Through ages and centuries: the long, challenged and threatened life of *Posidonia oceanica*

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Abstract: *Posidonia oceanica* (L.) Delile, the Mediterranean's endemic seagrass, is one of the most ancient and ecologically irreplaceable organisms on Earth. A survivor of geological upheavals, mass extinctions and millennia of environmental changes. This review synthesizes current knowledge of its evolutionary origins, unique biological characteristics, and the multiple pressures now threatening its persistence. Drawing on recent literature spanning genomics, ecophysiology, climate science and conservation biology, we examine the dual reproductive strategy that has sustained clonal meadows, and the mounting evidence of simultaneous direct and indirect anthropogenic impacts across the Mediterranean basin. The challenge is to survive at compounding climate drivers as thermal stress, ocean acidification, stratification, and sea level rise. Despite a 34% regression of meadow extent in the last 50 years, the species retains adaptive potential through epigenetic stress memory, phenotypic plasticity, and stress-induced mass flowering. The convergence of climate change with coastal development, pollution, invasive species and overexploitation, however, is occurring at a pace that far exceeds the species' capacity for recovery. Effective conservation requires urgent, coordinated action across the 21 Mediterranean nations, before the trajectory becomes irreversible.

Keywords: *Posidonia oceanica;* Mediterranean Sea; climate change; seagrass conservation; marine heatwaves; ocean warming; seagrass restoration; anthropogenic pressure.

1.
The Ancient Survivor

Thalassotaenia notophyllum sp. nov., fossil

In the summer of 2025, an article was published about fossils discovered in the lower part of an exposed coastal cliff, in a location called Isla Escondida, in remote Patagonia (Panti et al., 2025). Under various sedimentary deposits, a layer of tuff dated 20.5 ± 0.46 Ma, lies about 17 meters above a vegetation horizon where traces of seagrasses, with clearly recognizable epibionts, have been found, dating back to the beginning of the Miocene. Interesting data emerged from the analyses carried out. A new morphospecies *Thalassotaenia notophyllum* sp. nov. has been identified thanks to the beautifully preserved ribbon-like leaves with parallel veins, preserved epibionts on the leaves such as diatoms, bryozoans, coralline algae, polychaetas, and even the plagiotropic rhizomes with roots. Researchers recognized characters phylogenetically close to the genus *Thalassia* (Hydrocharitaceae), and they can better understand the southernmost environment where seagrass fossils have been found.

What fossils can reveal to us is always important, but when they show plant organisms it is, if possible, even more precious. Plants, especially those devoid or almost devoid of lignin, like seagrasses, are by their very nature destined to rapid decomposition and it is rare to find complete fossils of the various parts essential to the identification of the plant.

Thalassotaenia notophyllum sp. nov. is not a species of phanerogam closely related to *Posidonia oceanica*, although both belong to the Order Alismatales, the group that diverged from other monocotyledons in distant eras and underwent the evolutionary transition that brought some lineages back to the sea, becoming plants capable of modifying physiological functions and structures to adapt to the sea and to the context of that epoch.

Aquatic angiosperms are not frequent: flowering plant evolution involved more than 200 independent transitions from terrestrial ancestors to aquatic environments (Cook, 1999), a figure that more recent phylogenetic analyses suggest may be considerably higher (Tippery, 2026). Today aquatic angiosperms represent only about 2% of flowering plant species. The vast majority (recent estimates suggest 33 families and thousands of species) inhabit freshwater environments while seagrasses, a polyphyletic group,

comprise only about 60 fully marine species, encompassed in 4, to 6 families depending on the taxonomic treatment adopted: Zosteraceae, Hydrocharitaceae, Posidoniaceae, Cymodoceaceae and Ruppiaceae (Kuo & Hartog, 2006; Les & Tippery, 2013; Waycott et al., 2006).
The current overall geographical distribution of the various families includes the temperate coastal zones of the North Atlantic, the North Pacific, the Southern Oceans; the tropical areas of the Atlantic and the Indo-Pacific; and the Mediterranean (Short et al., 2007).

Genetic links have been studied to try to understand the connections and the distances between land plants, freshwater plants, seawater plants and have revealed a remarkable pattern: the transition from land to sea happened at least three separate evolutionary times (Les et al., 1997; Ma et al., 2024). Molecular phylogenetic research gave a clear indication of the three independent origins of the seagrasses, with three different lineages:

1. The Hydrocharitaceae, including *Thalassia* – to which the Patagonian fossil is related;
2. The Zosteraceae-Potamogetonaceae clade;
3. The Cymodoceaceae complex which includes Posidoniaceae, Cymodoceaceae, and Ruppiaceae.

Certainly, seagrasses living completely submerged have accomplished one of evolution's most extreme challenges, because every lineage, evolved from freshwater or salt-tolerant ancestors, had to undergo the same suite of necessary adaptations scheme, to deal with increasing salinity, reduced light, underwater pollinations and resistance to the mechanical forces of waves and currents. It's quite easy to understand how rare and difficult it may have been to realize this evolutionary transition to survive marine conditions, especially considering how essential it was that all these skills act simultaneously.

To better understand the extent of this step, it is useful to remember the strategies that made it possible. Recently, it has been ascertained that a possible key to understanding the extent of the mutation is a consequence of a triplication of the entire genome, which took place about 86 million years ago, which established genetic redundancy allowing some gene copies to maintain essential functions while other genetic copies could modify the capabilities by acquiring or losing some functions. This macromutational event can be the facilitating element of a simultaneous evolution of very complex adaptations (Ma et al., 2024).

What has been gained from this evolution? Here are just some of the most notable examples. The aerenchyma, a specialized spongy tissue, with large air cavities (lacunae), which runs the entire length of the plant, from the leaf to the rhizome, from the rhizome to the root, and which performs multiple tasks simultaneously: it provides buoyancy, structural support and flexibility which, at the same time, allows the transport of oxygen to the roots, often growing in anoxic sediments (Kuo & Hartog, 2006).
Among the most crucial assets, it was indispensable to improve and refine the efficiency of proton pumps (Salt-tolerant H^+-ATPases) to generate electrochemical gradients between cell membranes, and Na^+/H^+ antiporters, NHX family proteins, membrane transporters that actively move sodium from the cytoplasm while maintaining the necessary low Na^+/K^+ ratio for enzymatic functions (Touchette, 2007).

Cell walls were redesigned, adding to polysaccharides shared with terrestrial plants polysaccharides like polyanionic, low-methylated pectins and sulfated galactans, which are absent in terrestrial and freshwater flowering plants, being more characteristic in macroalgae, whose function is to facilitate gas exchange through the leaf epidermis and also allowing nutrient uptake (Aquino, 2004).
This step is of particular importance because the evolutionary scheme required a radical simplification, losing the ability to build and use stomata, fundamental structures of terrestrial plants, but unnecessary or even detrimental for fully submerged plants (Olsen et al., 2016). Without stomata, CO_2 acquisition takes place directly through the leaf epidermis. Since CO_2 diffuses approximately 10,000 times more slowly in water than in air, and most dissolved inorganic carbon in seawater occurs as HCO_3^-, which cannot passively cross membranes, seagrasses evolved mechanisms to access this important carbon source. With enzymes on the leaf surface (external carbonic anhydrase, outside the outer plasmalemma), HCO_3^- is converted into CO_2. Simultaneously, proton pumps (H^+-ATPases) expel hydrogen ions, creating localized acidic microenvironments that further shift the equilibrium toward CO_2 concentrating it near the membrane surface to promote passive diffusion into cells. Internal carbonic anhydrase in the cytoplasm then reconverts CO_2 to HCO_3^-, trapping it inside the cell as it cannot cross lipid membranes, while stromal carbonic anhydrase in the chloroplast reconverts HCO_3^- back to CO_2 precisely where Rubisco requires it for photosynthesis. It should be remembered that in seagrasses photosynthesis takes place in the epidermis. This carbon-concentrating mechanism ensures adequate carbon supply even in CO_2-limited underwater environments though it imposes metabolic costs associated with ATP consumption for proton pumping and enzyme synthesis (Larkum et al., 2017; Touchette & Burkholder, 2000). There are several hypotheses about possible mechanisms of membrane transporters, cotransporters or symporters, that would directly import HCO_3^- inside the leaves. For example, anion exchangers have been characterized in kelp (macroalgae), but these proteins have not been identified or characterized for seagrasses (Beer & Rehnberg, 1997; Fernández et al., 2014; Rubio et al., 2017).

Endless studies could be conducted on each of these evolutionary acquisitions and losses to describe them in greater detail, and to understand how these adaptations have allowed seagrasses to persist across geological eras of millions of years. Many other fundamental aspects remain active areas of research, including structural hypolignification (Ma et al., 2024), light-harvesting systems optimized for the underwater spectrum (high PSI/PSII ratios, enhanced LHCII) and the dual reproductive strategy. It is very interesting that all seagrasses retain the common characteristic of reproducing both sexually – through underwater pollination, and the production of fruits and seeds that enable genetic recombination and dispersal – and asexually – through clonal growth of orthotropic genetically identical ramets via plagiotropic rhizomes (Kuo & Hartog, 2006). Both strategies respond to the limitations or the opportunities posed by environmental biotic and abiotic constraints: sexual reproduction promotes genetic diversity and colonization, while clonal growth ensures persistence in stable habitats. This flexibility has sustained seagrasses through past climate shifts, now it may represent sufficient evolutionary advantage to face the present era, where rapid changing conditions pose unprecedented challenges. Ocean warming, acidification, and intensifying coastal development occurring within decades rather than millennia are posing pressing questions for the future of these ancient and irreplaceable ecosystems. Recent discoveries reveal a more nuanced range of possibilities. The same ancient strategy of the whole genome triplication that enabled marine colonization may provide ongoing genetic redundancy that buffers populations and facilitates innovation (Ma et al., 2024). Moreover,

seagrasses employ rapid, non-genetic adaptive mechanisms: epigenetic modifications enable stress memory, allowing plants to “remember” and respond more effectively to repeated thermal challenges (Nguyen et al., 2020); phenotypic plasticity permits adjustments to photosynthetic machinery and morphology within individual lifetimes (Edgeloe et al., 2022); and crucially, environmental stress itself triggers sexual reproduction, as witnessed in mass flowering events generating genetic diversity precisely when populations need it most (Marín-Guirao et al., 2019; Tomas et al., 2024).

In the complex evolutionary context of seagrasses, briefly described so far, it’s time to focus on *Posidonia oceanica*, an endemic species of the Mediterranean, to understand where and when “she” comes from, and what the present looks like.

P. oceanica inflorescence

2. From the Cretaceous to Us: One Species, One Sea

Let's start again with fossils. Of the scarce finds associated with *Posidonia*, recorded from the Cretaceous to the Miocene (Gessner, 1971), some have been associated with three extinct species of the Tethys Sea: *Posidonia cretacea* Hosius & Von der Marck (1880), *P. perforata* e *P. parisiensis*. Some of these attributed to *Posidonia parisiensis* are currently preserved at the Muséum National d'Histoire Naturelle in Paris and relate to marine deposits from mid-Eocene – end of Oligocene (48–23 Ma).

What factors have favored the long process of evolution and then persistence through the ages, and which have prevented their territorial expansion? *Posidonia oceanica* is in fact a unique species endemic to the Mediterranean Sea, confined within its shores for tens of millions of years, at least since the Sea became how we know it now, with its present configuration. It has been a process which unfolded in many phases, starting back to the Miocene (23–5.3 Ma), when a series of major geological transformations reshaped the basin through very different scenarios. It took millions of years for the Tethys Sea to close and almost another one million to endure and survive the Messinian Salinity Crisis. The dramatic lowering of the sea level fragmented the basin into lagoons and isolated brackish water bodies, environments that probably hosted and, in some way, selected the ancestors of *Posidonia oceanica*, capable of withstanding fluctuations in salinity, light availability, and temperature. The Messinian crisis ended approximately 5.3 Ma when the connection with the Atlantic Ocean was restored. Since then, one should recall the subsequent repetition of countless glaciations and deglaciations, culminating in the Last Glacial Maximum approximately 20,000 years ago, when sea levels dropped by over 120 meters. That affected the Mediterranean area, along with the interaction between tectonics and climate-induced sea-level oscillations and modified the environment as a result of temperature fluctuations and repeated sea level variations (Anzidei et al., 2014; Charles-François Boudouresque, et al., 2025). It is highly probable that the severity of these conditions left a lasting imprint on the genetic variations observed by contemporary analysis, between the populations of the eastern regions, compared to those located in the western Mediterranean (Arnaud-Haond, Duarte, et al., 2007; Serra et al., 2010).
These transformations were complete long before the first humans walked the Earth.

Posidonia oceanica is a witness to a Mediterranean that no human eye has ever seen.
While *Posidonia oceanica* remains the sole representative of its genus in the Mediterranean, the family Posidoniaceae has its other living members in the southern waters of Australia, where eight species are distributed along the temperate coasts from *P. australis*, the most studied, to smaller and less known species grouped in two distinct complexes (Aires et al., 2011; Gobert et al., 2006).
The split between the Mediterranean lineage and the Australian ones is ancient, dating back, once again, to the Tethys Ocean, this time more than 60 million years ago, as estimated through molecular clock analyses calibrated on the fossil record of the genus (Aires et al., 2011). Yet, they are not genetically close but genetic divergence between them remains surprisingly low, a reflection of the extraordinarily slow evolutionary rates that characterize the entire genus, shaped by long generation times and the dominance of clonal reproduction (Larkum et al., 2006).
Today, these distant relatives share not only their ancestry but also a striking functional similarity: *Posidonia oceanica* so closely mirrors the Australian species that the two communities, geographically separated by 17,000 km (Celdran et al., 2015; Larkum et al., 2006), occupy remarkably similar ecological niches and moderately similar functional compositions despite complete species and lineage replacement (Bosch et al., 2025; Waycott et al., 2006). A living echo of the shared Tethyan origin.
Unlike the other seagrass species sharing its habitat, whose wider ecological tolerances and dispersal capacities allow them to extend beyond the Mediterranean basin (Kuo & Hartog, 2006), *Posidonia oceanica* lacks both the biological tools and the evolutionary flexibility to cross its boundaries: a prisoner, in the end, of its own specialization.
However, this does not mean that the tools available offer no prospect for the future. The very specialization that confines this single species to a single sea has also shaped a remarkable set of survival strategies, and that may yet be enough, but the challenge, however, is far from simple in the face of a rapidly changing Mediterranean.
The historical ability to adapt has attracted growing scientific attention for at least half a century. One of the most important strategies, of course, is the dual possibility of reproduction through both the clonal growth system and seed production and dispersal system. The benefits of these strategies are revealed by the age of existing meadows: clonal groups ranging from 1 to 15 km in size, whose age have been dated between 80,000 and 200,000 years (Arnaud-Haond et al., 2012).

Before analyzing the two reproductive strategies in detail, it is appropriate to fully describe the morphology, structural complexity, and rhythms of *Posidonia oceanica*, to understand its strength and vulnerability.
The plant is a true flowering one, monocot angiosperm, with hermaphrodite flowers. In early autumn the inflorescence emerges and arises from the base of the leaf bundle, the long peduncle supports 3–5 spikes, which can bear from 3 to 6 flowers each. The flowers are devoid of perianth, sepals and petals. Self-pollination is minimized through protogyny, with initial maturation of the carpel – female phase – with one ovule contained into the ovary, and the three stamens in the bisexual flower – arranged in a single whorl, one median-abaxial and two inserted transversely – only two lateral stamens if the flower is male (Remizowa et al., 2012). When the stamens mature, they release thread-like pollen. From late spring through early summer, fruits progressively mature and detach. They are olive shaped, soft and float on the sea surface for a variable period, from a few days up to several weeks depending on currents and winds, then settle on the ocean bed, where fruit dehiscence occurs, through splitting longitudinally and releases one green seed. It has a membranous coat, a primary embryonic root and two adventitious root primordia, which germinates soon after released and immediately

produces real roots (Kuo & Hartog, 2006). The seed epidermis contains chloroplasts, so good light conditions promote photosynthetic activity. The seed is fully able to survive thanks to the abundant reserve of starches and an efficient vascular system that allows the mobilization of what is necessary for growth (Belzunce et al., 2005, 2008a; Celdrán & Marín, 2011).
The 6 or 7 leaves sprout from the seed or from a vertical rhizome. In the first case, the seedling needs a few months (6–8) to be photosynthetically autonomous (Balestri et al., 2009; Sutera et al., 2024). The leaves are ribbon-shaped, a long lamina with rounded or truncated apex, crossed by 8–11 longitudinal veins parallel to each other, i.e. the vascular bundles. Leaves can be bright green from juveniles – smaller than 5 cm – to intermediate – longer than 5 cm. When a petiole (ligula) is formed between sheath and lamina, finally the leaf is adult, it may reach 80–100 cm in height, often darker green and colonized by various epiphytes (Boudouresque et al., 2012). So, leaves of different ages can grow in the same node and are formed throughout the year but at different speeds during spring/summer or autumn/winter (Celdran et al., 2015). In addition, leaf fall is a senescence process that allows the recovery of useful nutrients (resorption) (Hemminga et al., 1999).
The leaf grows from the basal part – sheath – surrounding the orthotropic rhizome that originates from the main stem, a creeping rhizome, usually horizontal – plagiotropic – with an apical meristem, which develops nodes at regular intervals for the emission of vertical rhizomes, also with their own apical meristem.
This distinction, however, is not rigidly determined: according to available space and local conditions, an orthotropic rhizome may assume a plagiotropic orientation and vice versa (Caye, 1980). Their directional flexibility may be itself an expression of the remarkable phenotypic plasticity of the species, a theme that will be explored further in relation to clonal growth and reproductive strategies. The plagiotropic rhizome remains anchored to the substrate thanks to the roots and the node can also have branched or unbranched roots.
Given their composition, mainly phenolic constituents based on p-hydroxybenzoic acid (p-HBA) – atypical for vascular plants – sheaths, rhizomes and roots are not easy to degrade (Kaal et al., 2016). Notable factors are both the rich presence of lignin-like phenolic compounds and the conspicuous presence of cellulose and hemicellulose, both in relation to a substrate that tends to be anoxic (Rencoret et al., 2020). The layered overlapping of alternate rhizomes creates an interlacing structure that favors the accumulation of organic material and traps sediment, thus constituting a dense biogenic structure, called “matte” with many consequences. The architectural structure takes on a complex shape over time, a bioconstruction that grows rather slowly, but its development gradually modifies its own aspect: the more crowded areas prefer to grow orthotropic rhizomes, while the borders of the colony create the plagiotropic form (Vacchi et al., 2017). Once established, the matte modified also the environment acting like a barrier against currents, protecting beaches and coastlines from wave erosion. At the same time the matte functions as the major natural sink of organic carbon (Kaal et al., 2018). However, if the sediment supply is too abundant, such as near the mouths of rivers with large transport, the meadow can disappear (Boudouresque et al., 2012). In addition, if meadows are located where there are intense wave motion and/or strong currents, the matte can be eroded and fragmented by internal channels, originated from that erosion.

There are many factors that govern the complex chemistry of *Posidonia oceanica*, only partially described so far. Dissolved nutrients are absorbed through the epidermis of the leaf blade, where the process of photosynthesis takes place too. Photo assimilates are then translocated through the phloem reaching the active rhizomes and the meristematic tissues, while nutrients absorbed by both leaves and roots, depending on their availability in the water column and in the sediment respectively, are transported via the xylem to the

rhizome and meristematic tissues, where they can be stored during winter, as documented for inorganic nitrogen, for subsequent utilization during spring, for the seasonal growth (Alcoverro et al., 2000; Invers et al., 2002).
The different growth rates of the modular plant are evident by comparing existing data about the seasonal growth of the leaves, the slow plagiotropic growth, the even slower orthotropic growth and that linked to the episodic phenomenon of flowering. It is precisely these differentiations that make it necessary to investigate more deeply the question of dual reproductive strategies.

Most of the *Posidonia oceanica* meadows scattered in the Mediterranean Sea have existed for millennia. Clonal colonies already witness a genetic procedure capable of resisting both general and local environmental changes, implementing complementary mechanisms of development and persistence. The clonal plant is so defined when the various modules are functionally independent, even if connected. The physiological interaction is determined by the rhizome advancing horizontally in the substrate and producing, at regular intervals, ramets formed by a piece of rhizome, a bundle from which new leaves will emerge, and a root system (Borum et al., 2004; Marbà & Duarte, 1998). The clonal offspring is called "ramets", the plant that includes a variable number of clonal ramets is called "genet". Thus, the same genet contains ramets that share the same genotype and with the possibility of acting as an independent individual (Ruocco et al., 2021). They can share resources and risks (Dodd & Douhovnikoff, 2016), studies demonstrated functional integration between neighboring ramets through translocation, reallocation of nitrogen, carbon, nutrients, and photosynthates to organs of increased metabolic activity to promote clonal growth and colony spread (Marbà et al., 2006).

Recently, the important genetic question has been better investigated. Classical evolutionary theory predicts that clonal lineages should accumulate deleterious mutations over time, a process known as Muller's ratchet, eventually leading to extinction. Yet the ancient clones of *Posidonia oceanica* appear to contradict this prediction. Several theories propose alternative perspectives to explain this resilience. The General-Purpose Genotype model suggests that clonal reproduction allows for the preservation of exceptionally well-adapted genetic complexes that are advantageous to preserve. The Frozen Niche Variation model offers a complementary vision, proposing that different clonal genotypes co-exist by occupying narrow, non-overlapping ecological niches, each specialized in local microhabitat conditions (Arnaud-Haond et al., 2012; Ruocco et al., 2021).

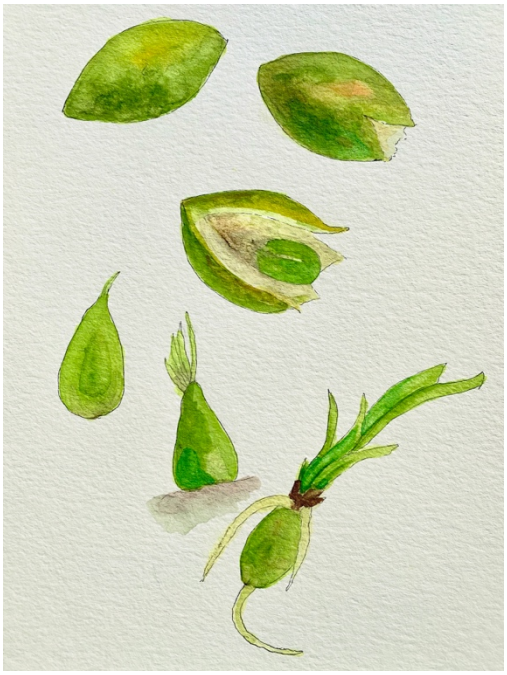
In the absence of frequent genetic recombination, adaptation to environmental change relies heavily on phenotypic plasticity, the capacity of a single genotype to express different morphological, physiological and behavioral responses to varying conditions (Pazzaglia et al., 2021). In *Posidonia oceanica* this plasticity is expressed at multiple levels: in the flexible orientation of rhizomes in response to available space, in the seasonal storage and remobilization of nutrients, and in the capacity to modulate growth rates according to light and temperature regimes.

The legacy left by ancient episodes of polyploidy is a genetic redundancy that can compensate for what was predicted by the Muller's ratchet theory. Evidence of this rapid adaptation mechanism during intense environmental stress comes from research in Australia's Shark Bay, where a single polyploid clone spanning nearly 180 km, the largest known clone on Earth, appears to have expanded into increasingly stressful habitats precisely through the combination of genome duplication and clonal growth

(Edgeloe et al., 2022). A clone that has survived thousands of years has done so not by changing its genome, but by remaining flexible in its expression.

Yet clonal growth is not, however successful, without its limits. The stability and persistence resulting from asexual reproduction constrain the development of evolutionary potential. Without genetic recombination adaptive variation cannot be generated and the clonal genotype may not be adequate when environmental change exceeds the boundaries of phenotypic plasticity (Arnaud-Haond et al., 2012; Pazzaglia et al., 2021). The very nature of clonal expansion makes it difficult to bridge geographical barriers, or colonize disconnected or distant habitats, or ensure recovery and recolonization following meadows loss, or serious disturbance (Ries et al., 2023). Moreover, any damage caused by pathogens or by some long-lasting stress factor (eutrophication, heatwaves), can compromise individual genets or the entire clone. The genetic uniformity renders the seagrass meadow or parts of it particularly vulnerable to disease and stress events (Hughes & Stachowicz, 2004; Reusch et al., 2005).

In response to these limits, sexual reproduction emerged as a complementary strategy available for *Posidonia oceanica*'s survival, even if it is a rather rare, episodic event. Previously, some of the principal phases were mentioned: the seasonal emergence of the hermaphroditic inflorescence, protogynous flowering strategy to avoid self-pollination, the winter to spring slow fruit formation, their detachment and dispersal, and the eventual seed settlement and germination. Each of these phases presents possible critical issues, beginning with the energetic investment required of each ramet to produce flowers and fruit. This investment is preceded by a prolonged accumulation of carbohydrate reserves in the rhizomes, a pattern that has led some authors to draw parallels with the mast seeding strategy described in terrestrial plants, characterized by infrequent reproduction and elevated shoot mortality in flowering years (Jahnke et al., 2015). The physiological cost is visible at the shoot level: flowering bundles carry an extra leaf, likely to meet the carbon demand of inflorescence production, while rhizome elongation slows markedly over an extended period (Calvo et al., 2006). Yet the probability of success at each stage is remarkably low. Only one mature and viable fruit results from 12 or 13 inflorescences; approximately 87% of the attempts are spontaneously aborted and about 10% is consumed by herbivores. The high abortion rate may be related to limited cross-pollination opportunities or to the occurrence of self-pollination (Balestri & Cinelli, 2003). In fact, protogyny prevents self-pollination within the same flower, but the problem arises equally in the context of pollination between flowers from genetically identical ramets (geitonogamy). Studies on *Posidonia australis* have revealed that hydrophilous pollen travels beyond the clone boundaries, so despite the clonal structure the meadow effective outcrossing prevails (Sinclair et al., 2014). This discovery is not yet demonstrated valid for *Posidonia oceanica.*



P. oceanica fruits and seeds, various phases

However, this is an energetically expensive process, and it may appear as a wasted investment, but other strategies intervene. The frequency and intensity of episodic flowering are very variable in space and in time, and there is seasonality, related to cooling water and shortening day length. In fact, some factors that favor flowering have been recognized: the age of the ramet, sufficient nutrients, and solar activity (Balestri & Vallerini, 2003; Gobert et al., 2005; Montefalcone et al., 2013). There is also the possibility of sexual reproduction as the most useful mechanism when climatic uncertainty alters stability. Intense heatwave-stimulated flowering events in the laboratory showed correlation with allelic richness and heterozygosity and this may be a capacity to respond in an adaptive way to temperature rises (Ruiz et al., 2018). The mass flowering also seems to follow far-reaching temperature rises, as in the heatwaves recorded in several recent years (1982, 1994, 1998, 2003, 2012, 2015, 2022, 2023 and 2024) across the Mediterranean Sea. After the unprecedented sea warming of 2022, mass flowering was extensively recorded across several sites (Stipcich et al., 2024). From January 2023 in the Balearic Islands, for the first time pseudovivipary was reported for *Posidonia oceanica*: the forming flower does not produce stamens or pistils but produces, with asexual behavior, a plantlet genetically identical to the maternal plant, which remains attached while developing its own leaves and roots before detachment and dispersal (Tomas et al., 2024). Only one previous observation of a comparable phenomenon had been reported, following a heatwave, in *Posidonia australis*, at Shark Bay, Western Australia (Sinclair et al., 2015).

At this point, having overcome the challenges of flowering, both fruits and seeds – and pseudoviviparous plantlets – face their own challenges before a new plant can establish. Their biology shows remarkable adaptations to making the effort more successful. The

fruit is not only a transporter and a reservoir: its pericarp, a compact outer hypodermis bearing chloroplasts, underlain by a thick spongy mesophyll traversed by air lacunae, is made
for buoyancy and, more than that, to allow light to reach the seed within, because the seed itself is already photosynthetically active before germination. This function persists and intensifies for a couple of months following seedling establishment, sustaining growth of roots and leaves of the developing plantlet (Celdrán & Marín, 2013). Even the seeds of *Posidonia australis* and *Posidonia sinuosa* have been confirmed as photosynthetically active, and this shared trait across genus suggests an adaptive mechanism inherited from a common ancestor during the Late Eocene (37.2–33.9 Ma). The larger seed size of the *Posidonia oceanica* compared to its Australian congeners may be a consequence of the Tethys basin closure with severe conditions of oligotrophic sea (Celdran et al., 2015).

The last step is a very crucial one. The result of this complex process depends entirely on the substrate where seeds come to rest. Various studies confirm that seed rooting succeeds in approximately 89% of cases on rocky substrates, while on sandy bottoms success drops to zero (Alagna et al., 2015). This seems counterintuitive but roots have adhesive capacity through root hairs that cling to hard, consolidated and immobile surfaces. Sand, by contrast, offers no resistance to displacement, being itself subject to movement by currents, and therefore it provides no stable anchorage for the developing seedling (Badalamenti et al., 2015). Of course, the site with greater hydrodynamics exacerbates the difficulty of anchoring the plantlet while a rock is a solid base to create, over time, a matte. In addition, plasticity was found in root hair response to substrate contact: tips of the root hairs acquire different morphologies (branched, digitiform) in relation to the type of substrate and exploiting its micro-roughness. Settlement occurs through adhesion and increasing mechanical interlocking, which provides anchorage strength of up to 2.4N (Zenone et al., 2020).

Prolonged research has shown that seedling establishments occurs in sites with a mixed substrate of sand and rocks or sand and dead matte, where attachment is also successful, but the high germinability demonstrated experimentally is rarely expressed in nature as additional favorable conditions must simultaneously occur and are strictly necessary, such as water movement, and availability of light and nutrients (Belzunce et al., 2008a; Piazzi et al., 1999). The spatial expansion proceeds slowly: about 10 cm in about 10 years has been observed in a location in Corsica. This growth rate agrees with study models where an 8 m diameter patch is expected to develop over 100 years (Balestri et al., 2017; Kendrick et al., 2012).
So, finally the new sprout is settled. What about its future?

P. oceanica seedling

3.
What on Earth is Going on Now?

The current knowledge of physiology, life cycle and specific characteristics of *Posidonia oceanica* has advanced considerably, compared to the first taxonomic and botanical descriptions of the late 19th century. Technological development now enables genomic studies, remote sensing and climate modelling. Ecological importance has progressively emerged from the underwater surveys of the 1960s through the

proliferation of studies in the 1980s. From the discoveries on clonality to the possibility of dating the matte of the 1990s and 2000s, the broadening of research fields and the advancement of investigative approaches have placed even more emphasis on the environmental role played by this ancient and still astonishing plant.
From the successfully rooted seed, the environmental importance of *Posidonia oceanica* meadows includes a long list of ecological services that have been recognized and increasingly defined over time:

- Carbon sequestration and long-term storage in the matte (Blue Carbon) (Fourqurean et al., 2012; Mateo et al., 2006; Pergent-Martini et al., 2021);
- High primary production, including contributions from the epiphytic community (Alcoverro et al., 2001; Pergent-Martini et al., 1994);
- Oxygen production supporting local aerobic communities (Pergent-Martini et al., 1994);
- Nursery habitat and biodiversity support for fish, invertebrates and epiphytes (Guidetti, 2000; Boudouresque, 2006);
- Coastal protection through wave energy attenuation and sediment stabilization (Infantes et al., 2012; Vacchi et al., 2017);
- Nutrient cycling and water quality improvement (Alcoverro et al., 2000);
- Food web support through exported leaf litter (Mateo et al., 1997);
- Bioindicator of environmental quality and ecosystem health (Gobert et al., 2009; Romero et al., 2007).

Beyond these well-recognized ecological roles, that make it fit perfectly into the definition of ecosystem engineer (Jones et al., 1994), recent research has begun to explore a more specific dimension of value. The sophisticated biotechnological techniques applied to chemical and molecular research have opened new perspectives for applications in the medical, cosmetic, agricultural and industrial fields, with consequent benefits for human beings. These potential advantages make the exploitation of *Posidonia oceanica* biomass even more appealing, also increasing its economic value.

- Biomedical and pharmaceutical applications: polyphenols, peptides and polysaccharides with demonstrated antioxidant, anti-inflammatory, anticancer and antimicrobial activity in preclinical studies (Abruscato et al., 2025; Leri et al., 2018; Messina et al., 2021; Punginelli et al., 2023; Vasarri et al., 2020);
- Cosmeceutical applications: photoprotective and skin anti-aging properties from leaf extracts (Barletta et al., 2015; Cornara et al., 2018);
- Neuroprotective potential: extracts showing protective effects on blood-brain barrier integrity under inflammatory conditions, suggesting applications against neuroinflammatory disorders (Abruscato et al., 2025);
- Valorization of beach-cast waste biomass (banquettes and egagropili): source of high-quality cellulose, lignocellulosic fibers for bio-based packaging, composite building materials and sound insulation, sustainable bioeconomy (Restaino et al., 2023; Benito-González et al., 2018; Khiari et al., 2010; Souii et al., 2023);
- Agricultural use: composting of banquette biomass as organic fertilizer (Castaldi & Melis, 2002);
- Heavy metal and pollutant adsorption: banquette waste as low-cost biosorbent for wastewater decontamination (Ferchichi et al., 2022);
- Bioethanol and synthesis of Cellulose Acetate production from lignocellulosic biomass as part of circular bioeconomy strategies (Coletti et al., 2013).

Most of these applications remain in experimental or laboratory stage. Although the research has noble and useful purposes, it is very likely that these innovative fields could add a further layer of pressure to the top of the many that already are acting on the *Posidonia oceanica* meadows, whose decline has been ongoing for decades and is, in large part, already attributed to multiple anthropogenic factors. The concern for the maintenance and preservation of *Posidonia oceanica* meadows, developed thanks to the multiplication of studies, began as early as the mid-70s.

The first legal regulations were issued to increase protection mechanisms. The international level starts indirectly with the Ramsar Convention (1975) for the protection of coastal wetlands, followed by the Barcelona Convention (1976), which flagged the threatened species. A little later, the Bern Convention (1979) declared the species as protected.

The European level provides for regulations and measures with different objectives:

1. The Habitats Directive 92/43/EEC (1992) classifies *Posidonia* beds (code 1120*) as a priority habitat in Annex I, forming the basis of Natura 2000;
2. It is listed in Annex II (endangered or threatened species) of the Barcelona Convention (1976, entered into force in 1978; updated in 1995) (SPA/BD Protocol). In 1999, the first action plan for the protection of the Marine Environment and the sustainable development of the coastal areas has been adopted;
3. *Posidonia oceanica* is listed (strictly protected flora) in Annex I of the Bern Convention (1979, updated 1996);
4. Under the Water Framework Directive (2000), *Posidonia* is used as a biological indicator to assess ecological status;
5. The Marine Strategy Framework Directive (2008/56/EC), establishes Good Environmental Status (GES) at marine scale, including seagrass habitats;
6. The Common Fisheries Policy (EC Reg. 1967/2006) explicitly prohibits the use of bottom trawls on *Posidonia* meadows.

Unfortunately, despite the attempts to protect them so far with legislative interventions, the decline of *Posidonia oceanica* meadows dramatically continues and its origins – direct and indirect – have a lot to do with the anthropogenic impact. However, various projects are trying to carry out mapping, measurements, monitoring and management plans at the local level. For example, the various EU-LIFE projects:

1. Posidonia Andalucia (LIFE09 NAT/ES/000534, 2011–2016), Spain, meadows in nine Natura 2000 sites in Andalusia;
2. LIFE SEPOSSO (LIFE16 GIE/IT/000761), Italy. First national-scale monitoring of *Posidonia* transplants in the last 20 years. It produced guidelines, technical manuals and the Posidonia Transplanting Web Platform;
3. LIFE SeaForest (2018–2023), Italy (ISPRA). Meadows as Blue Carbon reserves. It has installed sustainable mooring systems in three National Parks, restored over 100 small meadows areas and developed a protocol for quantifying sequestered CO_2, with prospects for a carbon market to finance conservation.

Moreover, at the Interreg level:

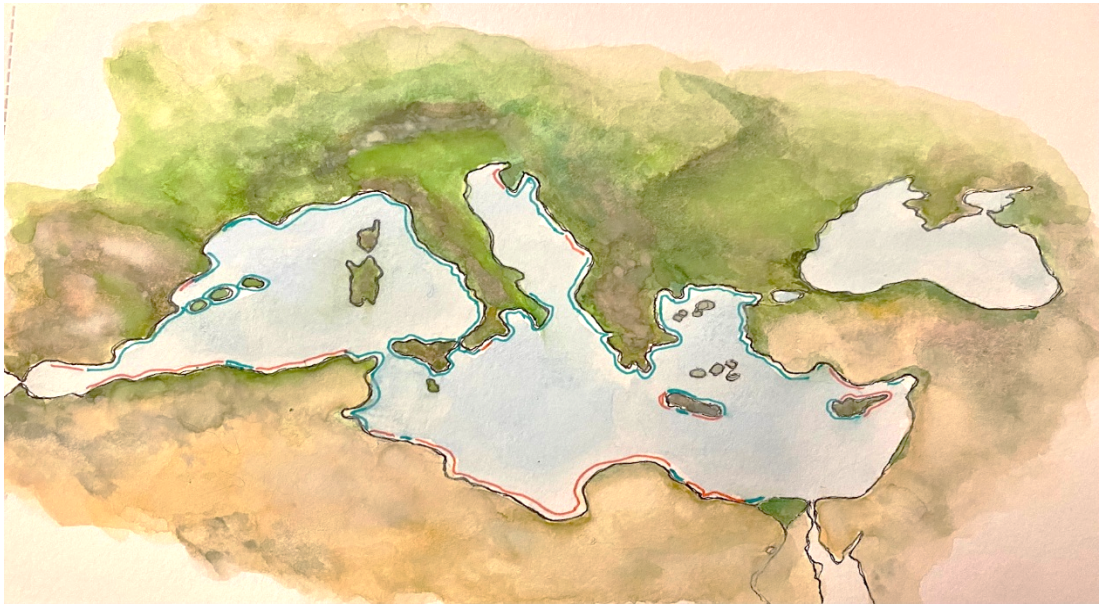
1. POSBEMED (2016–2018) and POSBEMED2 – Interreg MED Program, coordinated by IUCN. Focus on the management of banquettes on Mediterranean

beaches. The data collected revealed that 83% of local authorities remove *Posidonia* deposits every year, including protected areas;
2. ARTEMIS – Interreg Euro-MED is ongoing. Focused on meadows restoration using innovative techniques based on ecosystem services;
3. SASPAS – Interreg Italy-Croatia. Protection of meadows from anchoring in the Adriatic Sea.

There is also a coordination network: Mediterranean Posidonia Network (MPN) founded in 2019; it brings together about 60 members including scientists, authorities, NGOs and operators in the nautical sector. The declared goal: to protect 100% of the Mediterranean meadows by 2030.

As much as what has been done so far is appreciable and important, the existing rules and the projects in progress are not sufficient to solve a wide-ranging issue, which often manifests itself in inappropriate behavior at the local level. The enormous environmental danger represented by the reduced presence or absence of *Posidonia oceanica* for its dynamics, as we know them, is strictly related to its life cycle, slow growth and low recovery rate, as shown by conservation and replanting attempts. On a human timescale, the complete recovery of meadows is considered irreversible. In the last 50 years, regression has been estimated at 34% (Telesca et al., 2015).
What, and how many factors, such as the global changes already experienced by *Posidonia oceanica,* survived over millions of years, part of Earth's life, and what human intervention, actions, behaviors have been causing, and still are causing, this irreversible disaster? Can humans understand and correct this declining trajectory? Will it be possible to contain its dramatic consequences?

For *Posidonia oceanica* the Mediterranean is the only sea available.



Mediterranean Sea. Green line: *Posidonia oceanica* presence. Red line: absent or missing

A semi-closed basin, of almost 46,0000 km of coastline, islands included. Between 12,247 km^2 and 19,021 km^2 are colonized by *Posidonia oceanica* (Telesca et al., 2015; Traganos et al., 2022). The sea is surrounded by mainly narrow coasts and by rather high mountains, with many regional and local specific winds and microclimates. It is divided into eight sub-basins (Alborán, Algerian/Balearic, Ligurian, Tyrrhenian, Adriatic, Ionian, Aegean, Levantine) while an underwater ridge at a depth of about 360 m, between Sicily and Africa, "divides" the eastern basin from the western one. They are quite different because of the thermohaline circulation. Superficial, colder and less dense waters of the Atlantic enter through the Strait of Gibraltar, which is only 14 km wide, and progressively they move towards east, along the North African coasts until they reach the Levantine area.

Physical drivers (density variations, Coriolis effect, local winds) contribute to form stratification layers (superficial, intermediate, deep). The intermediate one moves back to west direction, along the Greek islands. This main current is the most constant factor of the Mediterranean circulation, warming, evaporating and increasing in salinity during its journey, with many local influences and variations. It is strictly connected with depth and marine topography, and, consequently, salinity differs significantly between the Eastern and the Western basins (Millot & Taupier-Letage, 2005). Furthermore, between the two basins, the eastern and western marine populations, including those of *Posidonia oceanica,* are significantly diversified at the genetic level (Arnaud-Haond, Migliaccio, et al., 2007).
Mediterranean Sea is a mosaic of ecosystems, hosting a high proportion of endemic species, consequences of its complex geological, geographic and civilizational history, whose human component has influenced the marine environment since antiquity. At first glance it might seem that in the last two centuries the appearance of the coast has been scarcely changed, but the reality is quite different. Mediterranean ecosystems have been profoundly modified by human activities (Boudouresque et al., 2009; Coll et al., 2010).
At the present time, the anthropogenic impact of the 21 countries bordering this sea consists of about 130 million coastal inhabitants, almost doubled with the tourist influx during the extended summer season (United Nations Environment Program, 2020). This population is expected to grow some 30% by 2050 (Aurelle et al., 2022). In the Mediterranean region the human presence also appears as a mosaic of very different social, political, and economic conditions. The existence of profound imbalances and inequalities makes the search for solutions even more complex. Accessing and using environmental resources equitably is a challenge for future generations, as is managing the impacts of climate change (Dos-Santos et al., 2020).

Of course, the growing number of inhabitants increases many different pressures on the environment: from a large to small, individual scale (Neeman et al., 2015). The creation of larger and busier ports or marinas, the creation of artificial seaside resorts and dredging provokes extra movements of sediment and seawater turbidity (Erftemeijer & Robin Lewis, 2006), in addition to altering shoreline profiles and modifying hydrodynamics, with growth or erosion phenomena of the coast itself (Biondo et al., 2020).

The fragile dune or sandy beaches are poorly considered as ecosystems. They are perceived as mere recreational surfaces while the secret life inside and outside sandy grains is often correlated with the Posidonia leaf litter accumulated on the beaches, the banquettes. Their systematic removal almost everywhere, driven by aesthetic and touristic demand, but now even for sustainable usage of what is generally considered “municipal waste” (Dentamare et al., 2025; Souii et al., 2023), deprive the coastline of a

very important natural protection against erosion, nutrient release and shelter for coastal flora and fauna (Rotini et al., 2020; Terracciano et al., 2026). Beyond the removal of banquettes, beaches are increasingly used as multi-purpose venues for tourism, entertainment and events, with compaction, artificial lighting and noise representing additional and largely unregulated disturbance factors for coastal wildlife. Moreover, mass tourism is tied up to high presence of UV filter cream chemical compounds widely used and released on every access into the seawater. Their accumulation in *Posidonia oceanica* tissues and in epiphytes too has been confirmed, both in laboratory and field tests (Agawin et al., 2022, 2024; García-Márquez et al., 2023).

The increase in fishing – literally overfishing – due to the food demands to be met, may be destructive and trawling is particularly harmful to the *Posidonia oceanica* meadows (González-Correa et al., 2005). The development of fish farms throughout the Basin, has negative effects on the quality of the seawater: wide installations with large discharge of organic matter, unused feed and chemicals into the surrounding waters, promoting eutrophication, reducing light availability and altering sediment conditions and each of these factors is directly harmful to *Posidonia oceanica* meadows (Delgado et al., 1999; Pergent et al., 1999). However, studies and monitoring reaffirm that sedimentation of organic material appears to be the fundamental negative factor for declining meadows (Holmer et al., 2008). A growing number of recreational boats moored at anchor can devastate many types of seabed. Crushing, tearing and abrasion produced by anchors or by their chains represent the major physical disturbance in *Posidonia oceanica* meadows, followed by the effects of fine particles resuspension, with localized siltation during re-deposition (Montefalcone et al., 2006, 2008; Pergent-Martini et al., 2022). Among the many difficulties that human activities impose on the marine environment, the unmanaged or inadequately treated discharges contribute significant quantities of pollutants, which now also reach even offshore and deep-water meadows, from the growing number of urbanized areas as well as from industrial sites (Jiménez-Casero et al., 2023).

The exponential increase in trade routes has also posed the problem of alien species released into the environment through their transport in ballast water and the washing of ships' holds, now better regulated but not applied with the same accuracy everywhere. The widening of the Suez Canal, which doubled in width in 2015, and the work on the southern sector completed in 2022–2023, has offered even more opportunities for the Lessepsian migration of non-native organisms. Among them the *Halophila stipulacea*, a tropical and subtropical seagrass species, arrived ~120 years ago (Winters et al., 2020) in the Mediterranean Sea, initially only in the eastern side. In 1995, it was recorded for the first time in the western Mediterraneo, close to Vulcano island (Aeolian Archipelago), representing the northernmost limit of its range at the time. In 2006 it was encountered further north in the harbor of Palinuro, Italy (Di Genio et al., 2021), and in 2021 it invaded a large area at Cannes, France (Thibaut et al., 2022). During time, its expansion can be considered slow, over 120 years its rate has been estimated in 12 km yr^{-1} (Georgiou et al., 2016). *Halophila stipulacea* mostly grows into the dead matte of native *Posidonia oceanica*, and alone on vacant sand or mixed with other native seagrasses (Winters et al., 2025), such as *Posidonia oceanica* and *Cymodocea nodosa*, or the green alga *Caulerpa cylindracea.* The recent warming of the Mediterranean water has a major role in *Halophila stipulacea* diffusion (Di Genio et al., 2021).

This warming trend introduces the most pervasive and far-reaching of all pressures: climate change. In the last two centuries, the Earth's climate has undergone increasingly faster changes. Natural processes, such as volcanic activities and solar shifts, have been

overwhelmed by human activities. The temperature of the atmosphere and oceans has risen, sea levels have risen as well, while the size of glaciers and polar ice caps have contracted. The causes of this change mainly depend on the exponential increase of greenhouse gas emissions produced by the use of fossil fuels in most, if not all, human activities (IPCC, 2021).

The Mediterranean Basin, with its unique geography, is recognized as one of the most important hotspots in the world for marine biodiversity: almost 18% of all known species, temperate and subtropical, are found there (Balzan et al., 2020; IPCC, 2021). Of these, about 20–30% are endemic, as is *Posidonia oceanica* (Coll et al., 2010), while ~666 are the reported as non-indigenous species by December 2019 (excluding Foraminifera) as is *Halophila stipulacea* (Zenetos & Galanidi, 2020). The same Geography also makes it a hotspot for climate change, according to the definition that a climate region is particularly sensitive to global change (Giorgi, 2006). According to climate models, a warming rate of ~20% higher than the global annual average is likely to happen in the region, with particularly hot summers, and a significant reduction in rainfall in all seasons, especially in southern areas (Lionello & Scarascia, 2018). The modifications of ecological responses in marine ecosystems due to climate change are provoked by variations – in average and/or in extremes – on the main drivers (temperature, salinity, pH, sea level). The increasing risks for marine and specifically for coastal environments is extremely high, especially for seagrasses (Hassoun et al., 2025; Henson et al., 2017). Biodiversity responds to changes across multiple timescales (from daily fluctuations to evolutionary transitions), but the current rate of change, a consequence of previously mentioned interacting pressure described above, is already causing documented species extinctions recorded, including the projected loss of Mediterranean seagrass habitat (Chefaoui et al., 2018; Templado, 2014).

At this point, it is worth considering in detail how climate drivers act and what are the effects on *Posidonia oceanica*, keeping in mind its distribution in the Mediterranean and its preferred habitat depth, from 0 to -40 m.
Rising water temperature represents the most identified and documented problem for *Posidonia oceanica*, whose thermal tolerance is quite narrow. Photosynthesis peaks between 28–30 °C and declines at higher temperatures until complete inhibition at 36 °C, while seeds show metabolic dysfunction from 26–28 °C onwards; a negative whole-plant carbon balance occurs above 32 °C in seedlings and plantlets (Marbà & Duarte, 2010; Rinaldi et al., 2023). So, while studies affirm that a consistent warming trend has been present in the Mediterranean SST for almost 40 years (Pastor et al., 2020), exceedance of these thresholds have been observed during the major marine heatwaves occurred since the early 2000s. A marine heatwave is defined as a prolonged period during which Sea Surface Temperature (SST) exceeds the local 90th percentile of long term climatology for at least five consecutive days (Hobday et al., 2016). Events can be classified as moderate, strong, severe or extreme based on multiples of the local difference between the climatological mean and the 90th percentile threshold (Hobday et al., 2018). Mediterranean heatwaves repeatedly happened in 2003, 2006, and most severely in 2022, when mass mortality events were recorded across multiple sites (Garrabou et al., 2022). At the meadow scale, the effects are measurable over decades. Rhizome production and leaf growth decline has been documented in western Mediterranean, while a two-decade record from the eastern basin, where warming is faster and baseline temperatures already higher, shows a progressive reduction in overall meadow productivity (Litsi-Mizan et al., 2023; Stipcich et al., 2022). Eastern Mediterranean populations of *Posidonia oceanica*, despite inhabiting warmer waters, show no greater thermal resilience than their western counterparts. Their upper thermal

limits are similar across the basin, but population near Cyprus, for example, persist where summer temperatures frequently approach or exceed those limits. This apparent paradox reflects a glacial legacy rather than recent acclimatization. Eastern and western population were isolated in separate refugia during the Pleistocene glaciations, accumulating genetic drift without developing local thermal adaptation (Bennett et al., 2022; Haverbeck et al., 2025). Since *Posidonia oceanica* occupies the water column from the surface to 40 m depth, understanding the full thermal threat to *Posidonia oceanica* requires looking beyond surface temperatures. It should be considered that the surface layer of the sea, between 0 and 10 m, is the most studied also through remote sensing. A temporal analysis between 1982 and 2019 showed a constant warming trend, about 0.035 °C·yr^{-1} (Pastor et al., 2020). Surface and intermediate layers combined (5–700 m) have been investigated with Argo floats, from 2005 to 2020. The western Mediterranean is warming faster than the eastern one (0.070 ± 0.015 °C·yr^{-1}). Significant warming trends are evident in the deeper layers (700–2000 m) of the two deep convection sites, the Gulf of Lione and the South Adriatic (Kubin et al., 2023). This cited study notes that an exceptional warming in the period 2013–2020 occurred in the southern Adriatic area.

The increase in atmospheric CO_2 intensifies greenhouse effects, more CO_2 is absorbed by seawater where the carbonate chemistry lowers pH through the formation of carbonic acid (H_2CO_3), with different consequences for many organisms, as happens for *Posidonia oceanica*. The plant itself appears relatively tolerant to reduced pH: shoot density and photosynthetic rates are largely maintained under moderate acidification, and in some experimental conditions the increased availability of CO_2 may even stimulate carbon assimilation (Cox et al., 2016). The more significant consequences concern the rich epiphytic community that colonizes *Posidonia* leaves (foraminifera, coralline algae, bryozoans, spirorbid polychaetas) most of which are calcifying organisms vulnerable to carbonate undersaturation. Studies conducted at natural CO_2 vents off the Italian coast, where pH is chronically reduced, consistently show that all calcareous epiphytes disappear or are strongly reduced, replaced by non-calcifying filamentous algae and hydrozoans (Mecca et al., 2020; Nogueira et al., 2017). This shift in epiphytic composition may generate cascading effects on the trophic network that depends on the meadow, and responses are not uniform across meadows: the degree of impact depends on local conditions and the health status of the plant community Under healthy conditions, *Posidonia oceanica* itself provides a partial refuge: its photosynthetic activity raises pH at the leaf surface, by up to 0.5 units during daylight hours, temporarily buffering the calcareous epiphytes against acidification (Hendriks et al., 2014). This protective capacity, however, is contingent on the plant's own health. A meadow already weakened by thermal stress loses its buffering function, exposing its associated community to the full impact of reduced pH (Apostolaki et al., 2014). The interaction between warming and acidification is therefore not additive but potentially multiplicative. However, before the overall assessment, further potential stresses induced by climate change remain to be considered.

A less visible but equally consequential dimension of climate change in the Mediterranean is represented by changes in salinity and water column structure. Although *Posidonia oceanica* has always been defined a stenohaline species, confined to a salinity range of approximately 36.5–39.5‰ (Boudouresque et al., 2012), but there are already different ranges of tolerated salinity in the east and west basins: 36.5–38 PSU in the western basin and 38–39.5 PSU in the eastern basin (Mancuso et al., 2023). Enhanced evaporation and reduced precipitation are expected, and with greater severity

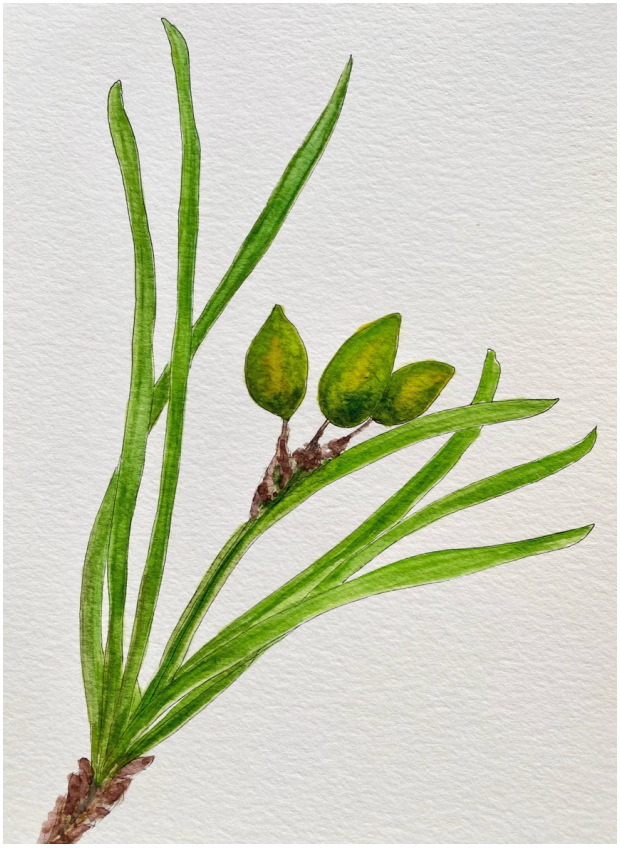
in the eastern and southern areas of the region, pushing conditions towards the upper tolerance limits of the species. *Posidonia oceanica* can cope with a variety of salinity concentrations, including hypersaline conditions found in coastal lagoon environments (Marín-Guirao et al., 2017). It has evolved osmotic regulatory strategies and considerable photosynthetic plasticity but is highly probable that the simultaneous presence of several stressors may complicate the functionality of any protective response in an era of rapid environmental change (Mancuso et al., 2023).

In nature nothing can really be isolated, and this is also true for salinity, which is linked to rising temperatures that reduce surface water density, thereby reinforcing thermal stratification and reducing vertical mixing between the upper and deeper layers of the water column (Kubin et al., 2023). The physical structure of the water column is another pathway for climate change to influence coastal ecosystems. Stratification is strongly seasonal: during spring and summer, intense surface heating produces a warm and relatively buoyant upper layer. A pronounced thermocline separates water masses based on temperature-driven density gradient (D'Ortenzio et al., 2005). Mediterranean surface waters are primarily oligotrophic because the thermocline restricts vertical mixing, and the colder, nutrient-rich waters remain isolated, below. In autumn and especially in winter, surface cooling and especially stronger winds contribute to eroding this stratification, allowing partial vertical mixing. Upwelling and mixing layers are particularly pronounced in some areas of the basin, such as the Gulf of Lyon and the North Adriatic Sea, where deep marine convection produces dense water masses contributing to the basin's thermohaline circulation (Durrieu De Madron et al., 2013). These seasonal processes play a crucial role in replenishing nutrients in surface layers and sustaining coastal productivity.
In fact, this timing perfectly aligns with the life cycle of *Posidonia oceanica*, which benefits from the increased availability of nitrate and ammonium during winter and early spring, when nutrient concentrations in the water column are highest (Lepoint et al., 2002). Climate change can easily alter this equilibrium. Milder winters may weaken the intensity of vertical mixing intensity and reduce the frequency or depth of convection events. The resulting decrease in vertical nutrient transport may further intensify the oligotrophic character of Mediterranean surface waters (Marty & Chiavérini, 2010). For shallow coastal ecosystems such as meadows of *Posidonia oceanica,* which typically occupy depths between the surface and approximately 40 m, these physical changes may have important ecological consequences. Rising sea surface temperatures reduce the density of surface waters, stabilizing the seasonal thermocline and extending its duration throughout the year (Kubin et al., 2023; Pastor et al., 2020). The Mediterranean thermohaline circulation, with a deep-water residence time of approximately 100 years (Malanotte-Rizzoli et al., 2014), has already undergone structural modification: since 2005, the so-called Western Mediterranean Transition has produced deep water masses warmer, saltier and denser than any previously recorded, with consequences that will propagate through the basin for decades (Schroeder et al., 2016).
The thermocline is only another one of the many physical boundaries being altered that are constantly investigated. Sea level rises because warming expands the volume of ocean water and accelerates the melting of glaciers and ice sheets. In the Mediterranean, these processes (today driven primarily by the thermal expansion of the waters, while in the future the predominant contribution will shift toward the melting of terrestrial ice) carry consequences that extend well beyond the shoreline (Galassi & Spada, 2014).

Sea level rises add a spatial dimension to the thermal and chemical stresses already described and the average level of the Mediterranean increased at a rate of 3.6 ± 0.8 mm/

year² during the period 1999–2024, an acceleration of 0.15 ± 0.06 mm/year² (Copernicus Marine Services, 2024).

Posidonia oceanica meadows occupy a well-defined bathymetric band, typically from the surface to 25–40 m depth depending on water clarity, with their lower limit set by light availability and their upper limit by wave action and substrate conditions. Both boundaries are now under pressure. At the lower limit, rising temperatures reduce water transparency through increased stratification and altered phytoplankton dynamics, pushing the light threshold shallower (Mateo et al., 2006; Pergent et al., 2015) At the upper limit, the combination of sea level rises and the progressive artificialization of Mediterranean coastlines, where natural sandy beaches and dune systems have been often replaced by seawalls, breakwaters and urban infrastructure, prevents landward migration (Pontee, 2013). In coastal sectors with gentle slopes, even the current modest rate of sea level rises has already been associated with regression of the lower meadow limit (Pergent et al., 2015). Moreover, projections suggest that by mid-century the terrestrial ice melt component will exceed the steric contribution to the rising of the Mediterranean Sea level, substantially increasing the rate of change (Galassi & Spada, 2014). Sea level rises thus add a further layer of pressure to an already stressed ecosystem, to a species whose slow growth and limited recovery capacity leave little margin for adaptation to compounding stressors acting simultaneously. Unlike terrestrial vegetation, which can migrate upslope, *Posidonia oceanica* meadows compressed between a rising sea and a fixed coastline, have nowhere to go. The result is a net reduction of available habitat, occurring on timescales far shorter than the species' capacity for recovery (Telesca et al., 2015).



P. oceanica ripening fruits

4. The Long Way Towards the Future

So, trying to find an answer to the "What's going on?" question, does not bring either easy answers nor relaxing scenarios. First, the Mediterranean Sea, connecting 3 continents, is a mosaic of countries, with different socioeconomic status, governance, culture and languages. Sometime that situation constituted an obstacle to a cooperative management of shared sea (Katsanevakis et al., 2015). Nevertheless, more than 50 years of studies have taught us a lot about physiology, biology and fundamental ecosystem importance of this marine angiosperm, which has survived epochal changes. Understanding its role and characteristics has contributed greatly to the various operations put in place to contain the damage, conserve the species, and restore the meadows where possible. For a long time, the results were rather discouraging, and this was largely due to incomplete information on fundamental aspects of the life cycle of *Posidonia oceanica* and also to very wide practices and methodologies applied during time (Pansini et al., 2022). Essential data such as seasonal nutrient and flowering cycles, carbohydrate dynamics in rhizomes, photobiological response at different depths and much more, have progressively emerged.

Nowadays, biochemical and physiological parameters are more sensitive and more reliable indicators of transplant success than simple morphological data. The attempt made with a sod transplant placed in 2017 (Monaco, France) was followed with monitoring for 8 years, evaluating both the structure and physiology of the meadow, as well as the chemistry of the surrounding sediments. After three years, flowering took place in synchrony with the natural meadow and, after eight years, an areal expansion of 25.8% beyond the initial expansion of the transplant area was documented (Descamp et al., 2025). A more recent research area follows the concept of *Posidonia oceanica* not as a "simple" clonal organism but as a true holobiont, i.e. an integrated system between roots, rhizomes and its own bacterial community. After two years from a transplant of cuttings from different donor population located in Calvi (Western Corsica, France), onto various biodegradable materials as anchoring structures, the bacterial communities associated with roots and rhizomes were characterized. The transplantation method must necessarily consider this factor because the lack of or limited contact with the sediment prevents the establishment of functional bacteria. This finding may explain many of the past failures while a substrate optimization intervention could significantly improve the resilience and long-term success of the restoration (Boulenger et al., 2025). Other studies have revealed the possibility for *Posidonia oceanica* to establish a specific fungal symbiosis, after years in which seagrasses were considered to be mycorrhizae-free. After

sampling in 32 localities in 7 countries (Spain, France, Italy, Croatia, Montenegro, Albania, Greece) a fungus that does not exist elsewhere*, Posidoniomyces atricolor* gen. et. sp. nov., has been discovered, which evolved only in association with this plant (Vohník et al., 2015, 2017, 2019).

Many aspects remain poorly understood, that need further study, while awareness has been gained about the preciousness of the ecosystem based on *Posidonia oceanica,* and of how technically demanding and costly restoration remains. Protecting existing meadows could be a more effective strategy, but at the same time, mitigating the multiple and concurrent stressors appears to be a difficult goal to achieve. Over time, monitoring instruments are increasingly advanced and calibrated for multiple measurements of chemical-physical parameters to assess water quality. Meanwhile, it also happens that a passive restoration, i.e. long-term monitoring, assesses potential natural recovery of two meadows. In 1986 at Prado Bay (Marseille, France), wastewater treatment was implemented and the construction of artificial beaches ended. Forty years of monitoring confirmed near-complete restoration of both meadows. So, if the drivers of decline are removed, *Posidonia oceanica* can recover well (Astruch et al., 2026).
The health and well-being of *Posidonia oceanica* meadows naturally depend on the health and quality of the water in which they are located. Today, new and more sophisticated control tools can effectively monitor the situation of the parameters hitherto indicated as essential.

As the knowledge on *Posidonia oceanica* has been progressively amplified thanks to synergies in the world of research, it would be appropriate to create greater institutional connection between all Mediterranean countries. It would be desirable in order to better defend the global ecosystem, starting from local realities, encouraging the adoption of shared protocols, just like the document “Guideline for the active restoration of *Posidonia oceanica*”, the result of a large collaborative working group, involving scientists, managers and conservation practitioners from multiple Mediterranean countries (Pergent-Martini et al., 2024). It is worth remembering that monitoring, sampling in the fields, such as laboratory technical extraction and analysis, at the various stages of research, are often carried out with considerable differences. Also in this case, the adoption of shared protocols would constitute a source of more reliable and better-quality data, in order to improve a comprehensive and necessary interpretation of the results (Renzi, 2025). New alternatives are being tested, such as restorations that start with recovery of stranded seeds along the coasts, often in large quantities after storms (Sutera et al., 2024) , with the advantage of not having to intervene on the donor meadow, and using genetically diversified material (Belzunce et al., 2008b) In this regard, a study has recently been published proposing a protocol to obtain the best shelf life and viability of the seed for always efficient restorations (Sutera et al., 2025). Working on a shared basis may be very helpful. So, the chances of success could really increase.

A further area of study that has been little mentioned so far, but is always of great importance, is linked to the presence of the microplastic pollution of the Mediterranean Sea. It has emerged that *Posidonia oceanica* meadows can act as sinks for microplastic particles, retaining pollutants in sediment, and in plant biomass. This absorption can both damage the plant, the sediments of the meadows, and even enter the food web with detrimental consequences for the entire ecosystem (Martinez et al., 2024). All components of the plant system, including detached leaves and egagropiles, have been investigated. The fibrous balls formed by dead, rolled-up leaves trap and accumulate microplastics, and have been proposed as biological indicators providing valuable

information on the presence and distribution of microplastics in coastal ecosystems (Alomar et al., 2024; Rigatou et al., 2025). Further investigations are needed to assess the intensity and severity of this recognized multi-lever absorption (Martinez et al., 2024).

So, how to evaluate the hypothesis of the future?
What are the risks that can be added to the existing problems? Studies in this regard are quite serious, mostly always related to temperature, acidification, eutrophication, possible sediment anoxia, increased water turbidity (Hassoun et al., 2025). But perhaps there are further ones, such as the increase in pressure that could derive from scientific research in the pharmaceutical, cosmetic or industrial fields, motivated by valid principles in theory but which, applied to a species in decline, could aggravate such a difficult situation as that of *Posidonia oceanica*. The species seems destined for an irreversible fate, unless effective reversals are implemented globally. We know with certainty that *Posidonia oceanica* has gone through many phases in very ancient times, almost unknown to us, overcoming incredible challenges with only its own tools, and slowly.
Perhaps this is what we still really must learn.

P. oceanica with inflorescence and rhizomes

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THE AUTHOR CONSULTED THE FOLLOWING WEBSITES ON THE MATTER OF LEGISLATION:

- https://eur-lex.europa.eu/eli/dir/1992/43/oj/eng
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