

## Essay

# How do rising sea temperatures affect *Posidonia oceanica* meadows in the Mediterranean ?



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*« Climate change is a global experiment in adaptive capacity, as species tolerate, adapt or die with changing conditions. While increasing temperatures are pushing many species to the very limit of their tolerance, it is also revealing a previously unimagined plasticity in the response of others. »*

from Ruiz *et al.*, 2018

## **Abstract**

*Posidonia oceanica* is a seagrass species thriving in the Mediterranean Sea since millennia. The integrity of *P. oceanica* meadows, in time and space, is essential to sustain the rich biodiversity of the Mediterranean, as well as to protect its shores and regulate the seawater's chemical composition. As all seagrass beds worldwide, *P. oceanica* meadows are progressively regressing alongside with the increase of seawater temperatures caused by climate change. Multiple *in situ* and *in vitro* observations revealed the strong impact of warming on the persistence and fitness of the seagrass' different life stages. The latter added to the impact of indirect actors such as sulfide stress, the synergies occurring between stressors and the high vulnerability of *P. oceanica*, worsens the status of the species in its rapidly changing environment. Nevertheless, some acclimation and/or adaptation possibilities seem to exist, for instance through the intensification of sexual reproduction and the activation of epigenetic processes. This literature survey gathers past and recent studies, giving a general picture of the diverse effects of global warming on *P. oceanica*. Although different trajectories for the fate of the meadows are proposed, all studies agree on the importance of protecting the meadows and acting for their conservation.

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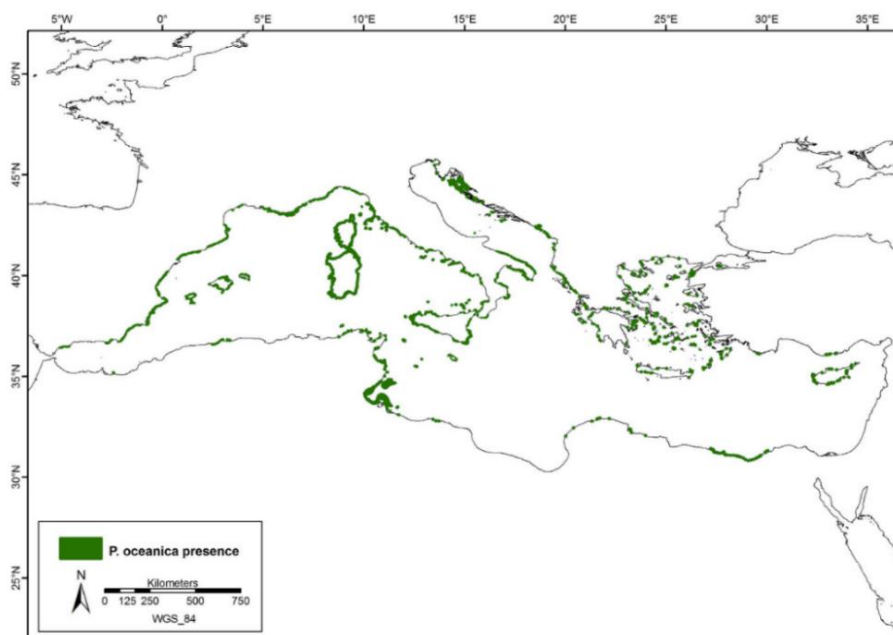
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## 1. Introduction

### 1.1 *Posidonia oceanica* : distribution, importance and biology

The Mediterranean basin shelters extensive meadows of the endemic seagrass species *Posidonia oceanica* (L.) Delile (den Hartog, 1970 ; Kuo and den Hartog, 2001). *P. oceanica* meadows were estimated to cover an area of approximately 12.200 km<sup>2</sup> along the Mediterranean coastline, dwelling in depth ranging from 0.3 to 45 m, depending on light availability and water dynamics (see Figure 1) (Duarte, 1991 ; Pasqualini *et al.*, 1999 ; Telesca *et al.*, 2015). The meadows distribution was accurately reported in the Western part of the Mediterranean (Telesca *et al.*, 2015). Data on the presence of *P. oceanica* in the Eastern basin is still scarce, although recent studies initiated the mapping of the meadows in Greek and Turkish waters (Topouzelis *et al.*, 2018 ; Traganos *et al.*, 2018 ; Akçali *et al.*, 2019 ; Duman *et al.*, 2019). The species is however not represented in the most Eastern part of the basin, along the coasts of Syria, Lebanon, Israel and around the Nile delta (Telesca *et al.*, 2015). Along the Northwestern shores of the Mediterranean, including around the islands, the seafloor is largely overlaid by *P. oceanica* meadows, as they thrive on both sandy and rocky bottoms (Badalamenti *et al.*, 2015 ; Telesca *et al.*, 2015 ; Ruju *et al.*, 2018). In this sector, the species is absent in only a few locations due to hydrological components or intense human activities. To these locations belong the northern Adriatic Sea, most shores of Languedoc (France) and the Gibraltar Strait (Boudouresque *et al.*, 2015). Along coasts where the meadows are abundant, huge quantities of dead *P. oceanica* leaves (leaf litter) are transported towards the shores in September-October. They get deposited by the water current on sandy beaches, where they form dense mats with peculiar shapes, the so-called *Posidonia banquettes* (Boudouresque & Meinesz, 1983 ; Romero *et al.*, 1992 ; Mateo *et al.*, 2003).



**Figure 1. Current distribution of *Posidonia oceanica* meadows.** Green areas indicate the presence of *P. oceanica* along the Mediterranean coastline, based on collated spatial information available on meadow presence. Coastlines represented with a dark line indicate the absence of *P. oceanica* or lacking data. (Source : Telesca *et al.*, 2015)

The importance of *P. oceanica* meadows is reflected in the numerous ecosystem services they provide (Costanza *et al.*, 1997 ; Campagne *et al.*, 2015 ; Boudouresque *et al.*, 2015). Together with the seagrasses' microbial epibionts, the meadows participate extensively to the primary production of the Mediterranean Sea (Pergent *et al.*, 1994 ; Personnic *et al.*, 2014 ; Boudouresque *et al.*, 2006, 2015). *P. oceanica* meadows are thus the basis of multiple trophic chains. The detached dead leaves are transported over great distances and towards depths, where they serve as source of food as well for abyssal species (Boudouresque *et al.*, 2006). The meadows' dense structure is used as shelter, spawning ground and/or nursery by many benthic and pelagic species, all relying on the healthy meadows for their life cycle (Harmelin-Vivien *et al.*, 1995 ; Boudouresque *et al.*, 2006). Multiple species interacting with the meadows, including crustaceans, cephalopods and teleosts, are targeted by local fishers, which adds to the seagrass' important economic value (Jiménez *et al.*, 1996 ; Boudouresque *et al.*, 2006 ; Vassallo *et al.*, 2013). The meadows also give shelter to threatened species, such as the beautiful noble pen shell *Pinna nobilis*. Furthermore, they ensure nutrient cycling (Romero *et al.*, 1992 ; Barrón and Duarte, 2009), oxygenize the seawater (Bay, 1984), improve water quality (Terrados and Duarte, 2000), enhance coastal protection from erosion (Gacia and Duarte, 2001), reduce the swell and wave strength (Stratigaki *et al.*, 2011 ; Manca *et al.*, 2012), stabilize dunes and provide indirect nutrient-inputs in-shore on which coastal vegetation depends (Boudouresque *et al.*, 2015). Last but not least, *P. oceanica* meadows are among the most efficient species for carbon fixation and sequestration (Pergent *et al.*, 1994 ; Mateo *et al.*, 1997, 2006 ; Fourqurean *et al.*, 2012 ; Pergent *et al.*, 2014). The biological, chemical, physical and geomorphological implications of *P. oceanica* meadows attest to their pivotal role in maintaining the stability and balance of the natural cycles occurring in the Mediterranean Sea (Orth *et al.*, 2006).

*P. oceanica* is an angiosperm species (Magnoliophyta). The seagrass growth relies mainly on clonal reproduction (Meinesz *et al.*, 1992 ; Balestri and Cinelli, 2003). The plants' rhizomes grow both horizontally (plagiotropy) and vertically (orthotropy). The former ensures the species asexual expansion, whereas the latter prevents the burial of the rhizomes due to the high amounts of sediment trapped by the canopy (Marbà and Duarte, 1998 ; Boudouresque *et al.*, 2015). *P. oceanica* shoots grow slowly (ca. 1 cm/yr) and can live up to 50 years old (Marbà and Duarte, 1998 ; Marbà *et al.*, 2005 ; Jordà *et al.*, 2012). Genotypes of *P. oceanica* clones were found to persist for millennia (Arnaud-Haond *et al.*, 2012).

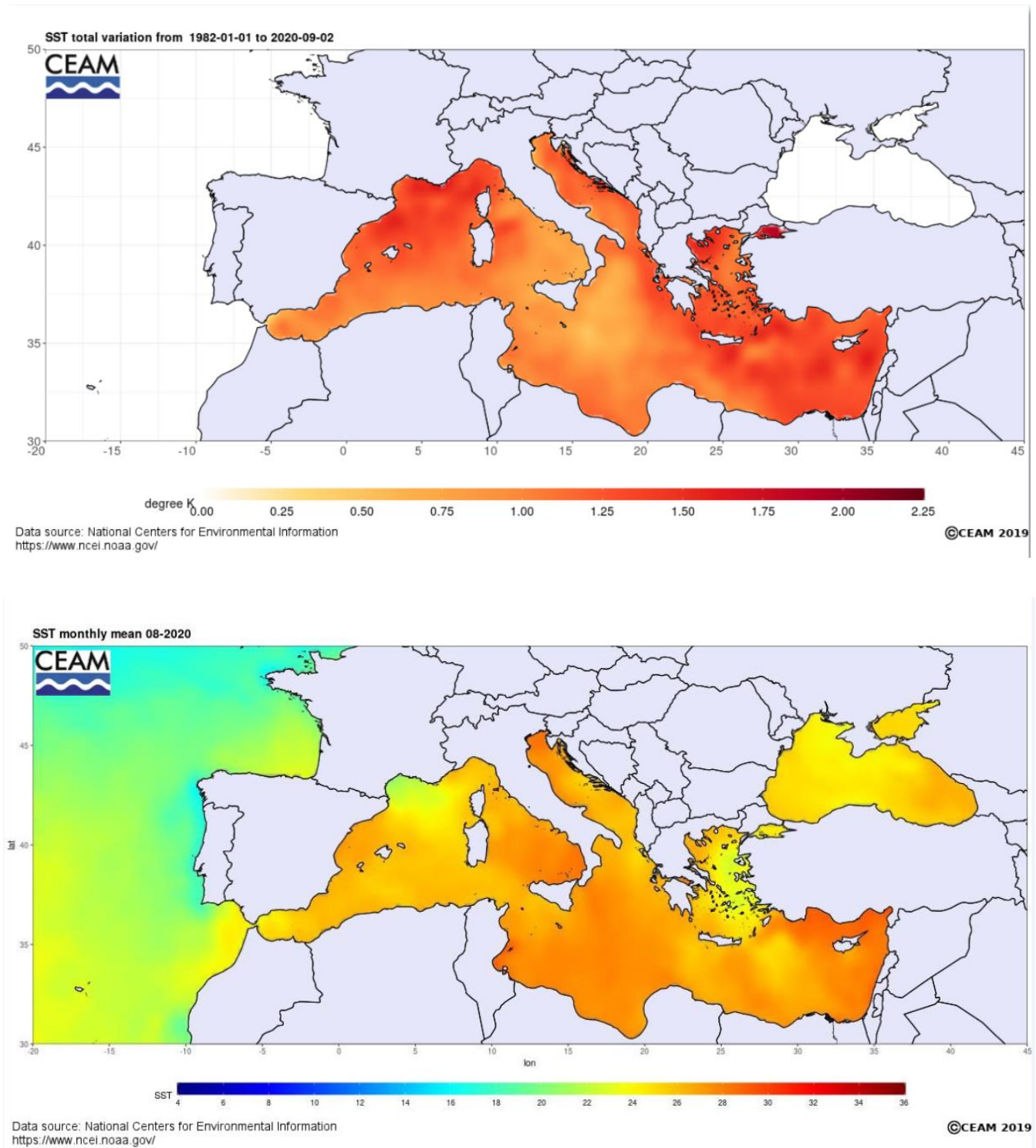
The global decline of seagrass beds critically concerns the Mediterranean *P. oceanica* meadows, for which a rapid loss has been reported since the end of the 20<sup>th</sup> century (Duarte, 2002 ; Orth *et al.*, 2006 ; Marbà *et al.*, 1996, 2014 ; Pasqualini *et al.*, 1999 ; Boudouresque *et al.* 2009). 34% of the beds are assumed to have disappeared over the past 50 years, with a few exceptions in Corsica (France), parts of the Sardinian coast (Italy) and the region of Valencia (Spain) (Telesca *et al.*, 2015). Investigations on the *P. oceanica* recession revealed the cumulative effect of multiple anthropogenic factors disturbing the seagrasses and triggering their decline (Marbà *et al.*, 1996, 2014 ; Pasqualini *et al.*, 1999 ;

Boudouresque *et al.* 2009). Among them are coastal urbanization causing eutrophication and excessive organic matter inputs, as well as mechanic disturbances due to fishing activities, dredging and aquaculture. Albeit important, these disturbances only partially contribute to the ongoing alarming regression of the meadows. Climate change, in contrast, is assumed to be the main driver of the *P. oceanica* beds' decline, as the warming of the Mediterranean seawater was recognized to be highly detrimental for the species (Duarte, 2002 ; Díaz-Almela *et al.*, 2007, 2009 ; Marbà and Duarte, 2010).

## 1.2 Warming of the Mediterranean : past and future

Oceans and seas stand on the front-line facing climate change. The warming of the atmosphere due to increasing atmospheric carbon dioxide (CO<sub>2</sub>) concentrations is closely followed by the warming of the globe's waters. The oceans act as buffer, as they absorb around 80% of the excessive atmospheric heat (Duarte *et al.*, 2018). The Intergovernmental Panel on Climate Change (IPCC) predicts a global increase of 2.58°C of the mean sea surface temperature (SST) by the end of the century (IPCC, 2019). The seawater warming leads to stronger and longer stratification of the water column, which can influence underlying biochemical and physiological processes (Coma *et al.*, 2009). While climate change involves a gradual increase of atmospheric and oceanic temperatures, it is also characterized by recurrent extreme weather events. Among them are heatwaves, during which aberrant high temperatures are reached over the course of a few weeks (15 days on average) (Darmaraki *et al.*, 2019). These local atmospheric events promptly warm up the air, oceans and seas (Darmaraki *et al.*, 2019). The occurrence of heatwaves has been increasing throughout the last century, and is expected to follow the same trend for the coming decades if climate change is not drastically mitigated (IPCC, 2012).

The bathymetry, geography and confined nature of the Mediterranean basin results in a faster warming relative to deeper open oceans (Meehl and Tebaldi, 2004 ; Girogi, 2006). The rates of warming of the Mediterranean Sea surface overshoot threefold those of oceans, with an average increase of 0.04°C per year (Giorgi, 2006 ; Díaz-Almela *et al.*, 2007). Long-term monitoring of the Mediterranean mean SST reported a global increase by 1.3°C between 1982 and 2020 (see Figure 2) (Pastor, 2020). Multiple intense heatwaves were recorded during the same period, such as during the summer 2003, 2006, 2015 and 2017 (Marbà and Duarte, 2010 ; Darmaraki *et al.*, 2019). The frequent heatwaves reaching the shallow waters of the Mediterranean generate high peaks of seawater temperature. These abrupt changes cause major ecological damages in coastal ecosystems, including in *P. oceanica* meadows (Duarte, 2002 ; Díaz-Almela *et al.*, 2009 ; Marbà and Duarte, 2010 ; Guerrero-Meseguer *et al.*, 2017).



**Figure 2. (Above) Mediterranean Sea Surface Temperature total variation from 1982 to 2020. The whole basin gained on average 1.3°C in 18 years. (Below) Mean Sea Surface Temperature in August 2020. Temperatures close to 28°C (dark orange) were reached in the Northwestern part of the basin where *Posidonia oceanica* meadows are present. (Source : Pastor, 2020)**



### 1.3 A vicious circle : the role of the *matte*

Underneath the canopy of *P. oceanica* meadows lies a unique structure : the *matte*. The *matte* is composed of the seagrass' leaf sheaths, rhizomes and roots (dead and alive), agglomerated into a dense layer with the sediment as matrix (see Figure 3) (Boudouresque and Meinesz, 1983 ; Mateo *et al.*, 1997). The orthotropic growth of the rhizomes coupled to the sedimentation occurring within the meadow induces the continuous rising of the *matte*, and accordingly of the whole bed (10 to 100 cm per century, Mateo *et al.*, 1997 ; Boudouresque *et al.*, 2015). The parts of the seagrass building-up the *matte* contain a fraction of the plants' primary production. Throughout its formation, organic and inorganic carbon is thus incorporated into the structure, where it can be stored from centuries to millennia (Romero *et al.*, 1994 ; Mateo *et al.*, 1997 ; Boudouresque *et al.*, 2015 ; Pergent *et al.*, 2014). This process confers to the *matte* the crucial role of carbon sink, which implies its participation in the mitigation of climate change (Boudouresque *et al.*, 2015 ; Pergent-Martini *et al.*, 2021). Owing to the significant size of the *matte* (up to several meters in height), the carbon sequestration rates by *P. oceanica* meadows are comparable with those of peatlands and mangroves (Mateo *et al.*, 1997 ; Pergent-Martini *et al.*, 2021). Pergent-Martini *et al.* (2021) estimated that 5 681 206 tons of CO<sub>2</sub> emissions are fixed every year by *P. oceanica*, with 21% of it being sequestered into the *matte* (Pergent-Martini *et al.*, 2021). Although the carbon fixation by the meadows only covers a small fraction of the CO<sub>2</sub> emissions of the Mediterranean countries, the seagrasses' contribution to the reduction of atmospheric CO<sub>2</sub> concentration cannot be neglected (Pergent-Martini *et al.*, 2021).

The *mattes'* role is however double-edged. The shoots' mortality, due to global warming for instance, can reverse the *matte's* status, from a carbon sink to a carbon source. Without the protection provided by the seagrasses' leaves, the *matte* is exposed directly to the water current, waves and swell, which altogether enhance its erosion. As a result, the *matte's* carbon content is slowly released into the water, where it can get remineralized and later on diffused back into the atmosphere in form of CO<sub>2</sub> (Pergent *et al.*, 2014, Pergent-Martini *et al.*, 2021). The mechanical disruption of the *mattes*, caused for instance by mooring or trawling, worsen the discharge of carbon (Ganteaume *et al.*, 2005 ; Pergent *et al.*, 2014). Hence, just as good as *P. oceanica* meadows are able to mitigate the CO<sub>2</sub> increase driving climate change, they also can accelerate it by releasing the carbon they have been storing for millennia (Pergent *et al.*, 2014, Pergent-Martini *et al.*, 2021 ; Boudouresque *et al.*, 2015). This particularity of the *P. oceanica* beds strongly reinforce the importance of preventing their degradation to avoid a local intensification of global warming.



**Figure 3. The *Posidonia oceanica* matte underneath the canopy.** The *matte* is composed of the seagrass' leaf sheaths, rhizomes and roots, with sediment filling the interstices. (Source : Ruitton *et al.*, 2017)

#### **1.4 Vulnerability of *Posidonia oceanica***

As the geography of the Mediterranean renders the migration of *P. oceanica* to cooler latitudes impossible, *P. oceanica* is left with the only alternative to adapt to its warming environment. As the most tangible scenario for the coming century does not predict the ending of climate change, the seagrass' tolerance and/or resilience capacity is most likely to determine the fate of the meadows. However, the species extremely slow growth (among the slowest growing seagrass on Earth) (Marbà *et al.*, 1996), sparse sexual reproduction (Marbà and Duarte, 1998 ; Díaz-Almela *et al.*, 2006) and low mutation rate (Aires *et al.*, 2011 ; Arnaud-Haond *et al.*, 2012) restrict the adaptive potential of *P. oceanica*, thus increasing its vulnerability towards rapid environmental changes and stressful conditions (Boudouresque *et al.*, 2009 ; Jordà *et al.*, 2012). Additionally, the low genetic diversity of *P. oceanica* limits as well the species' adaptative potential, although it was discovered to be higher than previously thought (Arnaud-Haond *et al.*, 2007 ; Serra *et al.*, 2010 ; Telesca *et al.*, 2015).

Hence, climate change constitutes a major threat for *P. oceanica* meadows. Therefore, understanding all the components influencing the seagrass survival is essential to set conservation goals congruent with the species' capacity to withstand this unstable environment. This work, based on a literature survey, aims at reporting how rising sea temperatures affect *Posidonia oceanica* meadows in the Mediterranean.

## **2. Effects of rising sea temperatures on *Posidonia oceanica***

### **2.1 Shoot mortality and reduced fitness**

Duarte (2002) emphasized in his review *The Future of Seagrass Meadows* the role of global warming in the worldwide regression of seagrass beds (Duarte, 2002 ; Short and Neckles, 1999). Long-term monitoring of *P. oceanica* shoot demography and annual maximum seawater temperatures around the Balearic Islands (Spain) highlighted the correlation between seawater warming and the species' increasing mortality rate (Díaz-Almela *et al.*, 2009 ; Marbà and Duarte, 2010). The *P. oceanica* loss observed on the field over the course of the study revealed the strong impact that climate change alone can have on the Mediterranean seagrass, as no other stressors were present in the area (Marbà and Duarte, 2010). An increase of the seawater temperature by 1°C was assumed to rise the shoot mortality by an additional 2.5% per year (Marbà and Duarte, 2010). The shoot recruitment of *P. oceanica* seemed however not to be affected by the seawater warming, as it only decreased with depth. Nevertheless, the average shoot mortality was estimated to be approximately twofold bigger than the average shoot recruitment, implying a negative net shoot growth rate (Díaz-Almela *et al.*, 2009 ; Marbà and Duarte, 2010). A seawater temperature of 28°C was recognized as a threshold above which *P. oceanica* shoot mortality increases drastically (Marbà and Duarte, 2010 ; Telesca *et al.*, 2015). This tolerance limit justified the high losses in *P. oceanica* meadows reported a few weeks after the heatwaves of summer 2003 and 2006, during which the Mediterranean reached temperatures above 28.5 °C (Marbà and Duarte, 2010). These two incidences led to the current assumption that *P. oceanica* meadows are, as most seagrass species, especially sensitive to short periods of extreme heat rather than to the gradual increase of seawater temperature (Díaz-Almela *et al.*, 2007, 2009 ; Marbà and Duarte, 2010 ; Guerrero-Meseguer *et al.* 2017).

Further analysis at molecular scale pinpointed the adverse physiological changes occurring in *P. oceanica* when exposed to heat-stress. In all marine plants, high temperatures can disrupt photosynthesis through the alteration of the photosystem II (PSII), lowering its capacity to capture energy from light (Bulthuis, 1987 ; Campbell *et al.*, 2006 ; Repolho *et al.*, 2017). Excessive thermal stress reduces the electron transport rate through the PSII, which restricts the carbon assimilation and thus lowers the plants' carbon fixation rate (Marín-Guirao *et al.*, 2016 ; Repolho *et al.*, 2017 ; Guerrero-Meseguer *et al.*, 2017). The lower photosynthetic activity coincides with the intensification of respiration, which in turn impacts the plants' carbon balance (Bulthuis, 1987 ; Marín-Guirao *et al.*, 2016, 2018). The increased respiration supports maintenance and repair cycles, as well as protein production, to compensate for the damages to the PSII (Collier and Waycott, 2014). For *P. oceanica*, short-term exposure (three hours) to temperatures above 27°C were experimentally shown to significantly lower the performance of the PSII and the oxygen production of seedlings immediately after the treatment (Guerrero-Meseguer *et al.*, 2017). The overall productivity of the *P. oceanica* early life stages is thus

assumed to be rapidly affected by temperatures corresponding to those measured in the field during past hot summers (Guerrero-Meseguer *et al.*, 2017). In the same experiment, long-term (one month) exposure of the seedlings to temperatures above 29°C, resulted in a high mortality rate (33% die-off), increased leaf senescence and reduced leaf growth (Guerrero-Meseguer *et al.*, 2017). The latter treatment simulated the effect of heatwaves that are expected to occur in a close future in the Mediterranean, and thus stressed their strong negative impact on the young plants' development (Guerrero-Meseguer *et al.*, 2017). The sensitivity of *P. oceanica* seedlings to heat-stress was furthermore attested in an earlier study, reporting 70% mortality in the species younger life stages in similar heated conditions (Olsen *et al.*, 2012).

The higher vulnerability of the *P. oceanica* seedling is directly reflected in the low colonization capacity of *P. oceanica* with increasing seawater temperatures, which worsen the species' resilience (Diaz-Almela *et al.*, 2007 ; Olsen *et al.*, 2012 ; Guerrero-Meseguer *et al.*, 2017). The overall low fitness and increased mortality rate of *P. oceanica* when exposed to high temperatures is likely to be caused by the above mentioned carbon imbalance, as it ensures the stability of metabolic processes, including growth, development and survival (Marín-Guirao *et al.*, 2018 ; Ontoria *et al.*, 2019 ; Pazzaglia *et al.*, 2020).

## **2.2 Gloomy perspectives for the meadows : model-based approach**

Multi-model-based approaches are used to estimate future variations in seawater temperature, under different plausible scenarios. Among them is the relatively optimistic Scenario A1B, in which the greenhouse-gas concentration stabilizes after 2050 (*Special Report on Emissions*, IPCC, 2000). Based on the temperature changes predicted under the scenario A1B and the studied relationship between seawater temperature and *P. oceanica* shoot mortality, Jordà *et al.* (2012) proposed a portrayal of the evolution of *P. oceanica* meadows in the Northwestern part of the Mediterranean (Balearic Islands) for the coming decades (Marbà and Duarte, 2010 ; Jordà *et al.*, 2012). The model projections predict a rapid increase of the Mediterranean seawater temperature, together with extended, more frequent and stronger heatwaves throughout the coming century (Jordà *et al.*, 2012). In these conditions *P. oceanica* shoot mortality rates are expected to follow the current increasing trend (Marbà and Duarte, 2010). Additionally, under scenario A1B, annual maximum SST in the Northwestern part of the Mediterranean are expected to recurrently reach 28°C (the species maximum tolerable temperature) within the middle of the century. The year 2050 would thus mark the start of an accelerated decline of the remaining meadows, susceptible to induce the species' extinction (Marbà and Duarte, 2010 ; Jordà *et al.*, 2012 ; Telesca *et al.*, 2015).

These predictions are in agreement with the meadows recession observed in the field (Marbà and Duarte, 2010). Marbà and Duarte (2010) measured a yearly net shoot loss of 5%. They estimated that it could reach 20% per year if the seawater temperature gained four additional Celsius degrees. According to the model's projections, the Mediterranean annual maximum SST will increase on average by  $3.4 \pm 1.3^{\circ}\text{C}$  by the end of the century (Jordà *et al.*, 2012). Under such variation, only 10% of the present density of *P. oceanica* is predicted to remain shortly after the middle of the century, which would imply the loss of the meadows' functionality and their disappearance soon after (Jordà *et al.*, 2012).

The critical consequences of seawater warming on *P. oceanica* meadows are thus assumed to have the potential to drive the decimation of the meadows before 2100 (Jordà *et al.*, 2012). Especially since the removal of local disturbances was shown to have very little effect on the seagrass resilience (Jordà *et al.*, 2012 ; Marbà and Duarte, 2010). These analyses strengthen the level of concern for the survival of *P. oceanica*, as they support a potential complete loss of the meadows in a close future if global warming is not drastically mitigated (Marbà and Duarte, 2010).

### **2.3 Sulfide stress**

Besides from generating direct physiological changes in seagrasses, the increase in seawater temperatures in the Mediterranean also involves substantial indirect effects. Biogeochemical processes, abiotic components and microbial activity for instance can be modulated under changing thermal conditions (García *et al.*, 2012). These indirect actors constitute a major threat for *P. oceanica* meadows as they undeniably influence the survival rate of the species (Marbà and Duarte, 2010 ; García *et al.*, 2012).

Sulphide is a highly toxic compound for eukaryotic cells (Fenchel and Finlay, 1995). Elevated sulphide concentrations in the marine sediment can inhibit photosynthesis and damage the meristem of seagrasses, resulting in a lower productivity and growth, and a higher mortality rate (Carlson *et al.*, 1994 ; García *et al.*, 2012 ; Calleja *et al.*, 2007 ; Garcias-Bonet *et al.* 2008). The sulphide concentration of marine sediment depends upon the reduction of sulfate by anoxic bacteria, whose activity is increased with higher temperatures (Knoblauch and Jørgensen, 1999 ; García *et al.*, 2012). Furthermore, the impact of sulphide is exacerbated when oxygen is depleted from the surrounding environment. The lack of oxygen prevents oxidation reactions to occur, which allows the accumulation of toxic reduced compounds within the sediment, including sulphides (Holmer and Nielsen, 2007 ; Mascaró *et al.*, 2009). Moreover, the seagrass' partial pressure in oxygen, which is reduced in anoxic conditions, prevents the entering of sulphides into its tissues (Pedersen *et al.*, 2004 ; Borum *et al.*, 2005 ; García *et al.*, 2012). High seawater temperatures trigger anoxia by lowering the oxygen solubility and enhancing its

consumption. Both oxidation reactions and the plants' protective mechanisms are thus disrupted with increasing temperatures (Vaquer-Sunyer and Duarte, 2011 ; García *et al.*, 2012).

Global warming hence fosters simultaneously oxygen depletion, as well as the production and accumulation of sulphide in the sediment. The latter conditions cause the intrusion of sulphide into the seagrass' tissues, which is transported through the plant's organs by gas diffusion through the meristem and up to the leaves (Pedersen *et al.*, 2004 ; Borum *et al.* 2005). In *P. oceanica*, sulphide intrusion in leaves was experimentally shown to increase with higher temperatures (García *et al.*, 2012). High sulphide intrusion rates were assumed to affect the plants' leaf production and to enhance shoot mortality, particularly after extreme heat events (García *et al.*, 2012 ; Marbà and Duarte, 2010). A sulphide concentration as low as 10  $\mu\text{M}$  was revealed to be sufficient for *P. oceanica* growth to be negative (Calleja *et al.*, 2007). Considering the predictions made on seawater temperatures for the 21<sup>st</sup> century, this concentration is likely to be reached and exceeded in the coming decades (García *et al.*, 2012, 2013). Sulphide-stress is thus assumed to greatly increase the vulnerability of *P. oceanica* meadows, especially since sulphide toxicity is expected to be exacerbated with climate warming (García *et al.*, 2012, 2013).

#### **2.4 Synergies between local and global stressors**

Intense coastal urbanization and the associated anthropogenic activities have driven the eutrophication of coastal waters across the Mediterranean basin (Karydis and Kitsiou, 2012). The excessive input of nutrients along the shores is known to negatively impact the functioning of coastal ecosystems by causing physiological changes in foundation species such as *P. oceanica* (Waycott *et al.*, 2009 ; Orth *et al.*, 2006). While the global climate change clearly affects the persistence of *P. oceanica* meadows, local stressors such as eutrophication, are assumed to have the potential to exacerbate the seagrasses' decline (Lloret *et al.*, 2008 ; Darling and Côté, 2008 ; Ontoria *et al.*, 2019).

Nutrient enrichment can, to some extent, enhance seagrass' growth, i.e. when the plants are growing under nutrient limited conditions (Alcoverro *et al.*, 1997). However, the high nutrient concentrations linked to anthropogenic eutrophication mostly overshoot the tolerance limit of the plants. Their growth and survival are thus negatively affected, in indirect and direct ways (Burkholder *et al.*, 2007). High inorganic nitrogen concentrations for instance allow extreme growth rates of phytoplankton, macroalgae and epiphytic algae, whose proliferation greatly reduces light availability for the benthic communities including *P. oceanica* meadows (Touchette and Burkholder, 2000). Simultaneously, excessive nitrogen concentrations cause negative physiological changes and alter cellular functions, both disrupting the seagrasses' growth (Burkholder *et al.*, 2007).

The concomitant activity of local and global stressors may result in a synergistic effect, which can drastically lower the plants' resilience and tolerance capacity under stressful conditions (Darling and Côté, 2008). The synergy between seawater warming and eutrophication on *P. oceanica* meadows was only recently attested through *in situ* experiments (Ontoria *et al.*, 2019). Ontoria *et al.* (2019) measured a decrease of 70% in photosynthetic performance in *P. oceanica* exposed to heat-stress and increased ammonium concentrations, whereas the effect of the isolated stressors was minor (Ontoria *et al.*, 2019). The combination of both stressors appeared to significantly amplify their individual effects on the seagrass' metabolism. Apart from greatly reducing the plant's productivity, the latter synergy also negatively affected leaf growth and the activation of photoprotective mechanisms, inducing the damage of the plants' tissues (Ontoria *et al.*, 2019). *P. oceanica* meadows collected closer to the shore, i.e. experiencing higher eutrophication levels, were additionally shown to have lower carbohydrates reserves when exposed to high temperatures relative to plants growing in oligotrophic waters, resulting in leaf senescence, lower growth rate and higher shoot mortality rates (Pazzaglia *et al.*, 2020).

Similarly, seed burial and overgrazing were identified to synergistically decrease the viability of *P. oceanica* seedlings when occurring concomitantly with seawater warming (Guerrero-Mesequer *et al.*, 2020). Seed burial is enhanced by increased sedimentation rates, especially along populated coasts where erosion is triggered by human activities, such as beach management, coastal deforestation and dredging (Cabaço *et al.*, 2008 ; Guerrero-Mesequer *et al.*, 2020). Overgrazing results in the same way from a cascade effect related to human pressure. As top-predators were extensively overfished in the Mediterranean, small grazers, such as the 'sea cow' *Sarpa salpa*, are now abundant and thrive in the *P. oceanica* meadows (Orth *et al.*, 2006 ; Short and Wullie-Echeverria, 1996). Adjacently, seawater warming together with eutrophication renders *P. oceanica* leaves more palatable for fish, which increases the grazing pressure on the species (Buñuel *et al.*, 2020).

Exposure to local stressors, such as eutrophication, seed burial or overgrazing, is likely to induce physiological adaptations in *P. oceanica*, which come with high energetic costs (Pazzaglia *et al.*, 2020). The investment of energy required for acclimation and the maintenance of metabolic processes potentially limits the plants' capacity to respond to further stressors, such as increasing seawater temperatures (Ontoria *et al.*, 2019 ; Pazzaglia *et al.*, 2020). The seagrasses' tolerance towards stress factors is hence presumably linked to the environmental conditions in which they develop. The experimental evidence of the existence of synergistic interactions between local and global stressors further reinforces the high level of concern for *P. oceanica* meadows, especially for those dwelling along the densely populated coasts (Ontoria *et al.*, 2019).

### **3. A glimpse of hope for the *Posidonia oceanica* meadows : adaptation possibilities**

#### **3.1 Heat-induced flowering**

Sessility constrains the capacity of plants to escape adverse or stressful conditions. Evolutionary pressure therefore granted these organisms with strategies to ensure the species' survival. Among them is the very efficient strategy of sexual reproduction. In the marine environment, clonal seagrasses, such as *P. oceanica*, rely on the latter to increase the species adaptive success in changing environments (Kazan and Lyons, 2016).

As a member of angiosperms, *P. oceanica* produces inflorescences for its sexual reproduction. The reproductive effort is twofold beneficial for the persistence of the meadows. On one hand, it allows long-distance seed dispersal, potentially towards more favorable conditions, which simultaneously increases the genetic connectivity between distant populations (Serra *et al.*, 2010 ; Kendrick *et al.*, 2016). On the other hand, it enhances genetic diversity among the clonal population. Recombination events during meiosis can potentially generate genotypes with higher tolerance and/or resilience capacities, or able to colonize new habitats (Hughes and Stachowicz, 2004 ; Reush *et al.*, 2005 ; Ruiz *et al.*, 2018 ; Marín-Guirao *et al.*, 2019). Moreover, seeds can act as a dormant stage for the seagrasses, which may contribute to the recovery of the species over time (Unsworth *et al.*, 2015 ; Ruiz *et al.*, 2018).

In all seagrass species, the occurrence of sexual reproduction varies in space and time, among and within species (Díaz-Almela *et al.*, 2006). In *P. oceanica*, past flowering events can easily be detected by the scars that inflorescences leave on the rhizome while they develop (Díaz-Almela *et al.*, 2007). Blooming in *P. oceanica* meadows is in general rare, sparse and unpredictable (Hemminga and Duarte, 2000 ; Díaz-Almela *et al.*, 2007).

Flowering is known to be triggered by genetic, physiological and environmental parameters including light and temperature (Searle and Coupland, 2004). Further external factors related to adverse environmental conditions were as well recognized as drivers of blooming events in terrestrial plants. Among these are abiotic components, such as drought, salinity, heat and cold, as well as biotic components, such as pathogens and grazers (Kazan and Lyons, 2016 ; Takeno, 2016). The irregularity of flowering events in seagrasses supported the role of external stressors in the transition to sexual reproduction in the marine environment (Díaz-Almela *et al.*, 2007 ; Kazan and Lyons, 2016 ; Ruiz *et al.*, 2018 ; Marín-Guirao *et al.*, 2019). In the global warming context, heat was soon identified as an environmental factor influencing the timing and intensity of blooming in seagrasses, including in *P. oceanica* (Buia and Mazzella, 1991 ; Díaz-Almela *et al.* 2006). The latter was supported by field observations, which provided evidence that extreme heatwaves (summer 2003 and 2006) were followed by extended flowering events of *P. oceanica* meadows in the Northwestern part of the Mediterranean



(Díaz-Almela *et al.*, 2007 ; Marbà and Duarte, 2010). The hypothesis of flowering being an adaptive response to heat-stress initiated further experimental investigations. Only heated *P. oceanica* plants bloomed in mesocosm experiments with individuals from identical provenance and with no genetic divergence (Ruiz *et al.*, 2018). Both observations *in situ* and *in vitro* suggested that flowering of *P. oceanica* meadows is rather associated to extreme seawater temperature anomalies (heatwaves) than to a gradual warming of the seawater. The higher the anomaly, the more prevalent and intense the flowering events appeared to be (Díaz-Almela *et al.*, 2007). Besides of inducing flowering, the plants' exposure to increasing temperatures in the above mentioned mesocosm experiments was also correlated with a reduction of leaf growth on *P. oceanica* (Ruiz *et al.*, 2018). The latter is considered as a typical response to stress in higher plants (Lichtenthaler, 1996). The heat-induced blooming of *P. oceanica* meadows was thus assumed to be a stress-driven response, enhancing the species' adaptive potential and survival, by respectively fostering genetic diversity and creating a seed bank persisting until environmental conditions stabilize (Jahnke *et al.*, 2015 ; Ruiz *et al.*, 2018 ; Marín-Guirao *et al.*, 2019).

In seagrasses, the transition from vegetative growth to sexual reproduction occurs through the modulation of gene expression and epigenetic reprogramming, as well as through the altered activity of phytohormones and further signaling networks (Marín-Guirao *et al.*, 2019). A transcriptomic analysis of seagrasses experiencing high temperatures revealed the activity of molecular cues responsible for flowering and flower development in *P. oceanica* (Marín-Guirao *et al.*, 2019). Altogether, the induced molecular changes detected led to higher heat tolerance and the induction of flowering two weeks after the beginning of the warm-up period (Marín-Guirao *et al.*, 2019). The *P. oceanica* flowers developed until their mature stage, which was reached within 6 weeks after the start of the experiment. However, their viability was not monitored in later stages and the sexual reproductive success could thus not be ascertain (Marín-Guirao *et al.*, 2019). Later occurring processes, such as pollination, seed dispersal and settlement, could likewise be influenced by the warming and negatively affect the seagrasses' reproductive success (Díaz-Almela *et al.*, 2007 ; Marín-Guirao *et al.*, 2019).

Additionally, allelic richness and heterozygosity in *P. oceanica* were shown to increase the intensity of flowering events (Jahnke *et al.*, 2015 ; Ruiz *et al.*, 2018). The intensification of sexual reproduction of *P. oceanica* in warming conditions could thus build-up a positive feedback enhancing the species flowering, as it allows a greater genetic diversity within and among the populations.

### **3.2 The power of epigenetic modifications**

Epigenetic modifications alter gene expression without changing the underlying DNA sequence, through histone modifications, non-coding RNAs and DNA methylations (Bossdorf *et al.*, 2008). The activation of specific epigenetic mechanisms under stressful conditions has the potential to enhance the

overall resilience, tolerance and adaptive capacity of clonal species such as seagrasses (Bossforf *et al.*, 2008). These processes for instance may result in early-flowering phenotypes, increasing the survival chances of species undergoing critical environmental changes such as *P. oceanica* (Dodd and Douhovnikoff, 2016 ; Ruiz *et al.*, 2018). The methylation of cytosines across the DNA sequence is especially known to contribute to evolutionary adaptations in changing environments (Verhoeven *et al.*, 2016 ; Duarte *et al.*, 2018). Moreover, epigenetic mechanisms are involved in heat-stress memory, which is assumed to allow plants to “remember” exposure to heat and better resist future ones (Lämke *et al.*, 2016 ; Marín-Guirao *et al.*, 2019). The epigenetic reprogramming in response to stress is integrated in the plants’ genetic material and generates faster reactions when stress conditions are reiterated (Lämke *et al.*, 2016 ; Latzel *et al.*, 2016 ; Marín-Guirao *et al.*, 2019).

As epigenetic modifications are unaffected by meiosis, they accumulate throughout the plant’s clonal expansion and are transmitted to offspring in the event of sexual reproduction. Therefore, epigenetic processes are susceptible to enhance the seagrass’ adaptive potential despite low sexual reproduction rates (Dodd and Douhovnikoff, 2016 ; Marín-Guirao *et al.*, 2019). Considering the thermal changes predicted for the 21<sup>st</sup> century, these mechanisms could play an essential role for the persistence of seagrass species, including *P. oceanica* (Dodd and Douhovnikoff, 2016 ; Marín-Guirao *et al.*, 2019). Alternatively, understanding the molecular basis of these protective processes could contribute to conservation and management efforts for seagrass meadows (Marín-Guirao *et al.*, 2019).

#### **4. Discussion**

*P. oceanica* meadows are efficient bioindicators. Their condition directly reflects the health of the Mediterranean coastal ecosystems (Montefalcone, 2009). The alarming status of the meadows demonstrates yet again the sheer size of human impact on the biosphere. The ongoing recession of *P. oceanica* meadows related to the direct and indirect effects of increasing seawater temperatures shows that global warming has the potential to cause the decimation of the species across the Mediterranean basin. The latter assumption strengthens the crucial and urgent need to limit anthropogenic greenhouse gas emissions, especially when considering the essential ecological and economical roles of *P. oceanica* meadows.

Fortunately, the early studies revealing the vulnerability of *P. oceanica* mediated their protection. In 1988, the species was added to the list of protected plant species in France (Boudouresque *et al.*, 2015). The species was later on protected under multiple European, national and regional legislations, and Marine Protected Areas were created along the coasts. Conservation plans aiming at maintaining or reestablishing the biodiversity of the Mediterranean were progressively put in place and allowed to mitigate to some extent the recession of the meadows (Boudouresque *et al.*, 2006). *P.*

*P. oceanica* beds are now classified as an “endangered” habitat under the IUCN Red List Criteria for Ecosystems (Gubbay *et al.*, 2016). Even though these measures will not allow to meet the conservation goals for the meadows, they certainly helped to change the general opinion on *P. oceanica*, which accelerated the efforts for their protection.

Restoration projects of *P. oceanica* meadows are ongoing and supported by research on seedling development (f.e. Alagna *et al.*, 2020). Different strategies were established and tested for the ecosystems’ rehabilitation (Boudouresque *et al.*, 2006). However, the recovery of disrupted meadows is difficult to reach, due to the high vulnerability of seedlings and the species’ very slow growth (Olsen *et al.*, 2012). For instance, a *P. oceanica* meadow of 1.13 hectares across the harbor of Marseille (France) destroyed by a bomb in the year 1942 had not recovered 50 years later (Boudouresque *et al.*, 2006).

Clones of *P. oceanica* are believed to have persisted for millennia under changing environments (Arnaud-Haond *et al.*, 2012 ; Dodd and Douhovnikoff, 2016). However, the pace of the ongoing climate change is susceptible to be too fast for the seagrasses to adapt to the current and future conditions (Walther *et al.*, 2002). Nevertheless, analyses of the genetic structure among *P. oceanica* populations revealed a higher genetic diversity within the species’ than was previously thought. The distribution of the genetic diversity is assumed to result from past vicariance events, which hypothetically occurred about 5.5 million years ago. From a genetic perspective, two distinct populations of *P. oceanica* exist, each of them residing on one side of the Messina Strait (Italy) (Arnaud-Haond *et al.*, 2007 ; Serra *et al.*, 2010 ; Duarte *et al.*, 2018). As the two populations are not reproductively isolated, their mixing may contribute to increase the species’ adaptive capacity towards global warming, especially since the Eastern population experiences slightly higher seawater temperatures. Moreover, the more frequent sexual reproduction observed among *P. oceanica* meadows with increasing temperatures could foster the inter-population crossing.

The adaptive potential of *P. oceanica* meadows is generally assumed to be low. However, the gloomy picture can change when considering the power of non-genetic mechanisms. Epigenetic modifications, as well as transposable elements and the seagrass’ microbiome can lead to rapid micro-evolution processes, which may allow the local acclimation of the plants (Duarte *et al.*, 2018). By modulating gene expression, epigenetic modifications and the activation of transposable elements trigger phenotypic plasticity and influence the resistance and adaptivity of the plants (Latzel *et al.*, 2013). The microbial community associated to the seagrasses is also susceptible to increase the plants’ fitness through the production of bioactive compounds, as observed for kelp forests (Ji *et al.*, 2017 ; Duarte *et al.*, 2018). Interestingly, *P. oceanica* meadows on the coastline of the Spanish region Valencia exhibited a hopeful trend. Despite their regression reported between 1990 and 2000, the meadows’ demography appeared to stabilize between 2002 and 2011, with some beds increasing in density and span (Guillén *et*

*al.*, 2013). Further analyses on the epigenomic material and microbial composition of these meadows may reveal processes responsible for the acclimation of *P. oceanica* in this area. Similarly, González-Correa *et al.* (2007) suggested a positive population dynamics in *P. oceanica* meadows from multiple protected and pristine areas across the Mediterranean basin (France, Spain, Tunisia and Cyprus) (González-Correa *et al.*, 2007). Their work emphasized the capacity of *P. oceanica* to accommodate to local environmental variability when anthropogenic disturbances are removed (González-Correa *et al.*, 2007). Analyzing the seagrasses' fitness within those protected areas could therefore reveal positive and hopeful trends for the species.

To conclude, rapid evolution through non-genetic mechanisms and inter-population mixing may theoretically neutralize the multiple effects of global warming on *P. oceanica* meadows. It is however far from certain that these processes will occur in a close future. The warming of the Mediterranean Sea could soon reach a critical threshold outpacing any possibility of adaptation for the seagrass. The death of the meadows could have dramatic consequences, particularly when considering the role of the underlying *matte*. The conventional protection of the meadows is essential and can still be broaden and reinforced. Especially since the tourism industry often does not strictly follow the regulations and is thus still having an important impact on the meadows. Mitigating global warming stands however on the front line for the conservation of *P. oceanica* meadows and therefore, for keeping the integrity of the Mediterranean coastal ecosystems. The huge importance of the *P. oceanica* meadows for the Mediterranean Sea and coasts, as well as for the regulation of the Earth's atmospheric CO<sub>2</sub> concentration clearly shows how crucial it is to care and to act for their protection.

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