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


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## Article

# The Heatwave of Summer 2022 in the North-Western Mediterranean Sea: Some Species Were Winners

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**Abstract:** The warming trend of the Mediterranean Sea is a long-term process. It has resulted in a northwards and westwards range expansion and abundance increase of thermophilic species, both native and non-indigenous, and in a shrinking of the range of cold-affinity species. Marine heatwaves (MHWs) are relatively short-term extreme episodes that are responsible for spectacular mortality events in some species and have been extensively reported in the literature. In contrast, the species that benefit from MHWs (the ‘winners’) have been much less studied. A record-breaking MHW occurred in 2022 in the north-western Mediterranean Sea. We focus on three ‘winner’ species, the thermophilic green macroalgae *Penicillus capitatus* and *Microdictyon umbilicatum* and the endemic seagrass *Posidonia oceanica*. *Penicillus capitatus*, which is mainly present in the area as an inconspicuous turf of entangled filaments (espera stage), produced the erect paintbrush-like stage where sexual reproduction takes place. *Microdictyon umbilicatum*, usually uncommon, bloomed to the point of clogging fishing nets. Finally, a mass flowering of *P. oceanica* occurred in late August–September, followed the following year (April–May 2023) by the extensive production and dissemination of fruits and seeds. Both processes, the long-term warming trend and one-off heatwaves, both ‘losers’ and ‘winners’, shape the change in structure and functioning of Mediterranean ecosystems.

**Keywords:** flowering; marine heatwaves; Mediterranean; *Microdictyon umbilicatum*; *Penicillus capitatus*; *Posidonia oceanica*

## 1. Introduction

### 1.1. Mediterranean Warming Trend and Heatwaves

Although the climate warming since the beginning of the 19th century has been partly natural (the end of the Little Ice Age—LIA), there is little doubt that greenhouse gas emissions due to human activities have amplified this warming, until they became the main

warming driver in the late 20th century and early 21st century [1–6]. The rate of warming is higher in the terrestrial realm than in the global ocean, including the Mediterranean Sea [6,7]. The Mediterranean is a hot spot for climate change [8], and all simulations point to a rapid warming of the Mediterranean by the end of the 21st century (e.g., [9]). In the upper layer, the simulated warming ranges from 0 to 2 °C under scenarios RCP2.6 and RCP4.5 up to 2 °C to 4 °C under scenario RCP 8.5 (see Table 4 of [9] for details), with trends ranging from ~0.2 to ~0.6 °C/decade (e.g., [10]). The warming anomalies display heterogeneity in intensity as well as in space at the Mediterranean basin scale (see Figure 2 of [9]; Figure 1 of [10]). One of the consequences associated with global ocean warming is the increased occurrence of marine heatwaves (MHWs), both longer and more frequent in the following decades [11–21]; see [22] for a review. Note that there is no consensus on the definition of MHWs, nor on the way to compute them (e.g., [10,23]), primarily since the definition depends on the time span considered for the climatology, hence, on time series availability. It is also worth noting that heatwaves, terrestrial and probably marine, are not a new phenomenon: they have been reported for almost a millennium [3]. In any case, MHW occurrence, intensity and duration have significantly increased over the last 20 years, beyond as well as within the Mediterranean (e.g., [24–28]). MHWs impact both the upper and the deeper layers (e.g., [10,29]), with dramatic ecological and economic consequences [19,20,30–38].

Long-term sea water warming of the Mediterranean has three main ecological consequences. (i) The spread of thermophilic native Mediterranean species, long confined to the warmest areas (the east and the south), whose range has been expanding westwards and northwards. This is the case for some teleosts, e.g., the ornate wrasse *Thalassoma pavo* [39,40], the parrotfish *Sparisoma cretense* [41,42] and the scorpaenid *Scorpaena maderensis* [43]. The thermophilous painted comber *Serranus scriba*, absent in 1990–1993 from the Côte Bleue Marine Park west of Marseilles, is now six times more common than *S. cabrilla* in shallow habitats (Éric Charbonnel, unpublished data). (ii) The spread of non-indigenous thermophilic species introduced to the Mediterranean Sea via, e.g., the Suez Canal and shipping, such as the seagrass *Halophila stipulacea* [44–46] and the red alga *Lophocladia trichoclados* (as *L. lallemandii*) (kingdom Archaeplastida) [47,48]. And (iii) the shrinking of the range of cold-water species, such as some teleosts (e.g., the common sole *Solea solea* and the European seabass *Dicentrarchus labrax* [49]), the eelgrass *Zostera marina* Linnaeus [50,51] and the brown alga *Fucus virsoides* (Fucales, kingdom Stramenopiles) in the Adriatic Sea [52–54]. For the latter species, most authors have only attributed its decline to pollution; it is a doxa dating from the middle of the 20th century (pollution was then claimed to explain everything; see [55]); but global warming must also be considered for this cold-affinity species.

The basket star *Astrospartus mediterraneus* is a filter-feeder endemic to the Mediterranean, although also present in the neighbouring Atlantic Ocean (Morocco, Portugal) [56]. It was considered as rare. From 2013 to the present, an impressive outbreak occurred in Catalonia; its abundance also conspicuously increased in Liguria (Italy) [56]. No correlation was found between basket star occurrence and the sea surface temperature (SST); however, it mainly dwells at depths ranging from 50 to 80 m, a depth where water temperature is poorly known; in addition, a correlation was found with summer rainfall [56]. As a result, the basket star could be a candidate species for the status of ‘global change winner’.

Relatively short-term extreme events, such as heatwaves, rather account for local mortality within a narrow depth range of sessile invertebrates, such as gorgonians (e.g., *Paramuricea clavata*, *Eunicella singularis*), sponges (*Spongia officinalis*) and the precious red coral (*Corallium rubrum*). Recovery has proved to be very slow or absent, at least in some localities, with mortality even worsening after the end of the surface heatwave [57,58]. The heatwave of 2003 had a severe impact on the leaf epibionts of the seagrass *Posidonia oceanica* in Liguria (Italy): the red calcified alga *Hydrolithon* sp. declined by more than 60% but quickly recovered, while the bryozoan *Electra posidoniae* declined seven-fold and took 16 years to recover [59]. On the other hand, heatwaves can work in favour of some species. Here, we develop this last point, much less often addressed in the literature than the issue of mass mortality, focusing on three species,

the ‘flowering’ of the green alga *Penicillus capitatus*, the bloom of the green alga *Microdictyon umbilicatum* and the exceptional flowering event of the seagrass *Posidonia oceanica*.

### 1.2. The Record-Breaking 2022 Marine Heatwave

The meteorological (and climatological) processes behind this extreme event are beyond the scope of this paper, so readers are referred to [60,61] and references therein.

The description of the 2022 MHW is only tentative, firstly because there is as yet insufficient literature to serve as a basis for a global survey, and secondly because the criteria for MHW detection and characterization vary according to the authors or the aims. The MHW affected the Western Basin more severely (see Figure 1 from [61]; T-MedNet website).

There is general agreement [60–62] that the intense warming of the surface layer started early, during May 2022, since by June SSTs (sea surface temperatures, based on satellite data) were already above normal in the western Mediterranean. Martinez et al. [10] even compute that the first 2022 severe MHW started by 15 June 2023. Then, in the NW part of the Mediterranean as well as throughout the Mediterranean, the SST has constantly been higher than the climatological baseline until spring 2023 (at least). The MHW displayed several peaks, impacting various areas. In the NW Mediterranean, the preceding average temperature/SST record (25.6 °C) dating back to 2003 (for the period 1982–2011) was broken with 26.1 °C, and maximum daily anomalies could exceed 4 °C. A main factor for the occurrence of the MHW was the negative anomaly of wind episodes [60], as mistral and tramontane wind episodes mix the upper layer and generate upwelling cells in the Gulf of Lions that prevent overheating in the surface layer (note, however, that in the stretches of coastline where they induce cascading [63], the MHW stress on benthic populations should be increased).

At the Mediterranean scale, the SST anomalies ranged between 1.5 and 2 °C during the meteorological summer, and until April 2023 all anomalies ranged between 0.5 and 1.5 °C. At the local scale, some SST anomalies higher than 2 °C persisted in the south-western part. In their Mediterranean main MHW catalogue, Martinez et al. [10] found two MHW events classified as ‘severe’ (as in 2003): from 15 June to 21 August 2022 and from 24 October to 22 November 2022. Whatever the domain considered and the criteria applied, this extreme event had a record-breaking duration.

The T-MedNet website ([64]; <https://t-mednet.org/visualize-data/temperature?view=ttfigure>, accessed on 7 December 2023) clearly showed that, by the end of 2022, the temperature anomalies reached deeper than 40 m. This resulted in the event with the highest cumulative intensity just after the well-known 2003 event [10].

## 2. Material and Methods

This work is based on the opportunistic observations of the authors, spread across the entire studied area (Occitania, Provence, French Riviera and Corsica; France), who dive frequently and all year round, from very shallow to deep (30–40 m) habitats (sand, reef, seagrasses, coralligenous outcrops), in the course of various field research and monitoring programs. They have also collected testimonies from artisanal fishermen, managers of marine protected areas and owners of diving clubs.

## 3. Results and Discussion

### 3.1. The Green Alga *Penicillus capitatus*

The green alga *Penicillus capitatus* Lamarck (Ulvophyceae, Viridiplantae, kingdom Archaeplastida) occurs as two stages. The first stage is a tangled turf of filaments that carpet the substrate; it is called the *espera* stage as, for a long time, it was regarded as a distinct species, *Espera mediterranea*. The second stage, which arises from the basal filaments, is a simple stalk terminating in a capitular tuft of bright green, free, dichotomously branched filaments, looking very like a paintbrush (hereafter: paintbrush stage) [65–69].

As shown by Alexandre Meinesz, in *P. capitatus*, the sexual reproduction is holocarpic: all the cytoplasm of the plant turns into gametes, after which the plant dies. This process

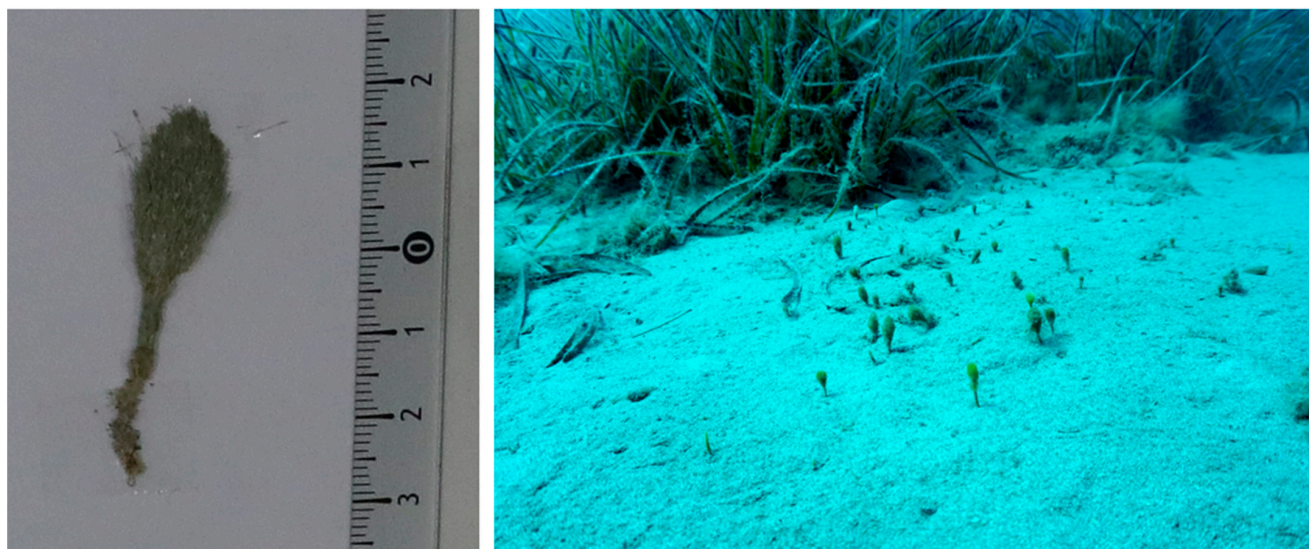


occurs in the paintbrushes, which in a way are the sexual organs of the plant, a kind of flower—although the term is of course inappropriate for algae [70,71].

*Penicillus capitatus* is a thermophilic species, occurring worldwide in tropical and warm seas: the Indian Ocean, Pacific Ocean and Atlantic Ocean [65,71]. It is present in the Mediterranean Sea, especially in its warmer areas, the eastern and southern basins. The espera stage is relatively common; it appears in the form of a turf of branched and intertwined filaments. In contrast, the paintbrush stage, relatively common although very localized in the eastern Mediterranean, is quite uncommon in the western Mediterranean; there, it is localized at a very few sites: Sainte-Maxime in eastern Provence, Villefranche-sur-Mer, Antibes and Golfe Juan (Croton Cove) in the French Riviera; Taverna, Portivechju Gulf and Sant’Amanza Gulf in Corsica; Elba Island and Secca della Meloria in Tuscany, Italy; Korbous, Hergla, Kerkennah Islands, Jerba Island, Zarzis and Ras-el-Ketef in Tunisia; and Cala Blava, south of Mallorca, Balearic Islands ([66–68,72–78]; Gérard Pergent and Thierry Thibaut, unpublished data). The occurrence of the paintbrush stage is on the increase [78].

The range of the espera stage is more extensive than that of the paintbrush stage, the occurrence of which is very sporadic, at least in the western basin of the Mediterranean. The paintbrush stage generally occurs between August and December in shallow (1–5 m) and soft-bottom areas: dead matte of the seagrass *Posidonia oceanica*, meadows of the seagrass *Cymodocea nodosa* and meadows of the green alga *Caulerpa prolifera* [66,68,78]. However, especially in the eastern Mediterranean basin, the paintbrush stage can also be observed in much deeper sites (Gérard Pergent, personal observations).

It seems that the formation of paintbrushes from the underlying espera turf could be uneven, occurring after hot summers, then absent for several years, at least in the north-western Mediterranean. The occurrence of the espera stage has been interpreted as a stress response induced by suboptimal environmental conditions [79]. Unfortunately, long-term monitoring of the presence, abundance or absence of paintbrushes is lacking. This is probably the case in Sant’Amanza Gulf (southern Corsica). In September 2022, paintbrush stages were observed at 14 m depth on dead matte of *Posidonia oceanica* at a site where they were definitely absent the previous years (2020 and 2021) (Figure 1).

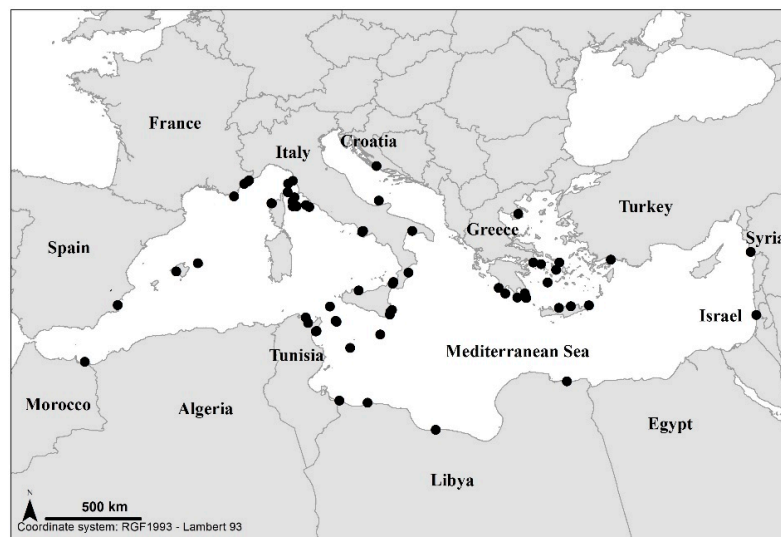


**Figure 1.** Paintbrush stage of *Penicillus capitatus*, Taverna, eastern Corsica, August 2023. Left: a voucher specimen; centimetric scale. Right: in situ aspect of the stand. Photo © Gérard Pergent.

### 3.2. The Green Alga *Microdictyon umbilicatum*

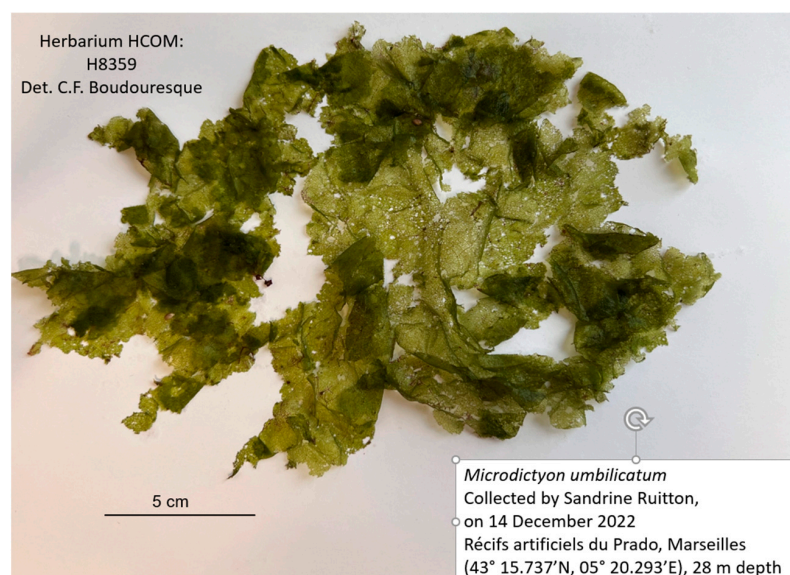
The green alga *Microdictyon umbilicatum* (Vellay) Zanardini (Ulvophyceae, Viridiplantae, kingdom Archaeplastida), also referred to as *M. tenuius* [80,81], is a thermophilic species that has been reported from all tropical and warm marine areas: the Atlantic Ocean, Pacific Ocean, Indian Ocean and Red Sea [82–85].

In the Mediterranean Sea, *M. umbilicatum* seems widespread, with the exception of the north-western basin, although it is usually uncommon everywhere; it thrives at various depths, from the deep infralittoral zone (up to 30–40 m) to the circalittoral zone (beyond 30–40 m depth) [69,80,81] (Figure 2). In Corsica, the only record is that of Coppejans [86] at Calvi; it was collected in September 1977 at 25 m depth. In mainland France, *M. umbilicatum* has only been reported from Mala Cove and Golfe Juan (French Riviera) in June 1927 [72,87], then from Port-Cros Archipelago (Eastern Provence) in October 2019 [88].



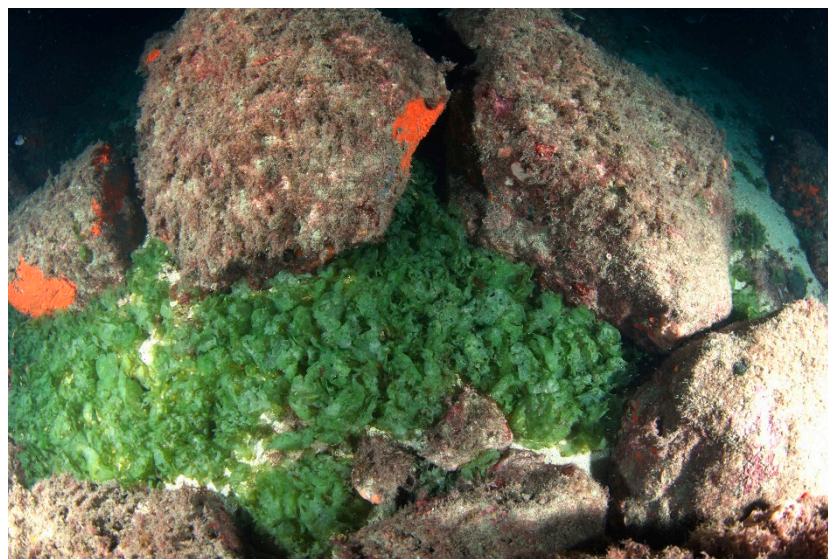
**Figure 2.** Location of *Microdictyon umbilicatum* known records (black points) in the Mediterranean, according to the *Plateforme macrophytes* database (OSU Pytheas, Aix-Marseille University). Its rarity in Spain, France and Turkey, well-explored regions, is undoubtedly not an artefact. On the other hand, its absence in Algeria and Egypt perhaps constitutes an artefact.

From late summer to fall 2022, *M. umbilicatum* proliferated off the Provence coast. Many fishermen found it trapped in their nets and some of them, intrigued by this alga, brought it to our institute. We also directly observed *M. umbilicatum* in situ (Figures 3 and 4). Since then, *M. umbilicatum* is still present, sometimes abundant, in several localities along the Provence coast, e.g., Prado Bay at Marseilles (Sandrine Ruitton, personal observations).



**Figure 3.** *Microdictyon umbilicatum* from Prado Bay, Marseilles (France).



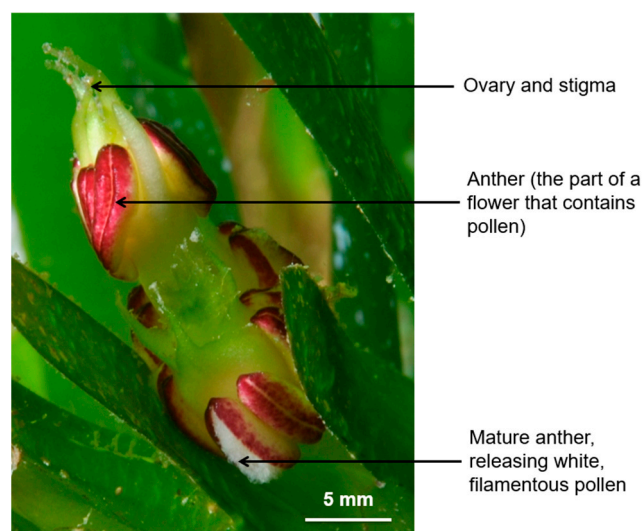


**Figure 4.** An accumulation of *Microdictyon umbilicatum* within the artificial reefs of Prado Bay, Marseilles (France), 28 m depth, on 14 December 2022. Photo © Sandrine Ruitton.

### 3.3. An Exceptional Flowering of the Seagrass *Posidonia oceanica*

The seagrass *Posidonia oceanica* (Linnaeus) Delile (Magnoliophyta, Viridiplantae, kingdom Archaeplastida) is endemic to the Mediterranean Sea [89]. It constitutes extensive meadows from sea level down to 10–40 m depth, depending on the water transparency, throughout the Mediterranean, with the exception of Lebanon, Israel, the northernmost Adriatic, the westernmost Alboran Sea, part of the Gulf of Lions and the vicinity of the mouths of rivers, such as the Rhone river in France [90,91].

The flowering of *Posidonia oceanica* occurs in fall, usually between September and November; an autumnal flowering is a not-uncommon feature for land plants in the Mediterranean area. Hermaphrodite flowers are grouped in an inflorescence at the tip of a 10–30 cm long stalk (Figure 5). The fruits, resembling green olives, are ripe in spring, usually between April and July, when they drop off, float and are dispersed by currents and winds over long distances [90,92,93].



**Figure 5.** An inflorescence of *Posidonia oceanica*. Each flower includes an ovary (with a stigma) and stamens (with an anther). Photo © Vincent Maran, courtesy of the author.

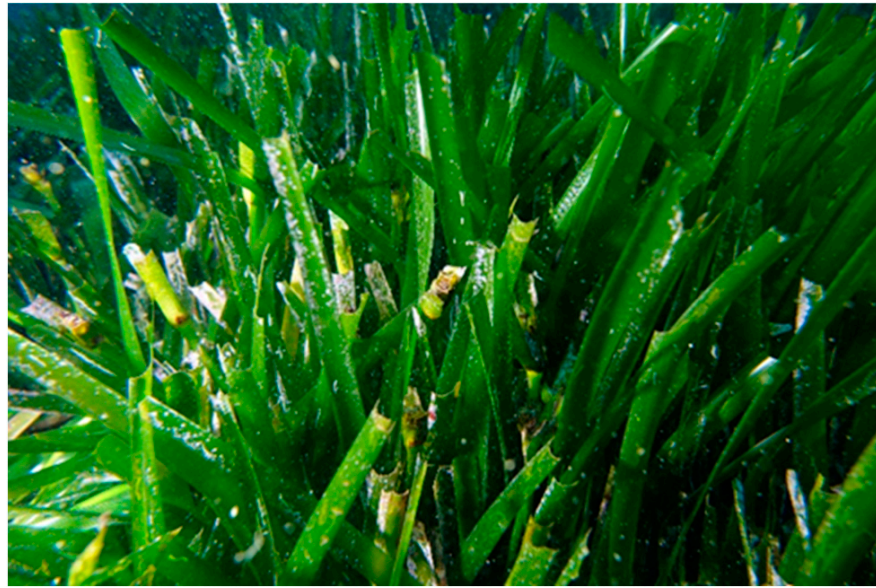
Flowering is not as rare as was believed in the mid-20th century (e.g., [94]), but its intensity is very variable, with mass flowerings generally spaced 5 to 12 years apart.

According to Diaz-Almela et al. [95]), they occur every 9–11 years. Mass flowering usually concerns a wide area, such as the north-western Mediterranean basin. Mass flowering has been reported, e.g., in 1975 [92,96], in 1993–1994 [97–101], in 2003 [91,95,101–105] and in 2009 [106]. However, the synchronism of flowering sometimes does not extend to the whole of the Mediterranean: for example, in Sicily, between 1974 and 1999, the most extensive mass flowering events were those of 1997 and 1998 [107,108].

In 2003, an unusual flowering was observed in July in the Bay of Calvi (Corsica), with flowers quickly aborting, followed by a new and massive flowering in fall and then by a massive fruiting in the spring of 2004 (G rard Pergent and Christine Pergent-Martini, unpublished data).

According to the literature, flowering may be triggered and/or enhanced by several factors, e.g., age of the orthotropic shoot, high summer temperature, peaks of annual SST, intense solar activity (with peaks every 11 years on average), the amount of carbohydrate compounds stored within rhizomes or a combination of these factors [95,100,103,104,108–110]. In the 1950s, the relative rarity of flowering was attributed to ‘the steady loss of adaptability of *P. oceanica* to the Mediterranean environment’ [94]. The assumption was somewhat naive, *P. oceanica* being a species that possibly resisted the partial drying up of the Mediterranean during the Messinian crises (5.7 through 5.3 Ma ago), then thirty glacial/interglacial cycles (since 2.5 Ma) and finally the succession of hot (such as the Medieval Warm Period—MWP) and cold (such as the Little Ice Age—LIA) episodes since the Last Glacial Maximum (LGM) 20 000 years ago. As to how *P. oceanica* possibly survived the Messinian crises, the debate remains open [111–113]: its presence in the Mediterranean is only formally attested by fossils after these crises [114,115]. Subsequently, the hypothesis in vogue was that flowering was the consequence of stress: sexual reproduction was seen as the last effort of the plant to survive in an environment that was becoming less suitable due, e.g., to pollution [116]. In fact, the most likely hypothesis to account for the irregularity and rarity of flowering seems to be the predator satiation strategy (PSS) (e.g., [117–121]). A regular production of offspring leads to the occurrence of predators consuming all of them. To be successful, be unpredictable! In the years when mass production of offspring occurs, predators are overwhelmed with potential prey (here inflorescences, fruits and seeds); they can consume only a certain amount, so that a significant number of them can escape being consumed. Obviously, for a long-lived species, such as many trees and *P. oceanica* (up to several millennia [122]), reproduction every year is unnecessary. Accumulating carbohydrate reserves during several years to allow an unpredictable mass production of offspring is a better strategy. As far as *P. oceanica* is concerned, while leaves are only moderately grazed [123], inflorescences are actively consumed by herbivores, such as the teleost *Sarpa salpa* and the sea urchin *Paracentrotus lividus* [100,110,124,125] (Figure 6). This high rate of consumption of the inflorescences is surprising, because they are better defended chemically, with higher levels of phenolic compounds, and have a lower nutritive value (proteins, nitrogen); in fact, the main factor in herbivore deterrence is the structural defences of the tissues [125]. The fruits are also consumed by sea urchins and the hermit crab *Clibanarius erythropus* [126]. The role of carbohydrate reserves and the reproductive cost are confirmed by the loss of rhizome elongation and production in the two years following mass flowering ([104,108]; but see [100]).

In late August–September 2022, an exceptional mass flowering of *P. oceanica* occurred from the Italian border to Camargue (mainland France), in the Gulf of Lions and in Corsica. We observed this flowering in situ (Figures 7 and 8) and on sand beaches, where broken inflorescences were massively cast ashore (Figure 9). The inflorescence density values reached may never have been recorded previously (Tables 1 and 2), with up to 100% of the shoots bearing an inflorescence at some sites (Figure 8). Of course, since the shoot density decreases with depth and is dependent on the health status of the meadow and micro-distribution patterns [90,127–129], the inflorescence density per m<sup>2</sup> can decrease with depth, while the percentage of flowering shoots actually increases [130]. In April and May 2023, large rafts of floating fruits were observed on the surface of the sea, together with fruits and seeds stranded on beaches (Figures 10 and 11).



**Figure 6.** Grazing of *Posidonia oceanica* leaves and inflorescences by the teleost salema *Sarpa salpa*. Reserve of Carry-le-Rouet, Côte Bleue Marine Park (west of Marseilles), 5 m depth, 1st December 2022. Photo © Bruno Belloni.

**Table 1.** Some historical data on inflorescence density of *Posidonia oceanica*.

Locality	Year	Depth	Inflorescence Density	Reference
Port-Cros Island (eastern Provence)	1975	2 m	5–20/m <sup>2</sup>	Giraud (1976) [96]
Port-Cros Island (eastern Provence)	1975	7 m	3/m <sup>2</sup>	Giraud (1976) [96]
Port-Cros Island (eastern Provence)	1975	13 m	10/m <sup>2</sup>	Giraud (1976) [96]
Port-Cros Island (eastern Provence)	1975	16 m	1/m <sup>2</sup>	Giraud (1976) [96]
Urla-Iskele (Turkey)	1983	1 m	Up to 210/m <sup>2</sup>	Pergent and Pergent-Martini (1988) [131]
Medes Islands (Spanish Catalonia)	1983	5 m	73/m <sup>2</sup> (mean)	Romero et al. (2012) [132]
Port-Cros Island (eastern Provence)	1985	1–3 m	125–500/m <sup>2</sup> (a)	Pergent and Pergent-Martini (1988) [131]
Rosignano (Tuscany, Italy)	1993	8–11 m	114–154/m <sup>2</sup>	Balestri and Vallerini (2003) [100]
Livorno (Tuscany, Italy)	1993	3–4 m	56/m <sup>2</sup> (mean)	Balestri and Cinelli (2003) [99]
Medes Islands (Spanish Catalonia)	1994	5 m	73/m <sup>2</sup> (mean)	Romero et al. (2012) [132]
Noli (Liguria, Italy)	1994	7 m	7/m <sup>2</sup> (mean)	Boyer et al. (1996) [116]
Noli (Liguria, Italy)	1994	10 m	28/m <sup>2</sup> (mean)	Boyer et al. (1996) [116]
Quinto (Genoa, Liguria, Italy)	1994	6–13 m	4/m <sup>2</sup>	Boyer et al. (1996) [116]
Livorno (Tuscany, Italy)	1994	3–4 m	137/m <sup>2</sup> (mean)	Balestri and Cinelli (2003) [99]
Akkum coast, Sigacık Bay (Aegean Sea, Turkey)	1994	1–3 m	0–24/m <sup>2</sup>	Dural (2010) [133]
Akkum coast, Sigacık Bay (Aegean Sea, Turkey)	1994	4–7 m	28–136/m <sup>2</sup>	Dural (2010) [133]
Los Amarillos, Almería–Granada (Spain)	1995	16–18 m	10/m <sup>2</sup>	Moreno and Guirado (2006) [134]



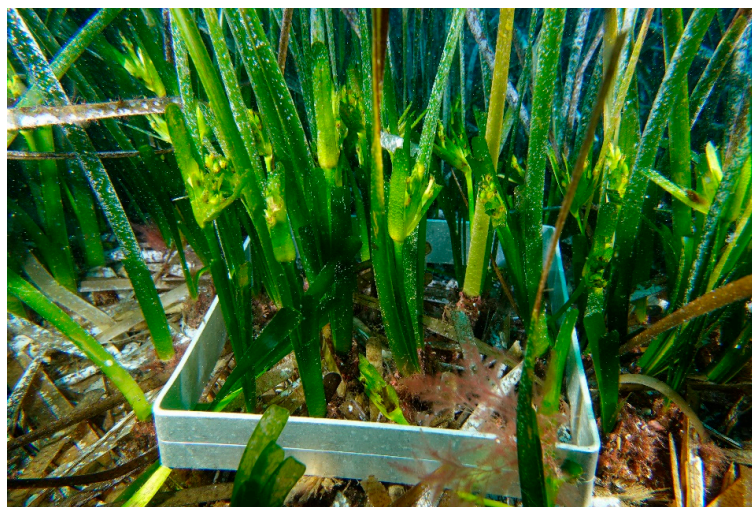
Table 1. Cont.

Locality	Year	Depth	Inflorescence Density	Reference
Capo Passero (Sicily, Italy)	1997	6 m	22–24/m <sup>2</sup> (mean)	Di Martino (1999) [107]
Capo Passero (Sicily, Italy)	1997	15 m	24–30/m <sup>2</sup> (mean)	Di Martino (1999) [107]
Capo Passero (Sicily, Italy)	1997	30 m	19–21/m <sup>2</sup> (mean)	Di Martino (1999) [107]
South-eastern Sicily (Italy)	1998	10–15 m	30–52/m <sup>2</sup> (a)	Calvo et al. (2006) [108]
Mataró (Spanish Catalonia)	2001	20 m	12/m <sup>2</sup> (mean)	Muñoz-Ramos (2002) [135]
Antignano (Livorno, Italy)	2003	2–3 m	193/m <sup>2</sup> (mean)	Balestri et al. (2005) [136]
Calaburras (Málaga, Spain)	2009	2–3 m	34/m <sup>2</sup> (mean)	Urrea et al. (2011) [106]
Calahonda (Málaga, Spain)	2010	2–3 m	69/m <sup>2</sup> (mean)	Urrea et al. (2011) [106]

Note: <sup>a</sup> Extrapolated from the authors' data.



**Figure 7.** Patrick Astruch observing the flowering of *Posidonia oceanica*, 10 m depth, Montremian, Bagaud Island, Port-Cros Archipelago (eastern Provence), on 17 November 2022. Photo © Bruno Belloni.



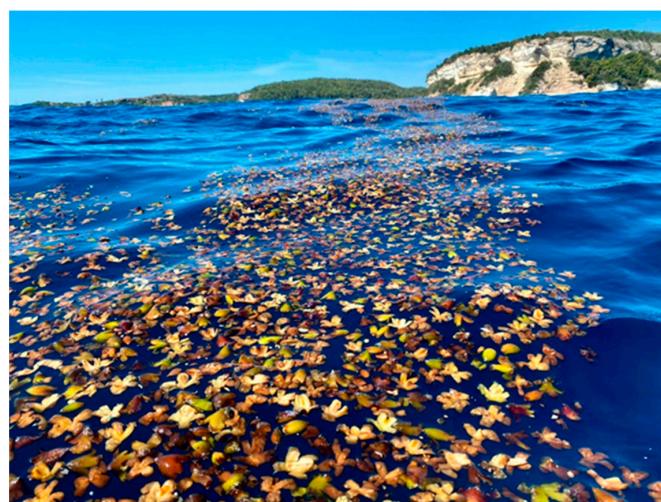
**Figure 8.** Mass flowering of *Posidonia oceanica* at Montremian, Bagaud Island, Port-Cros Archipelago (eastern Provence), on 17 November 2022. Almost all shoots bear an inflorescence. The metal frame measures 20 cm × 20 cm. Photo © Bruno Belloni.



**Figure 9.** Inflorescences—in fact, young fruits—cast ashore. Tamarone beach, Macinaghju, Corsica, 12 October 2022. Photo © Charles-François Boudouresque.

**Table 2.** Inflorescence density of *Posidonia oceanica* in fall 2022.

Locality	Depth	Inflorescence Density	Observers
Port-Cros Archipelago, eastern Provence (Montremian, Bay of Port-Cros and South side)	5–6 m	198/m <sup>2</sup> (mean)	Patrick Astruch, Bruno Belloni, Vincent Bardinal
	10 m	201/m <sup>2</sup> (mean)	
	15 m	182/m <sup>2</sup> (mean)	
Marseilles (Sormiou, Plateau des Chèvres and Rade Sud)	5–7 m	119/m <sup>2</sup> (mean)	Bruno Belloni, Serena André, Arthur Lazennec, Antonin Lefevre, Dorian Guillemain
	10–11 m	197/m <sup>2</sup> (mean)	
	15–16 m	119/m <sup>2</sup> (mean)	
Côte Bleue Marine Park (Sausset and Carry-le-Rouet) (western Provence)	5 m	253/m <sup>2</sup> (mean)	Éric Charbonnel, Bruno Belloni, Serena André, Arthur Lazennec, Nathan Portes
	10 m	201/m <sup>2</sup> (mean)	
	15 m	139/m <sup>2</sup> (mean)	
Cap d’Agde	4–6 m	87/m <sup>2</sup> (mean)	Édouard Chéré, Sylvain Blouet
French Catalonia (Porteils, les Elmes, Ste Catherine, Fourrat, Cerbère, Pin Parasol, Tancade and Peyrefite)	4–17 m	85/m <sup>2</sup> (mean)	Romain Hubert, Noémie Michez
Corsica (Taverna harbour and L’Isula—Île Rousse)	5 m	72/m <sup>2</sup> (mean)	Serena André
	9–10 m	58/m <sup>2</sup> (mean)	
	14–15 m	66/m <sup>2</sup> (mean)	



**Figure 10.** Fruits of *Posidonia oceanica* floating at the sea surface in late April 2023, after the massive flowering of fall 2022. Sant’Amanza Gulf, southern Corsica. Photo © Bruno Belloni.



*Posidonia oceanica* is a relatively thermotolerant species [137,138]; it tolerates temperatures as low as 9 °C and as high as 30 °C [139–141]. Interestingly, the populations from the warm (Cyprus) and cold (Catalonia) range limits of *P. oceanica* are the most resistant to extreme temperatures, whether low or high [142]. As far as 4- and 16-month-old germlings are concerned, photosynthesis is highest at 28–30 °C, the balance of photosynthesis/respiration becomes negative at 32 °C and photosynthesis ceases at 36 °C [143]. In the context of climate warming, the occurrence of sexual reproduction and the production of a number of offspring that escape predation owing to mass flowering could trigger better genetic diversity, with higher resistance to warming and other environmental changes [138]. Some modelling works predict, under the RCP8.5 scenario, the disappearance or very strong decline of *P. oceanica* from much of the Mediterranean [144,145], but debating the credibility of their conclusions is beyond the scope of the present article.



**Figure 11.** Fruits and seeds of *Posidonia oceanica* cast ashore in May 2023. Palombaggia Beach, southern Corsica. Photo © Bruno Belloni.

#### 4. Conclusions

Global warming is a long-term trend. In the Mediterranean Sea, it has resulted in the northwards and westwards expansion of the range of native species with warm affinity, e.g., the teleosts *Scorpaena maderensis*, *Sparisoma cretense* and *Thalassoma pavo* [39–43], together with many Lessepsian species introduced into the eastern basin. It has caused a shift in ecosystem functioning in the eastern part of the Mediterranean. One of the most spectacular species resulting from this upheaval are teleosts of the genus *Siganus* (rabbitfish), which are formidable herbivores that have completely disrupted the habitats of photophilous rocky reefs in the eastern basin [146–148], although their success could be a consequence of the pre-existing thermal conditions in this eastern basin (or much of it).

Marine heatwaves, however they are defined and delimited (questions that are open to debate), are discrete extreme events. They provide additional evidence of climate warming, highlighted by changes in their intensity, frequency and duration. However, it must be noted that marine heatwaves in the Mediterranean are not a new or recent phenomenon. The first documented event dates from 1983. But it is likely that for some of the heatwaves reported for centuries on land (see, e.g., [3] in western Europe) there may have been a corresponding phenomenon in the marine environment.

Most of the literature about Mediterranean marine heatwaves reports associated mortality events (e.g., [11,19] and references therein). Extreme events always induce extreme reactions from the public, from users (divers, fishermen) and from the media, but also from scientists when only the negative impacts are emphasized and perhaps sometimes exaggerated. The impacts on sessile invertebrates are localized to particular sites and within a relatively reduced depth range. Currently, these underwater mortality events, although spectacular for divers, have a relatively limited impact over time: the resilience of some (not all) of the impacted species must be considered, and no species is threatened with rapid extinction by these heatwaves because their distribution, in particular their depth range (e.g., *Paramuricea clavata*), goes well beyond the impacted areas and depths [149–152]. Cases of recovery following mass mortality events of gorgonians (*P. clavata*) have been reported in different locations after different MHWs over time [153,154]. In addition, these species may have dispersal capacities via planktonic larvae higher than expected, and connectivity between populations is maintained, since it is rare that all of the individuals are killed [155]. Resistance to thermal stress varies between individuals within a population and between populations, e.g., in *Corallium rubrum* and *Paramuricea clavata* [156–158]. Larval exchange between sites hundreds of metres apart and between different depths has occurred, supporting the hypothesis that deeper subpopulations unaffected by sea surface MHWs may provide larvae for shallower ones, enabling recovery after climate-induced mortality events [144,159,160]. Of course, the frequency and intensity of these events could have more significant long-term consequences in the future, such as regional species extinctions, especially when slow-growing and long-lived species are considered; this is already the case for the sponge *Spongia officinalis*, regionally extinct in western Provence [38]. Even if species impacted by MHWs are generally not threatened, the consequences are mainly related to the alteration of the seascape and the related ecosystem functioning [161]. After the collapse of animal forests such as gorgonian facies, ecological functions can be strongly affected in the long term [20,58].

The record-breaking 2022 heatwave had a spectacular impact on certain species (the ‘losers’) and probably on ecosystems yet to be described and analysed.

Parallel to the mortality of certain species, marine heatwaves may favour others, the thermophilic species (the ‘winners’), that may benefit from these extreme events to develop and disperse. Here, we have chosen three case studies in the north-western Mediterranean. (i) The possible induction of ‘flowering’ (in the form of the paintbrush stage) of the green alga *Penicillus capitatus*. (ii) The unprecedented bloom of the green alga *Microdictyon umbilicatum*. (iii) The massive flowering of the seagrass *Posidonia oceanica*. Other possible winners could have been proposed, but they require further investigation, and our aim was not to be exhaustive.

The equilibrium of ecosystems is a shifting status influenced by environmental factors. The current warming is obviously one of the main stressors affecting the Mediterranean Sea. In this context, heatwaves constitute milestones: unlike long-term warming, the consequences of which for ecosystems are often not perceptible in the short term, heatwaves cause spectacular, clearly visible events, either mortality or, on the contrary, the proliferation or massive reproduction of certain species. Both processes, the long-term warming trend and one-off heatwaves, both losers and winners, shape the change in structure and functioning of Mediterranean ecosystems.

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