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The 2022 mass flowering of *Posidonia oceanica* in the French Mediterranean Sea: is it unprecedented?

Serena ANDRÉ[1], Patrick ASTRUCH[1*], Charles-François BOUDOURESQUE[2*], Bruno BELLONI[1], Vincent BARDINAL[3], Jordi BOADA[4,5], Éric CHARBONNEL[6], Edouard CHÉRÉ[7], Jean-Michel COTTALORDA[8], Tristan ESTAQUE[9], Bruno FERRARI[10], Dorian GUILLEMAIN[11], Virginie HARTMANN[12], Romain HUBERT[10], Stéphane JAMME[13], Arthur LAZENNEC[1], Noëmie MICHEZ[10], Heike MOLENAAR[8], Briac MONNIER[14], Gérard PERGENT[14], Christine PERGENT-MARTINI[14], Alexis PEY[15], Thomas SCHOHN[1], Nuria TEIXIDÓ[4, 5, 16]

[1]GIS Posidonie, Aix-Marseille University, OSU Pythéas, Campus of Luminy, 13009 Marseille, France.
[2]Aix-Marseille University and University of Toulon, MIO (Mediterranean Institute of Oceanography), IRD, CNRS, Campus of Luminy, 13009 Marseille, France.
[3]Parc national de Port-Cros, 181 allée du Castel Sainte-Claire, BP 70220, 83406 Hyères CEDEX, France.
[4]Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Carrer d'Accés a la cala Sant Francesc 14, Blanes, 17300, Spain.
[5]Department of Integrated Marine Ecology, Stazione Zoologica Anton Dohrn, Ischia Marine Centre, Ischia, Naples, Italy.
[6]Parc Marin de la Côte Bleue, Observatoire PMCB, Plage du Rouet. 31, Av.J. Bart, BP. 42, 13620 Carry-le-Rouet, France.
[7]Ville d'Agde, Direction Gestion du milieu marin, Aire Marine Protégée de la côte agathoise, 34300, Agde, France.
[8]Centre National de la Recherche Scientifique (CNRS), Université Côte d'Azur, ECOSEAS UMR 7035, Parc Valrose, 06108 Nice, France.
[9]Septentrion Environnement, Campus Nature Provence, 89 Tra. Parangon, 13008 Marseille, France.
[10]Parc naturel marin du golfe du Lion / Office français de la biodiversité, 66700 Argelès-sur-Mer, France.
[11]Aix Marseille Université, CNRS, IRD, IRSTEA, OSU Institut Pythéas, Marseille, France.
[12]Réserve Naturelle Marine de Cerbère-Banyuls / Département des Pyrénées-Orientales, 66650 Banyuls-sur-mer, France.
[13]Aquanaute Expertise, 21 Rue des Palmiers, 06600 Antibes, France.
[14]UMR CNRS SPE 6134, University of Corsica, 20250 Corte, France.
[15]Thalassa Marine Research & Environmental Awareness, 286 F route d'Aspremont, 06690 Tourrette-Levens, France.
[16]Laboratoire d'Océanographie Villefranche, CNRS, Sorbonne Universtié, France.
Corresponding authors: patrick.astruch@univ-amu.fr, charles.boudouresque@mio.osupytheas.fr

***Abstract*.** The flowering of the Mediterranean seagrass *Posidonia oceanica*, which occurs in autumn, is known to be uneven, over space and time. Mass flowering events occur at about ten-year intervals. High summer seawater temperature seems to trigger flowering. However, flowering is not dependent on the summer seawater temperature alone, but also on the time elapsed since the previous mass flowering, as mass flowering needs the long-term accumulation of carbohydrate reserves within the rhizomes.

The 2022 autumn flowering of *P. oceanica* in the north-western Mediterranean Sea is consistent with this pattern: the summer of 2022 was characterized by a conspicuous marine heat wave, and the previous mass flowering dated back to ten years previously. Unfortunately, accurate data on previous mass flowerings, i.e. inflorescence density according to depth and shoot density, are not available, making comparisons difficult. The aim of this study was to describe the mass flowering of *P. oceanica* seagrass meadows observed along the French Mediterranean shore, to analyse the influence of depth and locality, and to determine whether it was unprecedented.

Inflorescences occurred at all studied localities and depths (from 0 to 21 m depth). The mean flowering intensity (FI) of the 2022 flowering along the French coast is 20.5% and the mean flowering density (FD) is 119 ± 128 inflorescences per m² (maximum at Sormiou, 10 m depth: 423 infl./m²). Differences between areas were observed: the highest mean flowering intensity reached 41% for Cap d'Antibes (French Riviera) and Sormiou (Marseille area). Flowering intensity was lower in the Gulf of Lions (which is unsurprising, due to lower winter temperature) and in Corsica (which is unexpected). Consistently with some previous flowering events, flowering intensity increased with depth. The question '*Was this flowering unprecedented?*' cannot be answered due to the lack of previous accurate data. In addition, the question is perhaps of no importance: it is possible that the flowering density is limited by the maximum carbohydrate reserve capacity in the rhizomes. Many signs of predation were observed, and as usual most flowers did not produce mature fruits; however, the mean fruit production, at the scale of French Mediterranean meadows, was 16 ± 45 fruits/m², which is extremely high. Fruiting intensity (FrI), at 13%, is much higher at depth, which can be explained by more intensive predation in shallow water.

Overall, even if not definitely unprecedented, the 2022 flowering can be qualified as exceptional. The high production of seeds will probably contribute to the natural recovery of threatened meadows.
Keywords: French Mediterranean Sea, fruiting, heat wave, mass flowering, *Posidonia oceanica,* predator satiation hypothesis.

***Résumé*. La floraison massive de 2022 de *Posidonia oceanica* en Méditerranée française est-elle sans précédent ?** La floraison de la magnoliophyte marine *Posidonia oceanica* se produit en automne. Elle est irrégulière d'une année sur l'autre et en fonction des localités. Des floraisons massives se produisent en moyenne tous les 10 ans. Les températures estivales élevées favorisent la floraison. Toutefois, la floraison ne dépend pas seulement de la température estivale élevée, mais aussi du temps écoulé depuis le précédent épisode de floraison ; en effet, une floraison massive nécessite l'accumulation à long terme de carbohydrates de réserve dans les rhizomes.

La floraison qui a suivi la vague de chaleur spectaculaire de l'été 2022, dans le nord-ouest de la Méditerranée, est cohérente avec ce modèle : la précédente floraison massive date de presque 10 ans. Malheureusement, il y a un manque de données précises sur les floraisons massives qui ont précédé celle de 2022 : densité des inflorescences, en fonction de la profondeur et de la densité des faisceaux, taux de production de fruits, etc. Cela rend difficiles les comparaisons. L'objectif de cette étude est de décrire la floraison massive des herbiers de *P. oceanica* observée sur le littoral méditerranéen français, d'analyser l'influence de la profondeur et de la localité, et de déterminer si elle est sans précédent.

Des inflorescences ont été observées dans toutes les localités explorées et à toutes les profondeurs (de la surface à environ 21 m). L'intensité moyenne de la floraison de 2022 atteint 20.5 % le long des côtes françaises et la densité de floraison (FD) est égale à 119 ± 128 inflorescences par m² (maximum à Sormiou à 10 mètres de profondeur avec un FD de 423 infl./m²). Des différences entre les zones sont observées : la plus forte intensité de floraison a été observée au Cap d'Antibes (Côte d'Azur) et à Sormiou (près de Marseille) : 41 %. L'intensité de floraison a été plus faible dans le Golfe du Lion (ce qui est logique, en raison des basses températures hivernales) et en Corse (ce qui est inattendu). En accord avec certains précédents épisodes de floraison massive, l'intensité de la floraison augmentait généralement avec la profondeur. Quoi qu'il en soit, la question : '*Cette floraison est-elle sans précédent ?*' ne peut pas être résolue en raison de l'absence de données précises sur les floraisons antérieures. Mais cette question est peut-être futile : il est possible que la densité de floraison soit limitée par la capacité maximale de stockage des carbohydrates par les rhizomes. De nombreux signes de prédation sur les inflorescences ont été observés et, comme c'est généralement le cas, la plupart des fleurs n'ont pas produit de fruits ; toutefois, la production de fruits, à l'échelle de la Méditerranée française, peut être estimée à 14 ± 45 fruits/m² d'herbier, ce qui est considérable. L'intensité de fructification (FrI), d'une moyenne de 13 %, est plus importante en profondeur, ce qui peut être expliqué par une plus forte prédation dans les eaux moins profondes.

Au total, même s'il n'est pas possible d'affirmer que la floraison de 2022 est sans précédent, elle peut être qualifiée d'exceptionnelle. L'énorme production de graines qui en résulte contribuera probablement à la recolonisation naturelle de *P. oceanica*, là où les herbiers ont été dégradés du fait de l'homme.
Mots-clés : floraison massive, fructification, Méditerranée française, *Posidonia oceanica*, théorie de la saturation du prédateur, vague de chaleur.

1. Introduction

Posidonia oceanica (Linnaeus) Delile is an engineer species of great ecological importance (Molinier and Picard, 1952). Endemic to the Mediterranean Sea, it provides many ecosystem services: primary production and an important role in the food chain, biodiversity hotspot, nursery, spawning ground and refuge for many marine species, oxygen production, sand factory which supplies the beaches, turbidity control (by hindering sediment resuspension), seabed stabilisation, wave and swell reduction, and protection of beaches against erosion (Boudouresque *et al.,* 2012, 2016). Moreover, in the current context of climate change, it plays a very important role in carbon fixation and sequestration (Pergent *et al.,* 2014; Pergent-Martini *et al.,* 2021; Monnier *et al.,* 2021). Despite a wide range of protection measures, including the Berne and Barcelona Conventions and a number of European Union Directives, *P. oceanica* remains threatened by direct or indirect anthropogenic pressures such as (i) increase in water turbidity, (ii) over-sedimentation and (iii) mechanical impacts such as trawling and anchoring (Boudouresque *et al.,* 2009, 2012; Giakoumi *et al.,* 2015). Conspicuous regressions have been observed, especially during the second half of the 20th century, in the Mediterranean Sea (Boudouresque *et al.,* 2009; Marbà *et al.,* 2009; Telesca *et al.,* 2015). Regression is not homogeneous throughout the Mediterranean and is more extensive in some areas than others (Boudouresque *et al.,* 2021). In France, although *P. oceanica* has the status of protected species, regression events are still observed mainly due to coastal development and anchoring in a number of bays which are very popular with recreational boaters. In the latter case, environment-friendly mooring zones with fixed buoys (ZMEL – *Zones de Mouillage et d'Équipements Légers*) are sometimes set up, but the process can take a long time and damage continues to be observed. Taking into consideration the natural slow growth rate of the plant (ten centimetres per year at best - Caye, 1980; Boudouresque and Jeudy de Grissac, 1983), natural recovery, although better than thought in the 1950-1960s (Boudouresque *et al.,* 2021), could require decades to centuries (Meinesz and Lefèvre*,* 1984; Pergent-Martini *et al.,* 1995).

As a seagrass, *P. oceanica* performs both asexual and sexual reproduction. The vegetative growth and the dissemination of cuttings, naturally detached, are the main spreading strategies (Molinier and Picard, 1952; Di Carlo *et al.,* 2005; Boudouresque *et al.,* 2012; Boudouresque *et al.,* 2021). Sexual reproduction does not occur yearly: it starts generally with a flowering in late summer or early autumn, with inflorescences bearing four to ten flowers (Boudouresque and Meinesz, 1982), with an average of four flowers per inflorescence according to Balestri and Vallerini, 2003 (Fig. 1). Next, some of these flowers will become fruits with a single seed (Fig. 2), bearing in mind that this species can be self-fertile (Sandmeier *et al.,* 1999). During the winter (fruiting period), the fruits grow and then detach from the shoot in the spring, March through June (Peirano *et al.,* 2001) but can exceptionally remain attached to the inflorescence where they germinate (pseudoviviparity *in* Ballesteros *et al*., 2005). Once detached, they reach the surface owing to positive floatability (Fig. 2a). For several days to weeks, carried by the currents, fruits can travel up to 100 km before the dehiscence (i.e. fruit opening) occurs (Micheli *et al.,* 2010) (Fig. 2b). The seeds, whose floatability is negative, sink randomly to the sea bottom. Under appropriate conditions (depth range, type of substrate), the seeds grow into seedlings producing new shoots (Fig. 3).

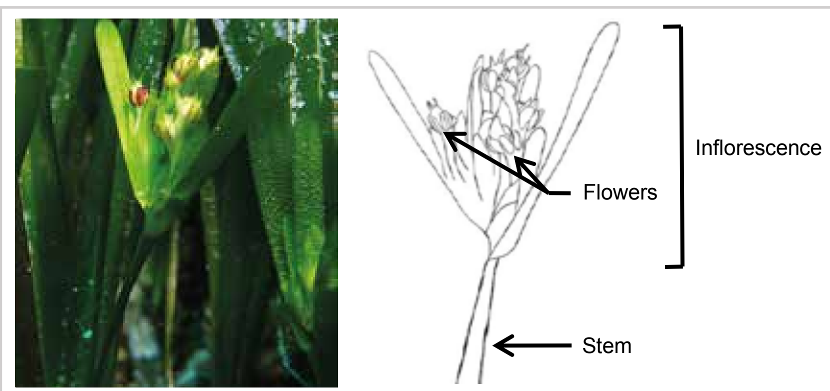

Figure 1. Left. Inflorescence of *Posidonia oceanica*. Photographs taken in Calanques des Salins at Port-Cros (Provence) on October 13th 2022 (© GIS Posidonie). **Right**. Original drawing of an inflorescence (© S. André).

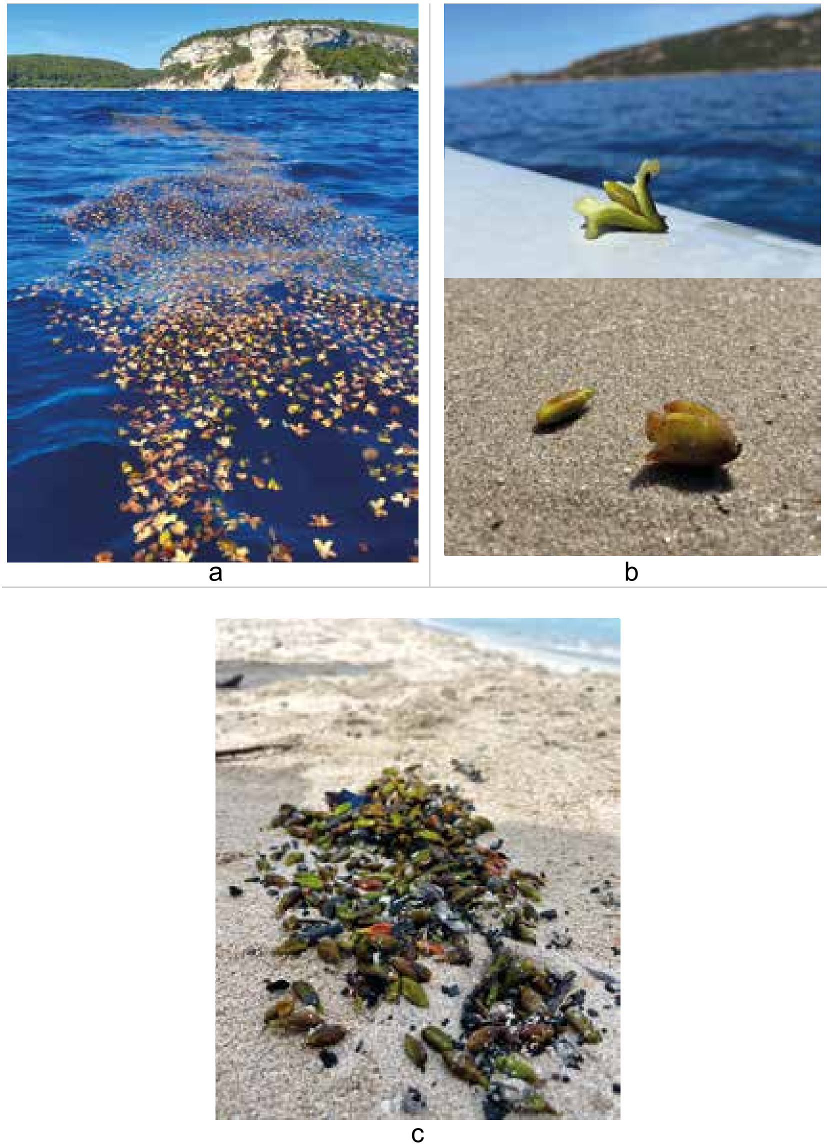

Figure 2. a. Floating fruits of *Posidonia oceanica* in Sant'Amanza Gulf (Corsica) on May 4th, 2023. **b**. Fruit opening at the top and seed detaching from the fruit (dehiscence) at the bottom. **c**. Seeds stranded at Santa Ghjulia beach (Corsica), on April 29th, 2023. Photos © S. André.

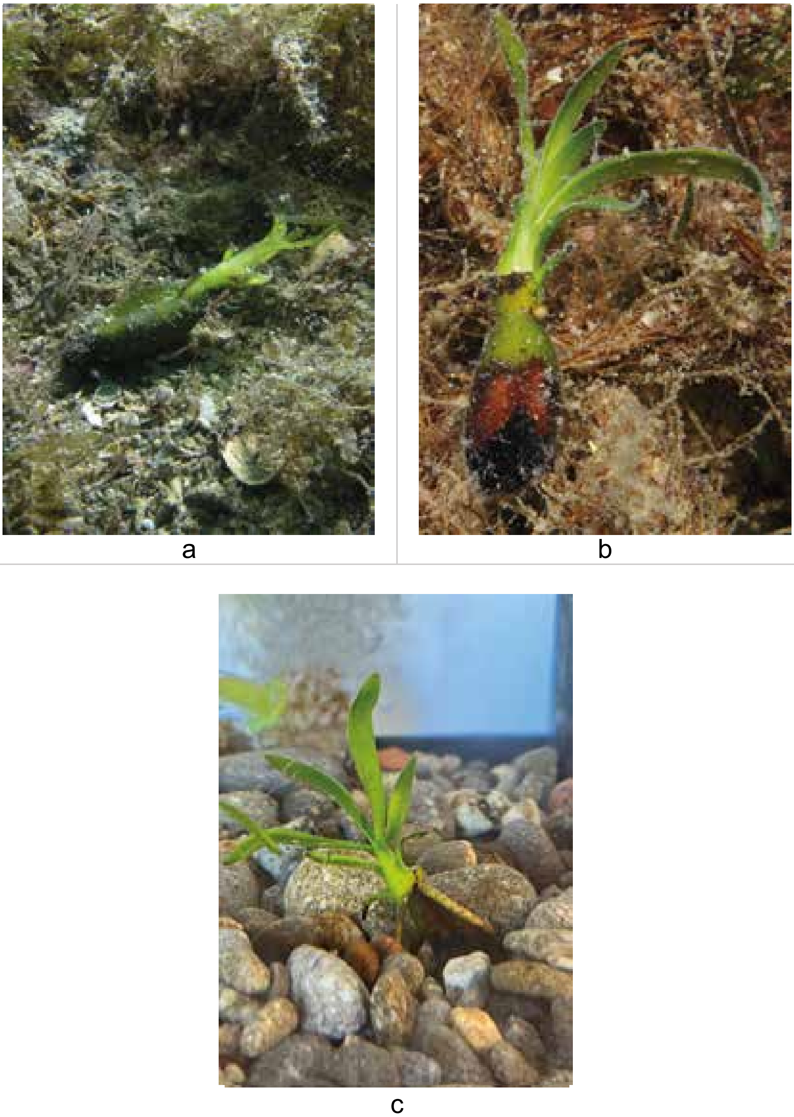

Figure 3. a. Germlings of *Posidonia oceanica* in Corsica, May 2023. **b**. Germlings of *P. oceanica* in Marseille, June 2023. Photos © GIS Posidonie. **c**. Germlings of *P. oceanica* after one month in an aquarium, May 2023. Photos © S. André.

Posidonia oceanica flowering events (whether massive and widespread or not) occur at time intervals of one to eleven years (Hamza *et al.,* 2000; Balestri and Vallerini, 2003; Díaz Almela *et al.,* 2007; Montefalcone *et al.,* 2013). Local flowerings can be observed every year (Cellini, 2001; Balestri and Vallerini, 2003), but a mass flowering, synchronized at larger scale (*e.g.*, north-western Mediterranean Sea), is much rarer (Díaz Almela *et al.,* 2007; Calvo *et al.,* 2010; Urra *et al.,* 2011; Montefalcone *et al.,* 2013).

Since August 2022, a mass flowering of *P. oceanica* was observed at numerous locations along the north-western Mediterranean coast and in particular, in France, around the Gulf of Lions, Provence, French Riviera, and the coasts of Corsica.

The aim of this study was to describe the mass flowering of *P. oceanica* seagrass meadows observed along the French Mediterranean shore, to analyse the influence of depth and locality, and to determine whether it was unprecedented. Fruiting rate and factors that could explain this event are also discussed.

2. Material and Methods

Types of flowering records

Quantitative, semi-quantitative and qualitative records were collected to gather the maximum of information concerning this flowering event such as occurrence, localisation, depth, density and, in addition, fruiting.

Quantitative records represent measurements of shoot and inflorescence densities assessed by SCUBA diving and more rarely by snorkelling. At each locality, sampling was carried out at different depths according to the configuration of the meadow: optimally 5, 10 and 15 m depth (so three sampling sites). The number of living shoots, then the number of inflorescences, were counted generally inside a 20 cm x 20 cm quadrat (sometimes a 25 cm x 25 cm quadrat) randomly placed in the meadow (Fig. 4a). Ten replicates per depth were performed, totalling about 30 quadrats per sampling locality (ten quadrats per sampling site). Other records were considered even if derived from a different or incomplete sampling method, corresponding to semi-quantitative records. At some localities, developing fruits (Fig. 4b) were counted in addition to inflorescence and shoot densities. To complete the quantitative assessment of the flowering, qualitative records with information on the occurrence of flowering were also noted, including photographs of *P. oceanica* inflorescences or beached aborted inflorescences or fruits (Fig. 5).

a b

Figure 4. a. Illustration of the sampling method for quantitative records by using a 20 cm x 20 cm quadrat, within the *Posidonia oceanica* meadow at Montremian, Port-Cros Archipelago (Provence), on November 17th, 2022, at 15 m depth. **b**. Developing fruits at Grande Quairolle (French Riviera) on February 15th, 2023, at 18 m depth. Photos © B. Belloni.

The inflorescence density or flowering density (FD – number of inflorescences per m²) is not a relevant proxy, as the shoot density steadily declines with depth (Pergent and Pergent-Martini, 1988; Pergent *et al.,* 1995). Flowering intensity (FI), also called flowering frequency (Urra *et al.,* 2011), corresponds to the percentage of inflorescence production in relation to the total number of shoots within the quadrats, that is to say, number of inflorescences / number of shoots. This percentage was calculated for all the quantitative and semi-quantitative records. In addition, the classification of Giraud (1977a, 1977b) was used to qualify the flowering density (Table I) and can be applied to some qualitative records. When possible, percentage of fruit production was established, referred to as fruiting intensity (FrI), corresponding to the number of fruits / number of inflorescences.

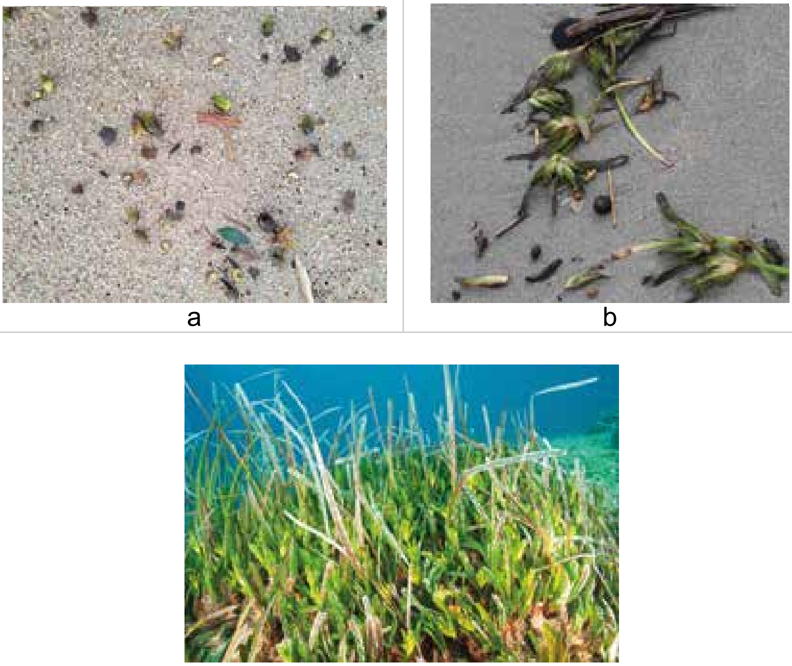

Figure 5. Examples of qualitative records by sightings of *Posidonia oceanica* flowering and fruiting. **a**. Photography of beached fruits at Pointe de la Parata (Aiacciu Gulf), Corsica on February 23rd, 2023 (© D. Guillemain). **b**. Photography of stranded inflorescences at Macinaghju (northern Corsica) on October 12th, 2022 (© C.F. Boudouresque). **c**. Photography of inflorescences at Rondinara (southern Corsica), on October 28th, 2022 (© Septentrion Environnement).

Table I. Giraud's classification of *Posidonia oceanica* flowering density (Giraud, 1977a, 1977b).

Inflorescence density (per m²)	**Flowering semi-quantitative scale**
1-20	(I) Isolated flowering
21-50	(II) Small flowering
51-100	(III) Moderate flowering
101-150	(IV) Large flowering
>150	(V) Exceptional flowering

Description of study areas

Study localities were grouped in five different areas (Fig. 6): Gulf of Lions, Marseille area (western Provence), Port-Cros National Park (eastern Provence), French Riviera and Corsica. Overall, data are available from 63 localities along the French Mediterranean coast. Among these localities, 31 are quantitative flowering intensity records, including four that also include records of fruiting intensity, two are semi-quantitative and 30 are qualitative (Table II).

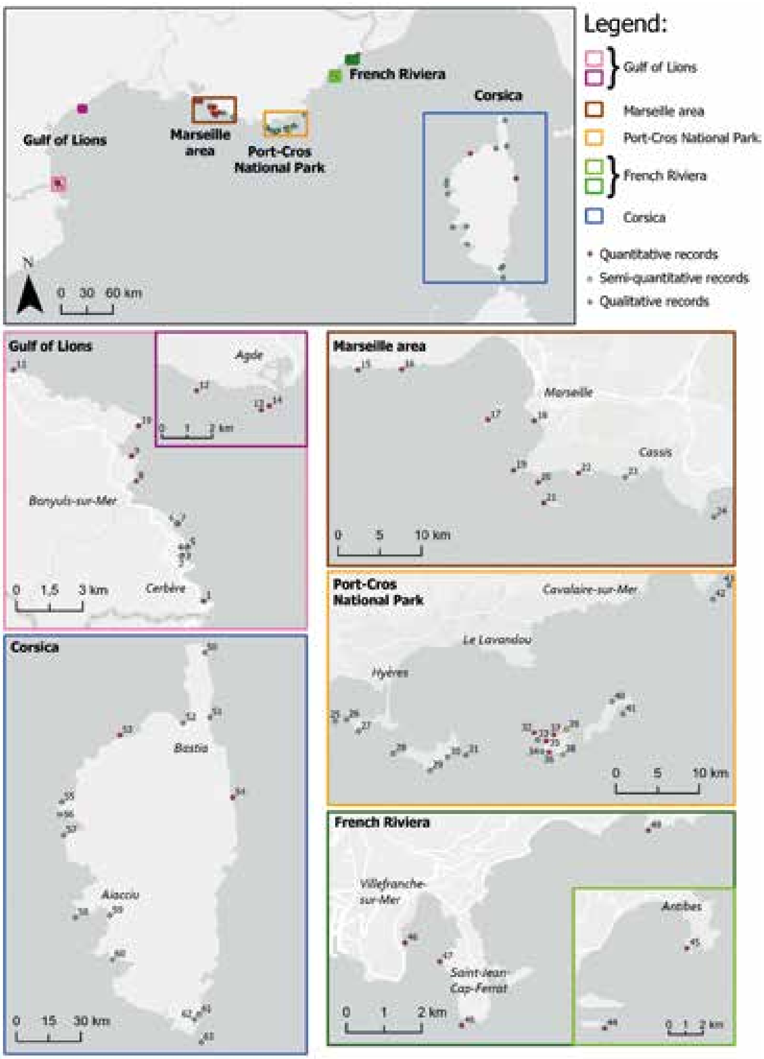

Figure 6. Location of study areas including quantitative, semi-quantitative and qualitative records.

Table II. Types of records concerning the 2022 *Posidonia oceanica* flowering event, according to area.

Area	Locality with quantitative records	Locality with semi-quantitative records	Locality with qualitative records	Total
Gulf of Lions	11 (including 3 with fruiting records)	/	3	**14**
Marseille area	8	/	2	**10**
Port-Cros National Park	4 (including 1 with fruiting records)	2	13	**19**
French Riviera	6 (including 3 with fruiting records)	/	/	**6**
Corsica	2	/	12	**14**
Total	**31**	**2**	**30**	**63**

The Gulf of Lions, corresponding here to the coastline from the Spanish border (Cerbère) to the city of Montpellier, includes three MPAs, the Natural Marine Reserve of Cerbère-Banyuls (NMRCB), the Natural Marine Park of the Gulf of Lions (NMPGL) and the Agde MPA (also called MPA Côte Agathoise). The NMRCB measures 650 ha including 65 ha classified as NTZ (No Take Zone). Within the reserve, there are three *P. oceanica* meadows (Tancade, Peyrefite and Pin Parasol) which are fragmented and where regressive limits were observed (*e.g*. at 19.6 m depth in 2000). Pin Parasol, the most extensive *P. oceanica* meadow (Ballesta *et al.,* 2000; Descamp *et al.,* 2005), is the only one to benefit from full protection status (all human activity banned including anchoring); the other two are in regulated fishing zones. Along the Albères coast (from Cerbère to Argelès), the other six meadows have similar environmental and physical characteristics (Pergent *et al.,* 1985; Ferrari *et al.,* 2008). Large areas of dead *matte* (living and dead rhizomes and roots, together with sediment which fills the interstices) can be observed, which confirms the meadow regression in this zone. The limited extension of the meadows is partly due to the high turbidity of the water and the severe hydrodynamic conditions. In Peyrefite Bay, the surface occupied by living *P. oceanica* is equal to that occupied by the dead *matte* (Ballesta *et al.,* 2000). In this area, *P. oceanica* meadows are described as rare, sparse and apparently subject to rather unfavourable abiotic conditions (water turbidity, hydrodynamism, low winter temperatures, lack of terrestrial sediment input). *Posidonia* meadows in the Agde sector (AMP Côte Agathoise) are also scattered in small patches of variable shape and size. Their depth distribution does not exceed 10 m (Blouet *et al.,* 2011).

The Marseille area (western Provence) includes two MPAs: the Côte-Bleue Marine Park (CBMP) where *P. oceanica* meadows cover a surface area of 1 198 ha and the Calanques National Park (CNP) with about 1 186 ha of *P. oceanica* meadow (Andromede Oceanologie, 2014). According to the sediment dynamic, numerous *P. oceanica* meadows along the coast appear to be possible sediment sinks (Vousdoukas *et al.,* 2011). This area, characterised by a predominantly rocky and steep slope, represents an active zone in terms of sediment dynamics with a high rate of agitation and erosion to the south, as well as dominant wave movements from southwest to north (Vousdoukas *et al.,* 2011). The Marseille area is impacted especially during summer by anthropic pressure such as touristic, recreational and commercial activities (Scemama *et al.*, 2020). The construction of the harbour of Marseille, artificial beaches and marinas prior to the 1990s are good examples of coastal development that has caused the decline of the *P. oceanica* meadows in the vicinity (Boudouresque *et al.,* 2021). Currently, thanks to the construction of an efficient sewage treatment plant, the remaining *P. oceanica* meadows are generally in good condition in this area (Boudouresque, 2021).

Port-Cros National Park (PCNP) includes the islands of Hyères (Porquerolles, Le Levant and the Port-Cros Archipelago) as well as the Giens Peninsula and the mainland shore facing the islands. The PCNP comprises two core areas representing 2 960 ha of marine area: Porquerolles Island and Port-Cros Archipelago (Boudouresque *et al.,* 2020). A large proportion of the sampling localities are located in the core area of Port-Cros, where trawling and almost all recreational fishing techniques are banned and professional fishing is strictly regulated (Cadiou *et al.,* 2009; Boudouresque *et al.,* 2020). They are also included in a Natura 2000 site and in a Special Protection Zone. Around the island of Port-Cros, the meadow was reported to extend in places to a depth up to 37-38 m (Harmelin, 1976; Harmelin and Laborel, 1976; Belsher *et al.,* 2005); a more recent report shows a lower limit at a depth of between 29 and 35 m, and more commonly between 31 and 33 m (Astruch *et al.,* 2012). Threats to the meadow are caused by recreational activities (Rouanet *et al.,* 2012). The area is also affected by introduced species such as the invasive algae *Caulerpa taxifolia* (Barcelo *et al.,* 2013), *C. cylindracea* (Klein *et al.,* 2005; Belloni *et al.,* 2023; Bonhomme *et al.,* 2006) and *Lophocladia lallemandii* (Boudouresque *et al.,* 2022), introduced species which concern more or less all the areas studied here, not only the PCNP. The Port-Cros Archipelago *P. oceanica* meadow is globally healthy, and covers most of the seabed, both on soft substrates and on rocks, reflecting the good overall quality of the environment (Astruch *et al.,* 2012; Belloni *et al.,* 2023). However, the lower limit of the meadow is regressing along the north coast of Port-Cros island (Bonhomme *et al.,* 2006, 2010). The *P. oceanica* meadow of the Gulf of Giens is similarly in an excellent state of health, according to Paillard *et al.* (1993) and to Boudouresque *et al.*

(2021), perhaps among the healthiest along the whole of the mainland French coast. However, signs of past pressure can be observed, as well as fishing pressure still occurring.

The French Riviera corresponds here to the coastline between Cannes and Menton, that is to say, the Alpes Maritimes *Département*. According to Boudouresque *et al.* (2021), the French Riviera region is one of the most human-impacted regions in the Mediterranean. The main causes of decline of *P. oceanica* are land reclamation for coastal development and the anchoring of cruise ships such as at Villefranche-sur-Mer (Meinesz *et al.,* 1991; Boudouresque *et al.,* 2021).

Posidonia oceanica seagrass meadows are extensively present in Corsica; the species covers an area of approximately 53 735 ha between 0 and 40 m depth. This corresponds to approximately 61% of the seabed in the Corsican infralittoral zone (Valette-Sansevin *et al.,* 2019). In Corsica, *P. oceanica* meadows often thrive beyond 35 m depth; the *matte* has for example an average thickness of 2.5 m and a maximum thickness of 8.7 m in one of the largest *P. oceanica* meadows in the Mediterranean Sea, that of the eastern continental shelf of Corsica (Monnier *et al.,* 2021). Corsica is a very popular destination for tourism, frequented by about 1/9th of the world's large yacht fleet in 2018 (Fontaine *et al.,* 2019). This high touristic pressure results in some meadows being heavily degraded by anchoring, for example in Sant'Amanza Gulf (Pergent-Martini *et al.,* 2022) and in the Bay of Calvi.

Statistical analyses

Statistical analyses were carried out using v. 4.2.3 of the R statistical software (R Core Team 2023). The Shapiro–Wilk test indicates a non-normal distribution of the dataset. Therefore, non-parametric tests were used to test the influence of depth and geography on flowering intensity (FI) and fruiting intensity (FrI). First, a permutational analysis of variance (PERMANOVA) on the qualitative data for depth range (Deep, Medium, Shallow) and areas was run using a similarity matrix based on the Euclidean distance of untransformed data and 999 permutations. A Spearman's correlation coefficient on the quantitative data was then calculated for depths and geographical coordinates (latitude and longitude) to determine the nature of the possible correlation (positive or negative). A cut-off p-value of 0.001 was applied to all tests.

3. Results

3.1. Quantitative and semi-quantitative flowering records

Table III includes the quantitative and semi-quantitative records collected after the 2022 mass flowering of *P. oceanica*.

Table III. Mean shoot density (shoot per m²), mean inflorescence density (FD - inflorescence per m²), semi-quantitative scale of flowering (Giraud, 1977a, 1977b) and *Posidonia oceanica* flowering intensity (FI) per sampling locality for each depth (each sampling site). N°: corresponds to the studied localities (see Fig. 6); N: numbers of replicates (quadrats); Inflo: inflorescence. Outstandingly high values (inflorescence per m² >150 and FI>40 %) are in bold and semi-quantitative records are mentioned in the table with an asterisk. Values are rounded off to the nearest whole number. All standard deviation has not been indicated but is available upon request.

Area	N°	Locality	Date	Depth	N	Shoot density	Inflo density	Giraud's scale	FI
Gulf of Lions	1	Cerbère	09/12/2022	5-7 m	10	765	18±21	I	2%
				10 m	10	455	30±35	II	6%
	3	Peyrefite cove (north of Cap Peyrefite)	21/12/2022	4-6 m	10	780	58±75	III	9%
				8-9 m	10	938	110±91	IV	12%
	5	Pin Parasol (south of Cap de Rederis)	12/12/2022	10-13 m	10	628	38±46	II	6%
				16-17 m	10	385	28±40	II	8%
	7	Tancade (south of Cap d'Abeille)	12/12/2022	7-10 m	10	835	118±141	IV	14%
				12-15 m	10	453	**163**±88	V	35%
	8	Les Elmes cove (north of Banyuls-sur-Mer)	28/11/2022	3-5 m	10	500	100±85	III	19%
				8-12 m	10	668	**200**±130	V	30%
	9	Fourrat (south of Anse de Paullile)	01/12/2022	4-6 m	10	588	20±31	I	3%
				10-11 m	10	513	100±117	III	18%
	10	Ste Catherine (south of Cap Béar)	30/11/2022	4-7 m	10	753	38±65	II	6%
				10-14 m	10	423	5±11	I	1%
	11	Porteils (west of Collioure)	24/11/2022	4-6 m	10	593	83±86	III	14%
				11-12 m	10	335	58±66	III	18%
	12	Cap d'Agde (southwest of Grau d'Agde)	25/11/2022	5 m	11	584	**177**±129	V	30%
	13	Cap d'Agde (close to a dead *matte* area)	25/11/2022	4 m	11	780	75±84	III	9%
	14	Cap-d'Agde (off the port entrance)	25/11/2022	6 m	11	559	9±23	I	2%
Marseille area	15	Sausset-les-Pins (Côte Bleue)	01/12/2022	5 m	10	740	135±92	IV	17%
				10 m	10	470	143±71	IV	30%

Area	N°	Locality	Date	Depth	N	Shoot density	Inflo density	Giraud's scale	FI
				15 m	10	458	113±40	IV	25%
	16	Carry-le-Rouet (Côte Bleue)	01/12/2022	5 m	10	1025	**370**±184	V	36%
				10 m	10	633	**260**±123	V	**41%**
				15 m	10	485	**165**±103	V	33%
	17	Calanque de la Crine (Frioul Islands)	06/02/2023	5 m	11	761	36±39	II	5%
				10 m	10	578	43±59	II	8%
				15 m	11	457	123±83	IV	28%
	18	Prado Bay (Marseille city)	23/11/2022	7 m	11	702	16±23	I	3%
				11 m	10	505	60±64	III	11%
				16 m	10	440	145±70	IV	37%
	19	Tiboulen de Maïre (island west of Les Goudes)	06/02/2023	5 m	11	475	39±66	II	7%
				10 m	11	507	57±70	III	12%
				15 m	10	385	5±11	I	1%
	20	Plateau des chèvres (between Jarre Island and Marseilleveyre)	23/11/2022	10 m	10	433	108±76	IV	25%
				15 m	10	355	100±57	III	28%
	21	Boulegeade (Riou Island)	06/02/2023	6 m	10	763	10±17	I	1%
				10 m	5	485	45±67	II	9%
				15 m	10	538	20±20	II	4%
	22	Sormiou cove	23/11/2022	5 m	10	718	**233**±162	V	32%
				10 m	10	710	**423**±134	V	**60%**
				15 m	10	378	113±54	IV	31%
Port-Cros National Park	32	Montremian (northeast Bagaud Island)	10/11/2022	6 m	10	825	**200**±146	V	25%
				10 m	10	940	**265**±160	V	29%
				15 m	10	495	**290**±102	V	**60%**
	35	Bay of Port-Cros (off the port entrance)	09/11/2022	5 m	10	360	130±63	IV	39%
				10 m	11	236	102±54	IV	**45%**
				15 m	10	295	83±58	III	28%
	36	South coast of Port-Cros	10/11/2022	5 m	10	1043	**263**±238	V	25%
				10 m	10	958	**245**±178	V	29%
				15 m	10	530	173±92	IV	36%

Area	N°	Locality	Date	Depth	N	Shoot density	Inflo density	Giraud's scale	FI
	37	Rascas (north coast of Port-Cros Island)	20/02/2023	5 m	10	640	**171**±95	V	27%
				10 m	10	472	114±55	IV	23%
				15 m	10	480	**258**±100	V	**54%**
	38	Pointe de la Croix (south Port-Cros, northeast of Gabinière Islet)*	08/12/2022	10 m	3	933	**317**±14	V	34%
				15 m	3	533	**292**±38	V	**57%**
	39	Pointe de la Galère (northeast of Port-Cros Island)*	07/12/2022	12 m	3	750	**167**±29	V	22%
	44	Saint Honorat Island (south of Cannes)	09/11/2022 10/11/2022	1-4 m	20	1033	216±188	V	24%
	45	Cap d'Antibes	28/12/2022	5 m	10	586	**229**±57	**V**	**40%**
				10 m	10	531	**248**±66	**V**	**47%**
				15 m	10	469	**173**±92	**V**	35%
	46	Laboratoire d'Océanographie de Villefranche	25/10/2022	2-3 m	10	546	43±134	II	5%
French Riviera	47	Lido Villefranche-sur-Mer	27/12/2022	5 m	10	712	**198**±151	V	32%
				10 m	10	533	38±24	II	7%
				15 m	10	424	35±26	II	9%
	48	Saint-Jean-Cap-Ferrat (near Villefranche-sur-Mer)	26/10/2022	1 m	7	878	94±65	III	10%
	49	Cap d'Ail	23/03/2023	5 m	10	1006	102±77	IV	10%
				10 m	10	565	114±80	IV	20%
				15 m	10	507	114±53	IV	23%
	53	Isula Piana (Isula Rossa)	22/02/2023	5 m	10	653	70±87	III	10%
				10 m	10	683	63±95	III	9%
Corsica				15 m	12	623	79±99	III	13%
	54	Portu di Taverna (eastern Corsica)	30/12/2022	5 m	7	911	75±58	III	8%
				9-10 m	10	655	53±62	III	8%
				14 m	10	613	50±31	II	8%

Records were collected between 25 October 2022 and 23 March 2023 at depths ranging from 0.9 m to 16.5 m. There are 31 quantitative and 2 semi-quantitative flowering intensity localities, totalling 72 sampling sites (different depths per locality) for quantitative records and 3 sampling sites for semi-quantitative records. It is worth noting that, although inflorescences were absent from some quadrats, there is no sampling locality or site (depth) without inflorescences. Mean inflorescence density varies from 5 to 423 per m² and FI from 1% to 41%. The highest mean FI observed on one sampling locality, all depths combined, is 41% for Cap d'Antibes (French Riviera) and Sormiou (Marseille area). Next were 38% at Montremian (Port-Cros), 37% at Bay of Port-Cros and Carry-le-Rouet (Marseille area). Among all the records collected, the highest mean inflorescence density has been observed at Sormiou at 10 m depth with 423 inflorescences per m² (FI = 60%) (Table III).

Combining all sampling localities and all depths, the mean flowering intensity of the 2022 flowering along the French coast is 20.5% and the mean flowering density is 119 ± 128 inflorescences per m².

Depth

To facilitate the interpretation of the results according to depth, a depth range has been established according to the following parameters: shallow between 0.9 and 7.5 m depth, medium between 7.5 and 12.5 m depth, and deep between 12.5 and 16.5 m depth. The average values in Table IV and Figure 7 have been ranked according to this depth range.

Table IV. Average flowering of *Posidonia oceanica* (FI and inflorescence density per m²) for each area according to the depth. Inflo: inflorescence.

Area	Depth range	Inflo density	Standard deviation	Shoot density	Standard deviation	FI
Gulf of Lions	Shallow	64.47	87.41	655.00	173.99	11%
	Medium	87.83	106.42	598.03	263.59	15%
	Deep	77.27	95.40	434.09	106.22	17%
Marseille area	Shallow	129.84	167.18	783.06	190.49	15%
	Medium	133.62	149.26	534.48	142.41	23%
	Deep	98.15	79.53	437.04	118.13	23%
Port-Cros National Park	Shallow	190.93	153.07	716.88	370.16	29%
	Medium	179.54	141.35	641.34	365.97	31%
	Deep	200.65	118.54	450.00	131.22	44%

Area	Depth range	Inflo density	Standard deviation	Shoot density	Standard deviation	FI
French Riviera	Shallow	160.58	146.53	832.16	331.68	21%
	Medium	133.33	106.41	542.93	99.69	25%
	Deep	107.20	83.63	466.67	111.41	22%
Corsica	Shallow	72.06	75.97	758.82	209.15	10%
	Medium	57.50	78.26	668.75	110.29	8%
	Deep	65.91	75.81	618.18	148.64	11%

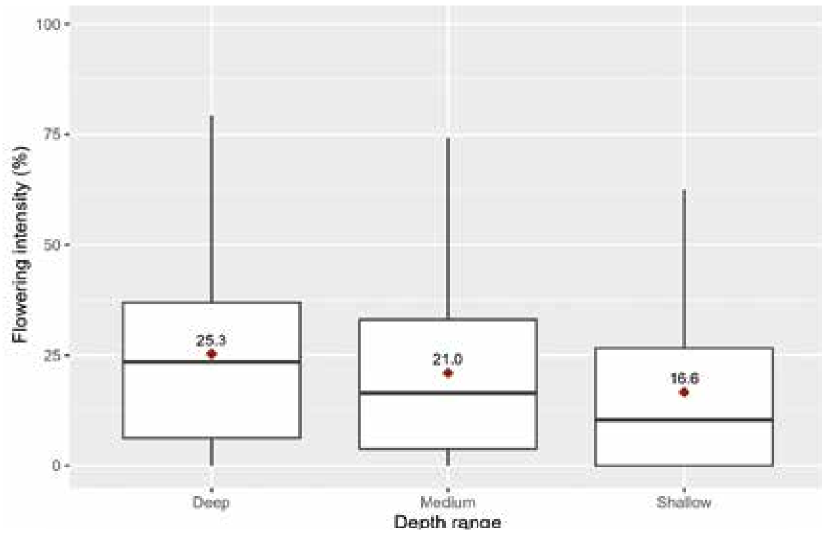

Figure 7. Flowering intensity of *Posidonia oceanica* in relation to depth range: deep (12.5 and 16.5 m depth), medium (7.5 and 12.5 m depth) and shallow (0.9 and 7.5 m depth).

A significant difference in FI is highlighted by PERMANOVA according to depth range (R^2=0.03, p-value=0.001; Table V). Results of Spearman's rank correlation (rho) do not display a depth effect on FD (p>0.001; Table VI). The flowering intensity (FI) is clearly a better proxy. In contrast with FD, FI increases with depth (Fig. 9): there is a significantly positive correlation between depth and FI (rho=0.15; p<0.001; Table VI).

Table V. Non-parametric permutational analysis of variance (PERMANOVA) on Euclidean distances for *Posidonia oceanica* flowering intensity and fruiting intensity according to depth range (Deep, Medium, Shallow) and areas. df: degrees of freedom F: overall F-statistic of the ANOVA; SumOfSqs: sum of squares; *: significant values.

Variables	Source of variation	df	SumOfSqs	R^2	F	p-value
Flowering intensity	Depth range	2	8731	0.03015	11.252	0.001*
	Areas	4	43812	0.15128	32.173	0.001*
Fruiting intensity	Depth range	2	19243	0.22992	17.466	0.001*

Table VI. Non-parametric Spearman's rank correlation coefficients (rho) for *Posidonia oceanica* flowering intensity, density and fruiting intensity according to depth and geographical coordinates (latitude and longitude) for the FI; *: significant values.

Variables	Source of variation	rho	p-value
Flowering intensity	Depth	0.1506595	4.532e-05*
	Latitude	0.1699399	4.07e-06*
	Longitude	0.1425586	0.0001148*
Flowering density	Depth	0.009182506	0.8048
Fruiting intensity	Depth	0.3025595	0.0007829*

Areas

The comparison of the inflorescence density between areas shows that Corsica has the lowest average FD value and the lowest FI (Table VII).

Table VII. Mean *Posidonia oceanica* inflorescence density (FD) and intensity (FI), according to areas. Areas are listed in descending order from highest to lowest FI.

Area	FD	Standard deviation	FI
Port-Cros National Park	190.28	137.54	35%
French Riviera	141.14	128.14	22%
Marseille area	120.11	135.23	21%
Gulf of Lions	75.13	96.34	13%
Corsica	64.83	75.59	10%

The PERMANOVA shows a significant difference between areas (R^2=0.15, p-value=0.001; Table V). The Spearman's correlation coefficients show a significantly positive relationship of FI with latitude (rho=0.17; p<0.001; Table VI) and then with longitude (rho=0.14; p<0.001; Table VI. This would mean that flowering intensity increases with increasing latitude and longitude, i.e., flowering is more intensive in the north than in the south and in the east than in the west at the scale of the north-western Mediterranean.

3.2. Qualitative flowering records

Table VIII includes the qualitative records, which were collected after the 2022 mass flowering of *P. oceanica.*

Table VIII. The 2022 *Posidonia oceanica* flowering event, as shown by qualitative records. N°: localities (see Fig. 6); Infl.: inflorescence.

Area	N°	Locality	Date	Flowering proxy	Depth	Giraud scale
Gulf of Lions	2	Peyrefite cove - south (north of Cap Peyrefite)	14/02/2023 10/03/2023	Observation of developing fruit	4 m 9 m	
	4	Pin Parasol - south (south of Cap de Rederis)	18/04/2023	Observation of developing fruit	7 m 11 m	
	6	Tancade - west	22/02/2023	Observation of developing fruit	6 m 12 m	
Marseille area	23	Oule (southwest Cassis)	27/10/2022	Infl. photograph		
	24	Roustaud (southeast La Ciotat)	28/10/2022	Infl. photograph		
Port-Cros National Park	25	Fourmigues de Giens (west Giens)	21/01/2022	Infl. observation		
	26	Ratonnière Island (west Giens)	11/10/2022	Infl. photograph		V
	27	Escampobariou (southeast Giens)	21/01/2022	Infl. observation		
	28	Langoustier (west Porquerolles Island)	21/01/2022	Infl. observation		
	29	Rocher de la Croix (south Porquerolles Island)	26/01/2022	Infl. observation		
	30	Calanques des Salins (southeast Porquerolles Island)	13/10/2022	Infl. photograph		V
	31	Petit Sarranier (east Porquerolles Island)	26/01/2022	Infl. observation		
	33	Bagaud cove (west Bagaud Island)	14/10/2022	Infl. photograph		V
	34	Pointe du Cognet (southwest Port-Cros Island)	12/10/2022	Infl. photograph		IV
	40	Pointe de Castellas (northeast Levant Island)	15/10/2022	Infl. photograph		V
	41	Sèche du Titan (southeast Levant Island)	22/02/2023	Infl. observation	20.5 m	
	42	Grande Quairolle (off Cap Lardier)	15/02/2023	Infl. photograph		
	43	Les Brisées de Taillat (east Cap Taillat)	15/02/2023	Infl. observation		

Area	N°	Locality	Date	Flowering proxy	Depth	Giraud scale
Corsica	50	Macinaghju (northern Corsica)	12/10/2022	Stranded infl. photograph	/	
	51	A Citatella (south of the Bastia port entrance)	17/09/2022	Infl. observation	5-10 m	
	52	San Fiurenzu (northern Corsica)	15/10/2022	Stranded infl. photograph	/	
	55	Cala Scàndula (south of Galeria, western Corsica)		Infl. observation		
	56	Punta Scàndula (west of Ghjirulatu, western Corsica)		Infl. observation		
	57	Calanche di Piana (west of Portu, western Corsica)		Infl. observation		
	58	Pointe de la Parata (Aiacciu Gulf)	23/02/2023	Stranded fruits photograph	/	
	59	Plage de Purtichju Grosseto-Prugna (Aiacciu Gulf)	22/02/2023	Stranded fruits photograph	/	
	60	Sec de Taravo, Porto Pollo Bay (north of Pruprià)	22/10/2022	Infl. photograph	3-6 m	V
	61	Rondinara (Sant'Amanza Gulf)	28/10/2022	Infl. photograph		V
	62	Balistra Bay (Sant'Amanza Gulf)	05/05/2023	Observation of developing fruit	15 m	
	63	Isule Lavezzi (southern Corsica)		Infl. observation		

Three qualitative records were observed in the Gulf of Lions, two in the Marseille area, 13 in the Port-Cros National Park and 12 in Corsica. They are mostly underwater observations or photographs of inflorescences. The deepest flowering observation was at 20.5 m depth at Sèche du Titan in Port-Cros National Park. A few others correspond to the stranding of inflorescences or of fruits and others to the development of fruits.

Although every sampling site had at least one inflorescence, some quadrats within these sites contained no inflorescence at all, while in some other quadrats almost all the shoots were bearing an inflorescence. All these records from each quadrat were converted into the Giraud scale (as far as possible) in order to take into account the qualitative and semi-quantitative records and then represent all the records in Figure 8 (n=746 values). Areas of the French Riviera and Port-Cros National Park had the most records corresponding to an exceptional flowering (Fig. 8). About 39% of data from the French Riviera and 53% from Port-Cros National Park corresponded to exceptional flowering (V). Gulf of Lions is the area with the highest number of quadrats without flowering (37%); in contrast, the Port-Cros National Park area had only three quadrats without flowering (2%); all the others had at least one inflorescence. In total, 29.5% of records, all areas included, correspond to exceptional flowering (V).

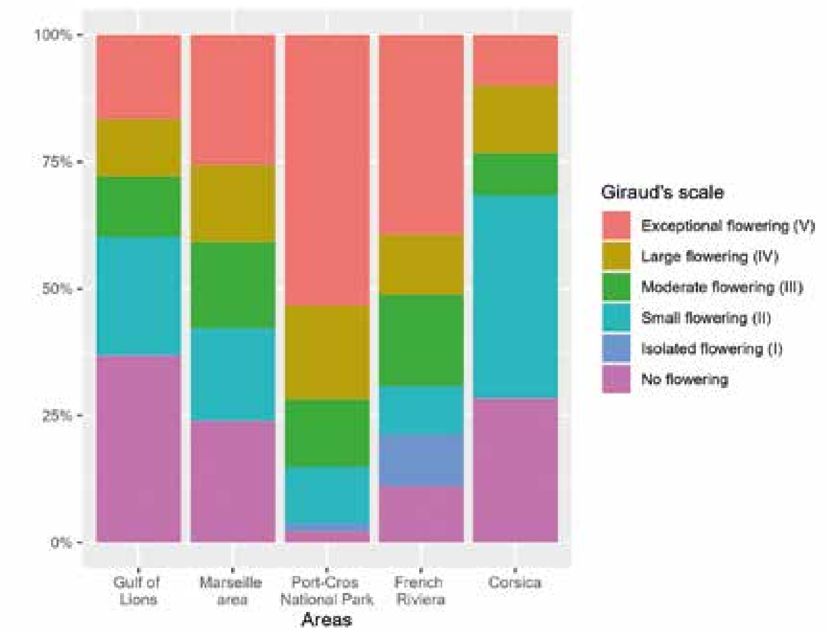

Figure 8. Giraud's scale of *Posidonia oceanica* flowering density according to areas, including semi-quantitative and qualitative records for quadrats.

3.3 Fruiting records

Fruiting records have been assessed in Gulf of Lions, French Riviera, Port-Cros National Park and Corsica (Table IX).

Mean fruit density values vary from 0 to 131 with a mean of 14 ± 45 fruits per m². Concerning the FrI, at Cap d'Antibes and Rascas (PCNP), means are about 27% and 24% respectively; in other words, about 1/4 of inflorescences produce at least one fruit. While at Lido Villefranche-sur-Mer and Cap d'Ail, the FrI was about 1%, the mean fruiting intensity (FrI) was 13%; values inside quadrats range from 0 to 100%, this maximum being obtained in two quadrats in the locality Rascas, Port-Cros with for example seven inflorescences and seven fruits. The lowest fruiting values were obtained in the Gulf of Lions and Corsica. The FrI is always much lower than the FI, and only three sampling sites (depth) obtained a percentage higher than 10%. Some sampling sites had a high flowering intensity but a very low percentage of fruiting intensity, such as Lido Villefranche-sur-Mer (FI=32% vs. FrI=0% at 5 m).

Table IX. Fruit density of *Posidonia oceanica* evaluated at eight localities and fruiting intensity (FrI) evaluated at four localities. N°: localities (see Fig. 6); N: numbers of replicates (quadrats); Inflo: inflorescence; FI: flowering intensity. Shoot, inflorescence and fruit density: per m². Values are rounded off to the nearest whole number. All standard deviation has not been indicated but is available upon request.

Area	N°	Locality	Date	Depth	N	Shoot density	Inflo density	Fruit density	FI	FrI
Gulf of Lions	2	Peyrefite - south	14/02/2023	4 m	10	/	/	3±8	/	/
			10/03/2023	9 m	10	/	/	0	/	/
	4	Pin Parasol - south	18/04/2023	7 m	10	/	/	0	/	/
				11 m	10	/	/	0	/	/
	6	Tancade - west	22/02/2023	6 m	10	/	/	0	/	/
				12 m	10	/	/	0	/	/
Port-Cros National Park	34	Rascas	20/02/2023	5 m	10	640	171	22±40	27%	26%
				10 m	10	472	114	3±7	23%	2%
				15 m	10	480	258	112±48	54%	45%
French Riviera	42	Cap d'Antibes	28/12/2022	5 m	10	586	229	11±8	40%	5%
				10 m	10	531	248	5±11	47%	2%
				15 m	10	469	173	131±88	35%	73%
	44	Lido Villefranche-sur-Mer	27/12/2022	5 m	10	712	198	0	32%	0%
				10 m	10	533	38	0	7%	0%
				15 m	10	424	35	2±5	9%	3%
	46	Cap d'Ail	23/03/2023	5 m	10	1 006	102	3±7	10%	1%
				10 m	10	565	114	0	20%	0%
				15 m	10	507	114	2±5	23%	2%
Corsica	62	Balistra Bay	05/05/2023	15 m	21	/	/	2±1	/	/

Quantitative records on fruiting made it possible to show a clear effect of depth ($R^2=0,23$; $p<0.001$), the Spearman's rank correlation showing a positive correlation (rho=0.30; $p<0.001$) (Fig. 9). A greater intensity of fruiting was observed at depth (Fig. 9).

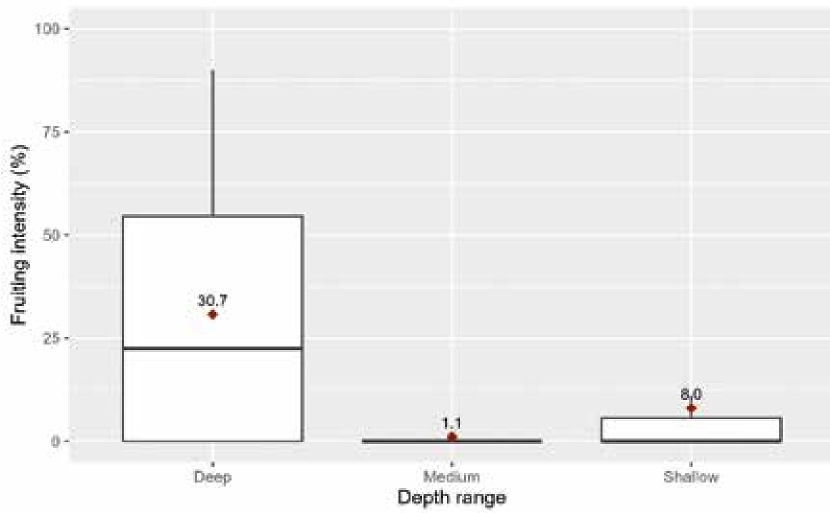

Figure 9. Fruiting intensity of *Posidonia oceanica* related to depth range: deep (12.5 and 16.5 m depth), medium (7.5 and 12.5 m depth) and shallow (0.9 and 7.5 m depth).

4. Discussion

4.1. Mass flowering along the whole French Mediterranean coast

Throughout the 2022-2023 late summer to winter, *P. oceanica* flowering and/or fruiting was observed in all 63 studied localities along the French Mediterranean coast. The study of 31 localities with quantitative records resulted in an average flowering intensity of 20.5%, with about 119 ± 128 inflorescences per m². The standard deviation is very high; the patchiness of the inflorescence was indeed high. Flowering intensity was very variable depending on locality and/or depth. In addition, signs of grazing of inflorescences by herbivores were observed at some localities. High grazing intensity on inflorescences was evidenced at Carry-le-Rouet in December 2022 (Fig. 10 Left). Grazing of inflorescences and fruits by herbivorous teleosts (the salema *Sarpa salpa*), sea urchins (*Paracentrotus lividus*) and the hermit crab *Clibanarius erythropus*, is a well-known fate for *P. oceanica* flowers and fruits (Verlaque, 1990; Piazzi *et al.,* 2000; Sanchez-Lizaso, 2004; Vergés *et al.,* 2007). Another observation, quite exceptional, concerns the presence of inflorescences on plagiotropic rhizomes and therefore colonisers (Fig. 10 Right). It is generally assumed that only orthotropic rhizomes may support flowering and seed production (Caye, 1980). Very few observations of inflorescence on plagiotropic rhizomes have been reported. One observation was made by Balestri *et al.* (2005) during the 2003 mass flowering.

Figure 10. Left. Inflorescences of *Posidonia oceanica* grazed by *Sarpa salpa* at Carry-le-Rouet reserve, Côte Bleue Marine Park (west of Marseille) on December 1st, 2022, at 5 m depth. Photo © B. Belloni. **Right**. Inflorescence growing on a plagiotropic rhizome at Porto Pollo, Corsica in October 2022. Photo © S. Jamme.

The flowering density (FD) is not a relevant proxy of flowering events, as shoot density steadily declines with depth (Pergent and Pergent Martini, 1988; Pergent *et al.,* 1995; Pergent-Martini *et al.,* 2005; Boudouresque *et al.,* 2012). According to the literature, the flowering density FD seems to decrease with depth, which is unsurprising (Pergent and Pergent-Martini, 1988; Díaz-Almela *et al.,* 2006; Romero *et al.,* 2012), or to be independent of shoot density and location of the meadow (Díaz-Almela *et al.,* 2006). Results of this study show that flowering intensity (FI) increased with depth; these results agree with those of Moreno and Guirado (2006), showing that shallow meadows flower more frequently, but deep meadows flower at a higher density, and of Di Martino (1999), showing an FI increase with depth, in Sicily. This can be explained by the fact that shallower meadows (e.g. less than 10 m depth) are more impacted by the grazing by herbivores (Boudouresque and Verlaque, 2020) and more exposed to the swell and water movement.

The low inflorescence density (FD) in the Gulf of Lions could be explained by a relatively lower temperature in this area: flowering seems to be triggered by a high summer temperature and by an October temperature of 20 °C or more (Caye and Meinesz, 1984; Thélin and Boudouresque, 1985; Pergent *et al.,* 1989; Stoppelli and Peirano, 1996). Looking at Giraud's scale including semi-quantitative and qualitative records for quadrats, the Gulf of Lions is the area with the highest number of quadrats without flowering (37%), which is far from being unexpected, as *P. oceanica* is a warm water species, the range of which is limited by low winter temperature (Pergent *et al.,* 2012).

Unfortunately, few quantitative data have been collected in Corsica, despite the extent of the coastline in Corsica, so these records are likely not representative of the flowering/fruiting event in Corsica. In fact, the qualitative records showed a high density of inflorescences as shown in Figure 11, and also numerous strandings of inflorescences and fruits (see Fig. 5).

Figure 11. High *Posidonia oceanica* flowering density in Porto Pollo, Corsica in October 2022. The fish school is of *Chromis chromis*. © S. Jamme.

Concerning the observed Spearman correlation with the GPS coordinates, this result is of course influenced by environmental differences. In fact, the environmental characteristics (typology, hydrology, etc.) of the different areas can be very different, as can easily be seen in the case of the Gulf of Lions. However, this result may be biased by the sampling strategy. In the same way, the results concerning the effect of depth are open to discussion because of these area differences, in particular the absence of deep seagrass meadows in the Gulf of Lions. It should also be pointed out that sampling was carried out over a long period, with the risk of minimising flowering intensity at some sites where data were collected later.

4.2. A flowering event of *P. oceanica* unprecedented for France?

Few *P. oceanica* flowering events have been reported in France (Giraud, 1977a, 1977b). Unfortunately, the intensity of inflorescences has rarely been reported. Hereafter, previous observations which mention the density or intensity of the inflorescences have been listed:

- Autumn 1961: Pointe des Oursinières (SE to Toulon), 12-25 m (6-8 infl./m²), an event apparently concerning the whole of Provence, following a particularly hot summer (Molinier and Zevaco, 1962; Giraud, 1977a).
- Autumn 1963: Lerins Islands (Cannes), on average 60 infl./m² (Stevenino *in* Giraud, 1977a).
- 1970, 1971, 1974 and 1975: Anse de Galeria (Corsica), FI of 0.2%, 0.7%, 0.2% and again 0.2% (Díaz-Almela *et al.,* 2007).
- November 1975: Calvi (Corsica), 6 infl./m² (D. Bay and W. Ravesteyn in Giraud, 1977a). Mourillon (Toulon), up to 100-200 infl./m² (on average 10-20 infl./m²) between the sea level and 6 m depth (Giraud, 1977a). Fruits were subsequently reported in early 1976 in many localities of Provence and Corsica, e.g. 1-5 fruiting inflorescences near Carry-le-Rouet (west of Marseille) at 6 m depth with a FrI < 1%, near Bandol, with 1-2 infl./m², at Port-Cros Island, 1-6 m depth, and in Elbu Bay (Scàndula Nature Reserve, Corsica), at 5 m depth (25/m²), 15 m (75/m²) and 20 m (25/m²), then absent deeper (Giraud, 1977a). It could be a massive flowering event.
- 1982: Anse de Galeria (Corsica), FI of 0.4%; Bay of Port-Cros, FI of 0.1%; and Banyuls-sur-Mer (Centre Heliomarin), FI of 0.1% (Díaz-Almela *et al.,* 2007).
- 1983: Anse de Galeria (Corsica), FI of 0.4%; Bay of Port-Cros, FI between 0.07% and 0.6%; Bagaud cove, FI about 0.07% and Banyuls-sur-Mer (Centre Heliomarin), FI of 10% (Díaz-Almela *et al.,* 2007).
- October 1985: Port-Cros, 5-20 inflo./m², 1-7 m depth (Pergent and Pergent-Martini, 1988). This flowering event was widespread, from French Catalonia to French Riviera and Corsica (Pergent and Pergent-Martini, 1988). The record from Centre Héliomarin (Banyuls-sur-Mer), in 1983, with a FI of 10% at 0.5-2 m depth (Díaz-Almela *et al.,* 2007) could be an error for 1985, as the authors do not mention the conspicuous and well reported 1985 flowering.
- 1994: Villefranche-sur-Mer (French Riviera), FI of 31% at 2-6 m depth (Díaz-Almela *et al.,* 2007). This event was noted in 1994, but it is possible that it was actually the data from the 1993 flowering.

Local flowerings have often been observed, according to Balestri and Vallerini, (2003); usually, less than 10% of the shoots flower in a given regular year. These flowerings often abort and therefore do not reach the fruiting stage, which has happened for example in Port-Cros in 1985 (Pergent and Pergent-Martini, 1988) and in Spain (Tabarca and Alicante) in 1988 (Sánchez Lizaso, 1992). This abortive event was also observed in 2003, just before the mass flowering which took place in

September-October, a first flowering having appeared in July (observed in Calvi, Corsica for example) which ended in complete abortion. The following (autumnal) flowering in 2003 led to fruiting (G. Pergent, unpublished data).

As far as the French Mediterranean is concerned, mass flowerings occurred in 1961, 1975, 1985, 1993, 2003 and 2012. Different dates were reported for other Mediterranean areas, such as the Tyrrhenian Sea and the Spanish Mediterranean (e.g. Díaz-Almela *et al.,* 2006, 2007; Boudouresque *et al.*, 2012; Montefalcone *et al.*, 2013).

Is the 2022 flowering unprecedented? Its extensive occurrence along the French Mediterranean coast, its high intensity (mean FI = 20.5%) and the ongoing fruiting process, support the exceptional character of this flowering. However, accurate data concerning previous mass flowerings are unfortunately missing. In fact, only the expert judgement of the senior authors, in particular CFB, CPM and GP, might perhaps provide an answer to the question raised. They have experienced most of the mass flowering events that preceded that of 2022. Their perception is that the latter, even if it was no more intense than any that preceded it in known history (which only goes back to the middle of the 20th century), was at least as intense as those from 1985 and 2003. Moreover, it is possible that the laws of physiology impose a limit on the intensity of flowering, which cannot be exceeded; for example, the storage capacity of reserves (carbohydrates and nutrients) by the rhizomes can determine such a limit in the inflorescence production per shoot.

In *P. oceanica*, non-structural carbohydrates (NSC), i.e. starch and soluble carbohydrates, such as sucrose, are stored within the rhizomes. Rhizomes are not specialized storage organs, unlike bulbs, and their storage capacity is therefore relatively limited. The NSC amount, which can reach 16% of the dry mass, is the highest in summer and the lowest in winter (Pirc, 1989; Renom *et al.,* 2000; Alcoverro *et al.,* 2001). These reserves make it possible to compensate for the insufficient primary production of certain years. Obviously, flowering and fruiting have an energetic cost (NSC, nitrogen and phosphorus), resulting in a lower number of leaves per shoot and lower growth during the two following years (Gobert *et al.,* 2001, 2005; Calvo *et al.,* 2006; but see Balestri and Vallerini, 2003). Unfortunately, a long-term survey of NSC and nutrients stored within rhizomes, between two mass flowering events, allowing validation of their possible control of flowering events, is not available.

According to the literature, such an event can be induced: (i) by the reproduction strategy of the plant, called predator's saturation strategy or predator's satiation strategy (Janzen, 1971; Karben, 1982; Curran and Leighton, 2000; Ostfeld and Keesing, 2004; Boudouresque *et al.,* 2021, 2023), which consists of producing a huge amount of seeds to saturate predators and consequently reduce the probability of all seeds being eaten; such a strategy is very common in the terrestrial realm for long-lived species such as the oak *Quercus* sp. (Koenig *et al.,* 1994; Sork *et al.,* 1993; Sork 1993; Koenig and Knops, 1995) or the bamboo *Bambusa vulgaris* (Janzen 1976); (ii) by the sea water temperature during summer and marine heatwaves (Díaz-Almela *et al.,* 2007; Ruiz *et al.,* 2018); and (iii) by the changes in solar activity through time; Montefalcone *et al.* (2013) suggest "*that intense solar activity, and not warmer temperature per se, is likely to be the main trigger for massive flowering events*".

It was thanks to this theory that Montefalcone *et al.,* (2013) predicted a massive flowering in 2022. In fact, temperature has often been linked to flowering event and there it is very likely that this is the case. However, due to regional differences, it is also interesting to consider whether another phenomenon on a larger scale could induce massive flowering at the scale of the Northern Mediterranean basin. Since solar activity influences the climate, and given that sunspot cycles are much more regular and predictable than climate fluctuations, the signal that can synchronise the start of the flowering process could well be represented by peaks in solar activity (Montefalcone *et al.,* 2013).

4.3 Fruiting

The higher FrD and FrI at depth could, in the same way as inflorescences, be related with lower water movement (that breaks inflorescence and fruit stems) and the lower abundance of herbivores (e.g. *S. salpa* and *P. lividus*) (Boudouresque and Verlaque, 2020). During the 2022 winter fruiting, fruiting data were measured in eight localities of the Gulf of Lions, Port-Cros National Park, French Riviera and Corsica; a fruit density average of 14 ± 45 fruits per m² was obtained. Concerning the FrI measured in four locality an average of 13% was obtained. Data from the literature show that 12-13 inflorescences are necessary for the production of one mature viable fruit of *P. oceanica* (Balestri and Cinelli, 2003), which is in line with the results presented here. However, the results obtained concerning the rate of fructification are not representative of all French coasts, as too few records have been collected to quantify the actual rate of fructification, and the results obtained here are probably overestimates. Even if the sexual reproduction strategy allows a lot of inflorescences during a mass flowering, only a small percentage of inflorescences of *P. oceanica* will produce mature fruits (Caye and Meinesz, 1984; Buia and Mazzella, 1991; Piazzi *et al.,* 2000). The two main reasons seem to be: (i) predation by herbivores (Fig. 8); Balestri and Cinelli (2003) estimated that about 84% of developing inflorescences are damaged by herbivores, and (ii) abortion of the flowers or of small fruits (Pergent and Pergent-Martini, 1988; Sánchez Lizaso, 1992; Caye and Meinesz, 1984, Pergent, 1985, Meinesz *et al.,* 1988, Romero, 1989). In 1994, abortion alone was responsible for the loss of about 87% of the reproductive material (Balestri and Cinelli, 2003); the very high abortion rate during the 1994 flowering, can be explained by the fact that there was a mass flowering the year before (1993), which exhausted the carbohydrate reserves of the plants. Furthermore, several factors could account for fruit abortion in *P. oceanica* such as limited pollination, resource limitation or competition, unfavourable local environmental conditions and inbreeding depression. In addition, elevated abortion rates of fruits could be of adaptive significance, in that they reduce the risk of loss of mature fruits to predation or provide a reserve of maturing into fruits if unpredictable resources become abundant (Balestri and Cinelli, 2003).

Before predation and abortion, Balestri and Cinelli, (2003) estimated the maximum potential seed production as between 84 to 487 seeds per m² during the 1993 flowering, and 340 to 945 seeds per m² in the 1994 flowering. Actually, fruit production was approximately 4.7 and 13.5 fruits per m² after the 1993 and 1994 flowering, respectively (Balestri and Cinelli, 2003), which is in line with the fructification rate measured after this 2022 flowering.

The trajectory from the flowering to the production of a new individual is a path full of pitfalls (Meinesz *et al.,* 1993). Seed germination, even on a favourable substrate, has been recorded very few times in the Mediterranean (Francour *in* Pergent, 1987; Buia and Piraino, 1989; Meinesz *et al.,* 1993). Once the seed has evolved into seedling, the growth of the first shoot with the first roots will still be vulnerable to different threats such as predation, water movements, competition with other macrophytes, etc.

Conclusion

Posidonia oceanica is a Mediterranean seagrass whose main spreading strategies are vegetative growth and dissemination of cuttings, naturally detached (Boudouresque *et al.,* 2021); sexual reproduction is rarer and starts generally with a flowering in late summer or early autumn. This flowering event, is known to be uneven, over space and time. In some isolated areas, flowering events are sometimes observed more frequently (Balestri and Vallerini, 2003), but given the existing data, massive flowering events, i.e. with high intensity and synchronised on a large scale, are rarer and occur at about ten-year intervals (Montefalcone *et al.,* 2013). High summer sea water temperature seems to trigger flowering. However, this event is probably not only dependent upon summer temperature, but also on the time elapsed since the previous mass flowering, as mass flowering needs the long-term accumulation of carbohydrate reserves within the rhizomes.

The 2022 summer flowering of *P. oceanica* in the north-western Mediterranean Sea is consistent with this pattern: the 2022 summer was characterized by a conspicuous marine heat wave, and the previous mass flowering dated back to ten years previously. Unfortunately, accurate data on previous mass flowerings, i.e. inflorescence density according to depth and shoot density, are not available, making comparisons difficult. This study has enabled us to describe, quantify and analyse the intensity of the 2022 flowering, providing density data, based on an accurate sampling strategy, in a wide geographical area, from the Spanish border to Corsica, in France.

Although there were differences between areas, inflorescences were present at all studied localities (n=63) and depths. The highest mean flowering intensity at a specific depth was observed in the French Riviera and Marseille area. With all records and depths taken together, Port-Cros National Park is the area where the most exceptional densities were observed (53% of values greater than 150 infl./m²). The low FI in the Gulf of Lions could be explained by a relatively lower winter temperature in this area. Concerning Corsica, a higher flowering pattern was expected but this may be explained by the scarcity of quantitative data in Corsica (only two localities). A general characteristic of the 2022 event was that flowering intensity increased with depth. The few fruiting data available give an idea of the difference between the rate of flowering and that of fruiting, with an average density of 14 ± 45 fruits per m² and an FrI of 13% (probably an overestimate).

The question '*Was this flowering unprecedented?*' cannot be answered due to the lack of previous accurate data in France. International efforts across the Mediterranean are welcome to enhance our knowledge of flowering. In addition, the question is perhaps trivial: it is possible that the flowering density is limited by the maximum carbohydrate reserve capacity in the rhizomes. As usual, most flowers did not produce fruits. Overall, even if not definitely unprecedented, the 2022 flowering can be qualified as exceptional. The high production of seeds will probably contribute to the natural recovery of threatened meadows.

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