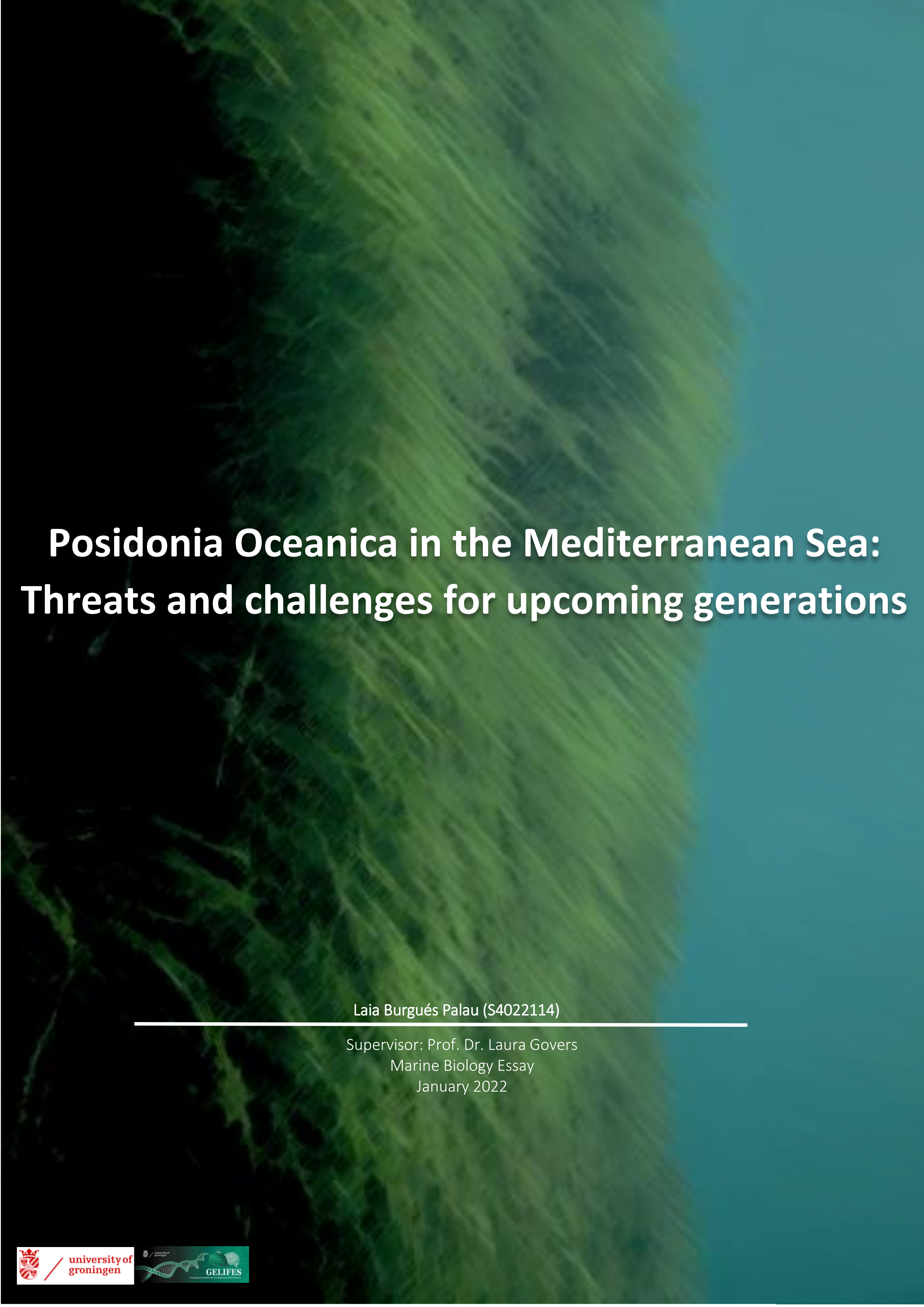

Posidonia Oceanica in the Mediterranean Sea: Threats and challenges for upcoming generations

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Posidonia Oceanica in the Mediterranean Sea: Threats and challenges for upcoming generations

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ABSTRACT

Seagrasses are essential parts of the Mediterranean ecosystems. *Posidonia oceanica* is the only endemic seagrass species of the Mediterranean Sea and forms dense and extensive green meadows. *Posidonia oceanica* ecosystems are extremely complex and unique marine environments and they constitute one of the most valuable submerged ecosystems on the earth providing biomass, oxygenating the oceans, acting as major CO2 sinks and providing suitable habitat for hundreds of species. Over the last decades, following increased coastal urbanisation and industrialisation and the uncontrolled use of unsustainable fishing methods such as trawling, as well as the invasion of alien species have caused the disappearance and/or alteration of many *P. oceanica* meadows. Additionally, ocean warming, sea level rise, eutrophication and extreme weather events are climate change effects that are hampering *P. oceanica* recovery and, in most of the cases, speeding up their decline. *Posidonia oceanica* meadows are identified as a priority habitat type for conservation and management is mainly focused on protective measures through the installation of artificial reefs and seagrass-friendly moorings for boats, in order to reduce the erosive pressure of otter-trawling and free anchoring in shallow meadows. However, scant attention has been devoted to palliate the effects of Climate change in the marine ecosystems until the Paris Agreement at the 21st Conference of the Parties (COP). This essay will explore the potential effects that climate change will have on *P.oceanica* by examining (i) the ecological and economic relevance of *P. oceanica* meadows in the Mediterranean ii) the current and historical known distribution of *P. oceanica* across the Mediterranean Sea, (iii) the magnitude of decline phenomena in the last decades and its consequences, iv) climate change-related challenges and pressures for the upcoming years. and (v) the conservation measures that are being implemented to palliate these decline.

KEYWORDS: Seagrass, *Posidonia oceanica*, Climate Change, Mediterranean Sea

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1. INTRODUCTION

The Mediterranean Sea *,* a *"sea in the middle of the land" (Mare Medi Terraneum)*, is one of the major reservoirs of marine and coastal biodiversity (Mannino *et al.,* 2017). Despite representing a small portion of the world's oceans, it is inhabited by an extraordinary rich and diverse biota (Mannino *et al.,* 2017). The Mediterranean Sea hosts roughly 17,000 species accounting for 4–18% of the world's marine biodiversity (Mannino *et al.,* 2017). As a result, it sustains high rates of endemism with an estimated 20–30% of the marine species being unique from the Mediterranean Sea (Boudouresque, 2004).

Seagrasses are essential parts of the Mediterranean ecosystems and are among the most valuable and endangered coastal ecosystems on the Earth (Manes *et al.,* 2021). Seagrasses structural and functional roles have been largely studied and their ecological importance is well-understood (Campagne *et al.,* 2014, Cullen-Unsworth *et al.,* 2014, Nordlund *et al.,* 2016; Unsworth *et al.,* 2018). Although seagrass morphology and anatomy differ among taxa as a result of different evolutionary pathways, there are many common structural adaptations of this

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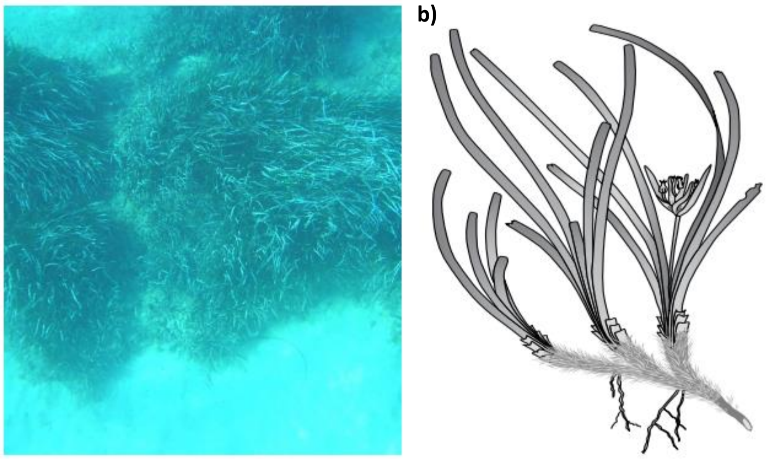

Figure 1. Posidonia oceanica forms very dense stands from the subtidal to depths down to 50-60 m in areas with clear water. The species is easily identified by the dense, broad leaves and the hairy remains around the rhizomes and lower parts of the shoots. **a)** Photo: P.B. Christensen **b)** drawing: redrawn from Luque and Templado 2004.

group to the marine environment (Badalamenti *et al.,* 2015). For instance, seagrasses have strap-shaped leaves with fibre strands that withstand the drag exerted by the water movements and they possess an excellent anchor system to withstand the hydrodynamic disturbances caused by waves and currents (Badalamenti et al., 2015). In this sense, seagrass meadows represent distinct and unique plant-based marine ecosystems whose structure and dynamics give rise to ecosystem engineering functions (Duarte, 2000a). Other adaptations include photosynthesis occurring primarily in the epidermis of the leaves, the loss of stomata, and the development of aerenchyma in response to reduced gaseous movements in the liquid medium or the ability to propagate in the marine environment through several unique mechanisms (Kuo, J. & den Hartog, 2006; Olsen et al., 2016). Four species of seagrasses are described to inhabit the Mediterranean Sea: *Zostera marina, Zostera noltii, Cymodocea nodosa* and *Posidonia oceanica* (Borum, 2006). However, during the last decades, special attention has been driven to

Posidonia oceanica (L.) Delile (Neptune grass) (Fig. 1) since it is the most abundant and the only endemic seagrass species in the Mediterranean Sea (Gobert *et al.,* 2006; Telesca *et al.,* 2015).

Posidonia oceanica forms meadows or beds extending from the surface to 40–45 m depth, some of them have been dated to be older than 6000yr (Picard, 1965). *Posidonia oceanica* needs clear, oligotrophic and oxygenated waters to survive and the depth to which the meadows grow is often limited by light (Díaz-Almela E & Duarte., 2008). It is known that *Posidonia oceanica* meadows can be found from 31°N in the coasts of Libya to 45°N in the Gulf of Trieste (Green and Short, 2003). Therefore, *P. oceanica* meadows are able to support a relatively wide range of temperatures ranging from 10ºC to 29ºC (Duarte, 1991, Duarte et al., 2007). The minimum light requirements of this plant are 0.1 - 2.8 mol PAR photons day^{-1} m^{-2} (Gattuso *et al.,* 2006). *Posidonia oceanica* tolerates a narrow range of salinity, from 33‰ to 39‰ (Fernández-Torquemada & Sánchez-Lizaso, 2005). In historical literature, *P. oceanica* was thought to occur mainly on soft and nutrient-rich substrates (Molinier & Picard *et al*., 1952; Boudouresque & Meinesz, 1982) and its presence in rocky reefs was limited to very particular conditions. For that reason, *P. oceanica* has been considered the "climax community" of soft sublittoral habitats in the Mediterranean Sea. Moreover, some authors reported that *P. oceanica* development is facilitated by precursor communities such as *Cymodocea nodosa* Asch. beds that accumulate sediment and organic matter (Molinier & Picard et al., 1952; Boudouresque & Meinesz, 1982; Badalamenti et al., 2015). Since 1997, *P.oceanica* seedlings have been reported on a variety of substrates, ranging from consolidated substrates such as rocky reefs covered by algae to unconsolidated substrates such as sand or gravel (Buia *et al.,* 2002; Alagna *et al*., 2013). Additionally, some seedlings were observed settled even at exposed sites and on bare rocks (Buia *et al.,* 2002; Alagna *et al.,* 2013). The type of substrate conditions the plantlets resistance to withstand the hydrodynamic disturbances, for instance, rocky substrates confer higher resistance than sand or gravel (Buia *et al.,* 2002; Alagna *et al.,* 2013; Badalamenti *et al.,* 2015). *Posidonia oceanica* propagates through both vegetative and sexual reproduction; however, vegetative propagation by rhizome elongation in established spots patches is considered the dominant process by which seagrass expands and maintain existing meadows (Marbà *et al.,* 1998; Sintes *et al.,* 2005; Badalamenti *et al.,* 2015). *Posidonia oceanica* flowering occurs in autumn and plants release the fruit in the late spring of the subsequent year (Peirano *et al.,* 2001). According to Pergent *et al.* (1989), *P. oceanica* flowering occurs about once in a decade; however, more recent studies have reported meadow flowerings in consecutive years (Semroud, 1993; Balestri & Cinelli, 2003). In addition, it has been observed high patchiness in flowering intensity at small spatial scales of a few meters (Gambi *et al.,* 1984; Balestri, 2004). Some studies indicated that flowering occurrence and intensity can vary with depth (Gambi *et al.*, 1984; Semroud, 1993). Therefore, literature suggests that *Posidonia oceanica* flowering is an irregular phenomenon both temporally and spatially and the factors that influence the flowering, remain largely unexplored (Díaz-Almela *et al.,* 2006).

Posidonia oceanica meadows play essential ecological and economic roles (Bell & Harmelin Vivien, 1983; Jeudy de Grissac and Boudouresque, 1985; Duarte, 1999; Duarte, 2002). Ecosystem services provided by *P. oceanica* are relatively well-studied and are listed as: nursery areas for fish and invertebrates, high biomass production, oxygenation of coastal waters, source of food for many species, sediment trapping and shoreline defence, oxygenation of coastal waters and carbon sink role due to slow decomposition rate (Vassallo et al., 2013). Despite the largely well-understood importance of preserving healthy *P. oceanica* meadows, it has been estimated that 46% of the underwater meadows in the Mediterranean have experienced some reduction in range, density and/or coverage, and 20% have severely regressed since the 1970s (Díaz-Almela E & Duarte., 2008). This alarming decline has been observed across all the Mediterranean Sea and has been attributed to direct human activities (e.g. coastal urban development, fishing activities, aquaculture) (Boudouresque et al., 2012). However , climate change has brought new threats and challenges that are adding extra pressure on *P. oceanica* ecosystems (e.g Short & Neckles et al., 1999). Changes in sea level, extreme weather events, eutrophication and ocean warming, can alter seagrass distribution, productivity, and community composition (Short & Neckles et al., 1999). In turn, potential changes in distribution and structure of seagrass communities may have profound implications for local and regional biota, nearshore geomorphology, and biogeochemical cycles, which can directly affect human economy and welfare (Short & Neckles et al., 1999). Some of the effects and responses to many of those environmental factors associated with global climate change are relatively well studied in *P. oceanica*. However, literature connecting all these effects is not that abundant. I aimed to review this literature to extrapolate the potential consequences of a changing global climate on *P. oceanica* ecosystems by assessing (i) the ecological and economic relevance of *P. oceanica* meadows in the Mediterranean ii) the current and historical known distribution of *P. oceanica* across the Mediterranean Sea, (iii) the magnitude of decline phenomena in the last decades and its consequences, iv) climate change-related challenges and pressures for the upcoming years. and (v) the conservation measures that are being implemented to palliate these decline.

2. IMPORTANCE OF P. OCEANICA IN THE MEDITERRANEAN

2.1. Ecological value

Posidonia oceanica meadows play an important role in climate change mitigation since they are the most relevant natural carbon sinks in the Mediterranean Sea. Recent reviews (Duarte et al., 2010; Kennedy et al., 2010) show that seagrass meadows sequester between 580 and 680 gCO^2 m^2 yr^1 due to seagrass community metabolic rates and the high efficiency of seagrass meadows at capturing and burying suspended particles in the water column.

Additionally, *Posidonia oceanica* meadows are hotspots of biodiversity which sustain extremely complex food web (Fig. 2). Moreover, a characteristic feature of Posidonia meadows is the combination of two kinds of primary production (Boudouresque *et al*., 2012). First, the primary production resulting from *P. oceanica* leaves and rhizome. The net primary production of *P. oceanica* is on average 420 g DM/m^2/year and may reach 1,300 g DM/m^2/year (it drops in relation to depth). *Posidonia oceanica* primary production is rich in lignin and cellulose, compounds that are not used much by herbivores, as well as in phenolic compounds, one of whose roles is to dissuade potential consumers (Piovetti *et al.,* 1984). Recent studies determined that less than 10% of the *P. oceanica* primary production is consumed by herbivores (Boudouresque *et al.,* 2012). These, include the fish *Sarpa salpa*, the sea urchin *Paracentrous lividus*, isopod crustaceans *Idotea hectica*, spider crabs *Pisa mucosa* and *P. nodipes*. Conversely, epibiota biomass is widely used by gastropods species such as *Calliostoma langieri, Cerithiu, vulgatum* and *Collumbela rustica* (Boudouresque *et al.,* 2012).

Secondly, the primary production produced by Multicellular Photosynthetic Organisms (MPOs) leaf epibiota, which is very palatable for herbivore species. The primary production from leaf epibiota is estimated between 100 and 500 DM/m^2/year. All in all, vegetal biomass results to be very high within the ecosystem (Boudouresque *et al.*, 2012).

Animal biomass is considerably lower than vegetal biomass and it is estimated to oscillate between 100-200 g DM/m^2 (the values for each taxonomical group or trophic compartment vary largely from one station to the next and according to depth) (Boudouresque *et al.,* 2012).

A substantial part of the primary production (24 to 85%) is exported in form of dead leaves to other ecosystems (Boudouresque et al., 2012). Verlaque & Nédélec (1983) found that 40% of the digestive content of the sea urchin *Paracentrous lividus* was *P. oceanica* biomass belonging to a meadow placed hundreds of meters away from the sea urchin community. In addition, the accumulation of dead leaves deposited on the shoreline (also called banquettes) can develop cushions up to 4 meters high, which can, in turn, sustain a complex invertebrate food web, protect the shoreline from erosion and, when transported further inland by the wind, act as seed material for dune formation (Borum *et al.,* 2004).

Part of the *P. oceanica* biomass remain inside the meadow forming the litter. Its mass increases with depth and represents up to 200% compared to the biomass of the leaves (Romero *et al.,* 1992). Litter decomposition is very slow (e.g at 20 m depth, only 11% of its biomass had disappeared in Ischia, Italy; Pergent *et al.,* 1994) and detritus feeders are the main path of energy transfer from *P. oceanica* to higher trophic levels.

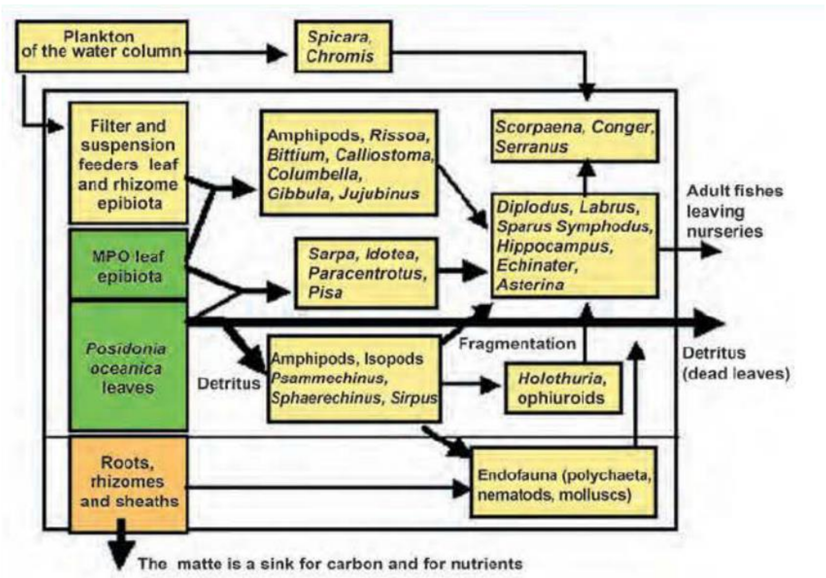

Figure 2. Trophic relationships and functional compartments in the *Posidonia oceanica* ecosystem. Reprinted from "Boudouresque C.F., Bernard G., Bonhomme P., et al. (2012) Protection and conservation of Posidonia oceanica meadow. RAMOGE and RAC/SPA publisher, Tunis: 1-202.", by L. Vassallo et al., 2013, *Marine Pollution Bulletin*, , 75(1–2), 157–167

2.2. Ecosystem services and economic value

Ideally, ecosystem services should be valued by how they contribute to human welfare. However, this conception is deceptive and too simplistic since a good deal of the intrinsic mechanisms and processes involved in ecosystem dynamics are still unknown (Odum & Odum & Odum, 2000b). It is extremely difficult to ascribe an economic value to ecological services independent of human appreciation of nature's work (Pascual et al., 2017). As a result of this complexity, performing valuation techniques based on ecological accounting principles must be introduced (Pascual et al., 2017). Taking that into consideration, several definitions, descriptions and classifications on how to quantify the economic value of an ecosystem (*Posidonia Oceanica* in this case) have been suggested throughout the last decades (Vassallo et al., 2013). There is a general literature consensus that *Posidonia oceanica* meadows provide direct economic benefits. For instance, the widely recognised role of *P. oceanica* beds as nursery grounds for several commercial species (Francour 1997; Vassallo *et al.,* 2013; Bell & Harmelin-Vivien, 1983; Bellan-Santini *et al.,* 1986; Boudouresque, 2004). A study from Vassallo *at al.,* (2013) assessed the natural capital of *Posidonia oceanica* using Emergy methodology (Brown & Herendeen, 1996). Ecosystem services traditional approach is an anthropocentric, user side approach, based on the subjective preferences (Vassallo at al., 2013). It does not consider the contribution of nature and its formation of the raw material used, nor the damage generated by the future exhaustion of the natural resource, nor the expenses resulting from the social exclusion of local communities (Vassallo at al., 2013; Nadalini et al., 2021). Conversely, Emergy methodology converts the thermodynamic basis of all forms of energy, resources and human services of an ecosystem into equivalents of a single form of energy, then are transformed into monetary values (Nadalini et al., 2021). They estimated Posidonia meadow value in 172 € m^2 yr^1 (Fig. 2). Additionally, they determined that sediment retention is the most valuable component of the system, making up almost 100% of the value of *P. oceanica* (up to 99%) due to the meadows attenuation of hydrodynamics, resulting in effective shoreline protection reefs.

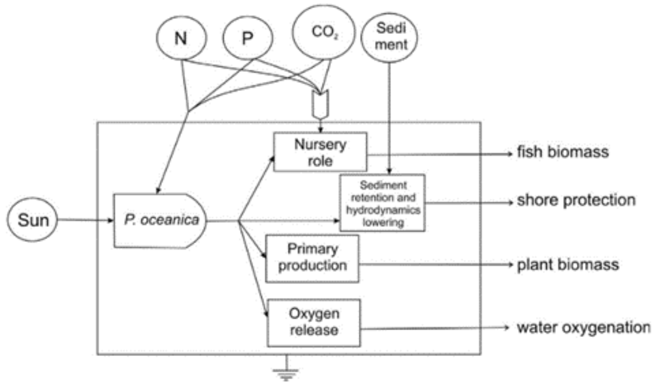

Figure 3. System diagram of *P. oceanica* services. The analysed system is represented as a box. The box contains the main components and is surrounded by all inputs that support the system, all located on left and upper boundaries. Outputs are located outside right boundary while heat losses are represented below. Reprinted from "The value of the seagrass *Posidonia oceanica*: A natural capital assessment", by L. Vassallo et al., 2013, *Marine Pollution Bulletin*, , 75(1–2), 157–167

Several studies have addressed how the presence of a meadow affects sediment properties (De Falco et al., 2008; Gacia et al., 1999) and wave energy (Basterretxea et al., 2004; Infantes et al., 2009; Vacchi et al., 2010). A meadow, in particular, dampens surge and acts as a barrier to sediment flow on the bottom (Brunel and Sabatier, 2009). It also plays an important role in the beach's sedimentary balance, supplying biogenic sand and/or trapping

sediments (Basterretxea *et al.,* 2004). There is evidence that *P. ocenaica* meadows can produce 60 to 70 gr m^{-2} yr^{-1} of calcium carbonate which translates to an important yield when scaled to the large area occupied (Canals & Ballesteros, 1997). For instance, Mallorcan beaches are composed of more than 70% bioclastic sediments, most of them associated with the P. oceanica meadows (Jaume & Fornos, 1992; Rodriguez-Perea *et al.,* 2000). However, the amount of 'new' biogenic sediment reaching the beach is nevertheless uncertain (Basterretxea *et al.,* 2004).
Many studies have tested the reduction of hydrodynamic forces, represented by waves and bottom currents, in both lab conditions (Boudouresque *et al.,* 2006) and in situ (Duarte, 2004; Jeudy de Grissac & Boudouresque, 1985). Results showed that the hydrodynamic forces are reduced from 10% to 75% under the leaves (Gacia *et al.,* 1999; Gambi *et al.,* 1989), and of 20% few centimetres above the meadow (Gacia &Duarte, 2001). In addition, the accumulation of banquettes across the shoreline, protects the beaches by mitigating the wave effect and, consequently, reducing coastal erosion.

Tourism in the west Mediterranean countries represents a major economic income, especially during summer season. Clean waters, white sands and its abundant biodiversity, are powerful touristic attractions, in part, derived from the presence Posidonia meadows. Therefore, the health status of Posidonia meadows may have important and direct ecological and economic implications for Mediterranean countries (Boudouresque *et al.,* 2012)

3. DISTRIBUTION AND TRAJECTORIES OF CHANGE

At least 1.5% of seagrass beds is lost every year and almost 29% of the areal extent of seagrass has disappeared globally since 1879 (Waycott *et al.,* 2014). This implies that 1/3 of European seagrass area was lost due to disease, deteriorated water quality and coastal development. (Los Santos *et al.,* 2019). In a study from Los Santos *et al.* (2019) they reported seagrass loss, recovery and stability for the four European native species *Zostera marina, Zostera noltii, Cymodocea nodosa* and *Posidonia oceanica* between 1869 and 2016 (Fig. 4). Across the observational record (1869–2016), they reported seagrass losses of 49%, increases of 22% and showing no change of 29%, when accounting for all the species.

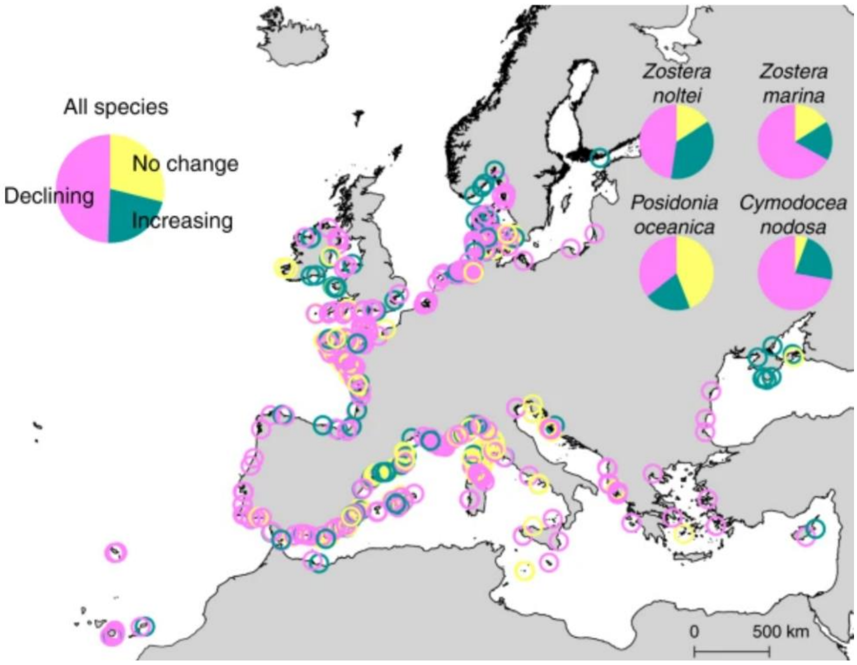

Figure 4. Distribution of compiled seagrass sites in Europe and their trajectories. Seagrass sites in Europe showing no change (yellow circles, *n* = 213), increase (green circles, *n* = 160), and decline (magenta circles, *n* = 364) trajectories based on the available time series reports between 1869 and 2016, thus corresponding to different time windows. Reprinted from: "Recent trend reversal for declining European seagrass meadows", by C. Los Santos et al., 2019, *Nature Communications*, *vol. 10, p. 3356.*

The predominant trajectory for the European seagrasses indicates a general decline. Loss rates of European seagrasses peaked in the 1970s and 1980s and started to slow down in magnitude toward the end of the century (Fig. 5) (Los Santos et al., 2019).

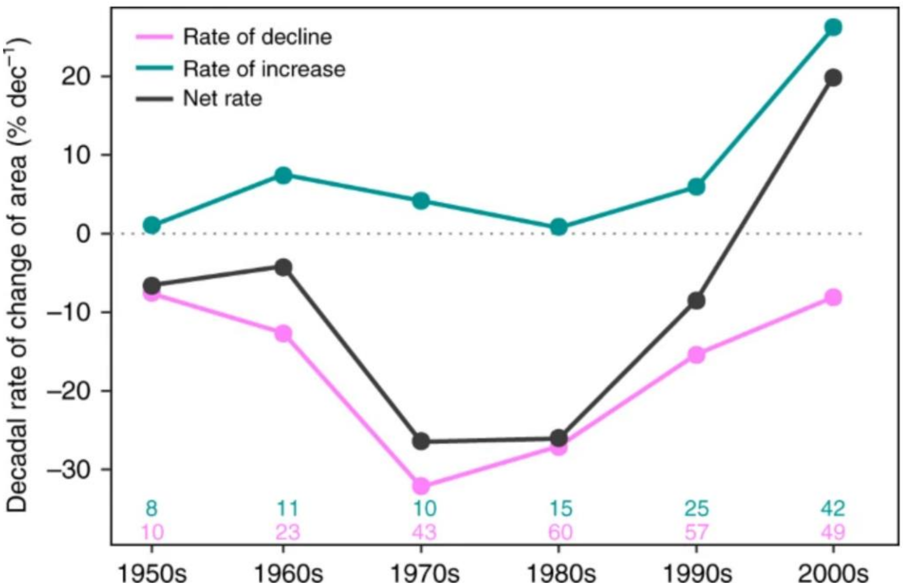

Figure 5. Decadal rate of change of area of European seagrasses (1950s–2000s). Decadal analysis includes time series >8 years. Number of sites per decade and trajectory are given at the bottom of the plot. Reprinted from: "Recent trend reversal for declining European seagrass meadows", by C. Los Santos et al., 2019, *Nature Communications*, *vol. 10, p. 3356.*

An accurate spatial information on habitat distribution is an essential prerequisite for a sustainable use of marine coastal areas. Abundant studies have been conducted assessing *P.oceanica* regression during the past decades (Marbà *et al.,* 2014; Marbà *et al.,* 2002; Gobert *et al.* 2006; Badalamenti *et al.,* 2011; Meinez *et al.,* 1976; Colantoni *et al.,* 1982; Ardizzone *et al.,* 2006; Boudouresque *et al.,* 2000; Guillén *et al.,* 2013; Gonzalez-Correa *et al.,* 2005; Arnaud-Haond *et al.,* 2007; Peres *et al.,* 1964; Jorda *et al.,* 2012; Los Santos *et al.,* 2019). Despite *P.oceanica* being one of the most relevant and well-studied seagrass species, there has been a lack of effort to combine all the spatial information available and provide a clear distribution overview across all the Mediterranean (Telesca *et al.,* 2015). First attempts to create a spatial record of *P. oceanica* meadows date back to the end of 19th century but the first maps did not appear until the 1970s in France and Italy. In 2015, a study from Telesca *et al.,* (2015) which is part of the European Research project Mediterranean Sensitive Habitats (MediSeH), finally provided a fine-scale assessment of the magnitude of this previously reported regression phenomena across all the basin. They provided an accurate current distribution of *P. oceanica* meadows and quantified the magnitude of losses based on historical records (UNEP-WCMC) (Fig. 6). The total current known area of *P. oceanica* meadows in the Mediterranean Sea was found to be 1,224,707 ha (12,247 km2) (510,715 ha in the western and 713,992 ha in the eastern part of the basin) (Telesca et al., 2015). Additionally, they realised that knowledge of *P. oceanica* meadows distribution was fairly comprehensive in north-western and central of the Mediterranean Sea but there was a clear gap of information regarding the southern (from Morocco to Egypt) and eastern (from Israel to Turkey) parts of the Mediterranean basin (Fig 6a). They estimated a total loss of *P. oceanica* of 124,091 ha over the past 50 years (Table 1), which corresponds to an average regression of 10.1% of the total known area (across all the Mediterranean basin). Considering only those areas for which they had historical information (368,837 ha), the estimated loss was of an alarming 33.6% in the past 50 years (Telesca et al., 2015).

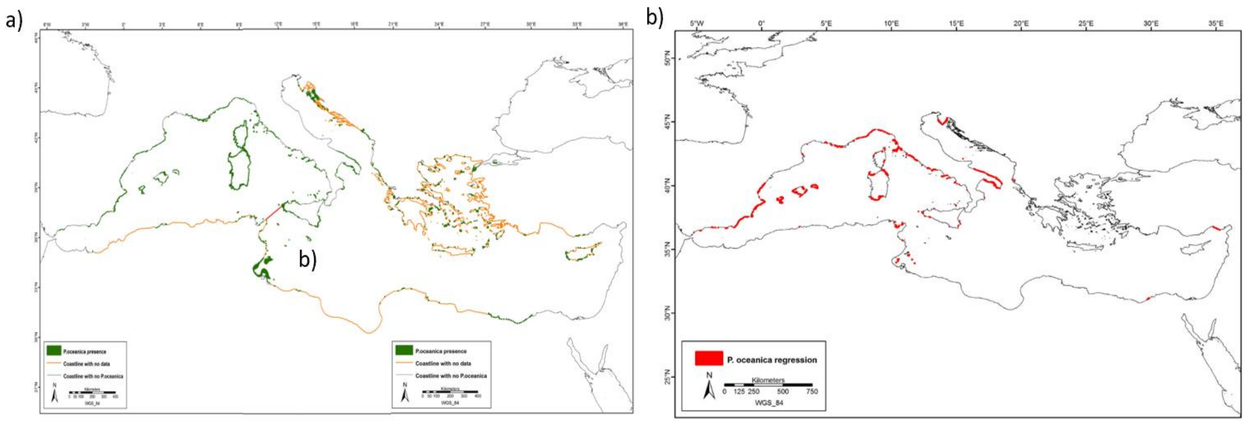

Figure 6. a) Current distribution of Posidonia oceanica meadows. The current distribution of *P. oceanica* (green areas) along the Mediterranean Sea coastline, based on collated spatial information available on meadow presence. **b)** Coastline with regression of *Posidonia oceanica* meadows. Maps created with ArcGIS® software by Esri (Environmental Systems Resource Institute, ArcMap 9.3, www.esri.com) using data from OpenStreetMap.org (© OpenStreetMap contributors). Adapted from "Seagrass meadows (Posidonia oceanica) distribution and trajectories of change", by L. Telesca et al., 2015, *Scientific Reports*, *5*, 1–14. https://doi.org/10.1038/srep12505.

Country	Currently surveyed coastline (%)	Historical surveyed coastline (%)	*P. oceanica* total current area (ha)	*P. oceanica* total historical area (ha)	*P. oceanica* regression (%)	Time range of data
Spain	100%	70%	172,669	222,254	29%[1]	1993–2011
France/Monaco	100%	60%	94,030	96,783	9%[2]	1980–2011
Italy	100%	42%	337,611	395,298	25%[3]	1990–2005
Slovenia	100%	—	9	—	—	2004
Croatia	14%[4]	—	31,437	—	—	2010
Montenegro	100%[5]	—	—	—	—	2004
Albania	100%	—	4,803	5,710	16%	2007–2008
Malta	100%	—	5,860	—	—	2002
Greece	8%[4]	—	44,939	—	—	2011
Turkey	29%[4]	6%	287	—	—	2009
Cyprus	30%[4]	—	9,040	—	—	2008
Syria, Lebanon, Israel	100%	Absent[6]	Absent[6]	—	—	2003
Egypt	63%[5]	3%	—	—	—	2006
Libya	11%[4]	—	1,235	—	—	2011
Tunisia	81%[4]	13%	518,685	531,844	2%	1972–2010
Algeria	16%[4]	—	4,072	—	—	2010
Morocco	100%[5]	—	—	—	—	2006

Table 1. Lengths of coastline with the known current and historical presence of *Posidonia oceanica*, the percentage of regression and the time range of data. Reprinted from “Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change”, by L. Telesca et al., 2015, *Scientific Reports*, *5*, 1–14. https://doi.org/10.1038/srep12505.

4. CONCEQUENCES OF CLIMATE CHANGE ON P. OCEANICA

The major causes of *P. oceanica* loss were widespread disturbances acting at local scale (e.g fish trawling, coastal constructions, dredging), but recently, global disturbances such as climate change are seriously threatening *P. oceanica* persistence in the Mediterranean Sea (Marbà *et al.,* 2014). Studies indicate that the Mediterranean Sea is warming every year at alarming rates (Cubash et al., 2001). Additionally, other observed trends such as a general reduction in water transparency and greater frequency of extreme weather events suggest that *P. oceanica* meadows will have to cope with enhanced climatic stress in the coming decades (Díaz-Almela E & Duarte., 2008).

4.1. Ocean warming

Rises in human-induced atmospheric CO2 are causing global warming. Based on global climate scenarios, the Mediterranean Sea has been listed as one of the areas most sensitive to global warming (Giorgi, 2006). Depending on the climate scenario and the season, an increase in atmospheric temperature from 2 to 6 °C by 2100 is expected in the Mediterranean basin. This rise in global temperatures entails a warming of the Mediterranean Sea surface which is currently estimated at 0.4 °C/decade for the period 1985-2006 (Nykjaer, 2009) (Fig. 4). *P. oceanica* has an upper tolerance limit of 29°C (Duarte 1991), which means that increases of sea surface temperatures (SST) above this limit cause stress, impairing plants metabolism (Procaccini et al., 2012; Tuya et al., 2016). The photosynthetic balance between the quantity of carbon fixed and respired is disrupted by this thermal stress, skewing the balance in favour of respiration and depriving the plant of valuable energy (Lee et al., 2007; Collier & Waycott, 2014; Jordà *et al.,* 2012). Since the turn of the century, annual maximum SSTs have consistently surpassed *P.oceanica*'s upper thermal limit increasing decreasing plant growth, indicative of plant stress (Jordà et al., 2012). In a study from Jordà *et al.,* (2012), they predicted a functional extinction, or a reduction to less than 10% of the current population size of *P.oceanica* by 2049 (±10 years) in the Balearic Archipelago. Other studies assessed whether reproductive mechanisms are affected by increasing water temperatures (Ruiz *et al.,* 2017; Carey *et al.,* 2002; Diaz-Almela *et al*., 2007). When *P. oceanica* is exposed to a temperature increase it transits from clonal grow to sexual reproduction (Carey *et al.,* 2002; Diaz-Almela *et al.,* 2007). For instance, Ruiz *et al.,* (2017) used controlled experiments to test if warming can effectively trigger flowering in *P. oceanica*. They simulated a heat wave under laboratory mesocosm conditions placing them in either elevated (27 °C, + 4 °C above control mean) or control temperature groups. After six weeks they returned to control levels to allow plants to recover from heat stress for another six weeks. Plants exposed to elevated temperatures displayed inflorescence whereas controls showed no signs of flowering (Ruiz et al., 2017). Sexual reproduction seems to be a stress-driven response

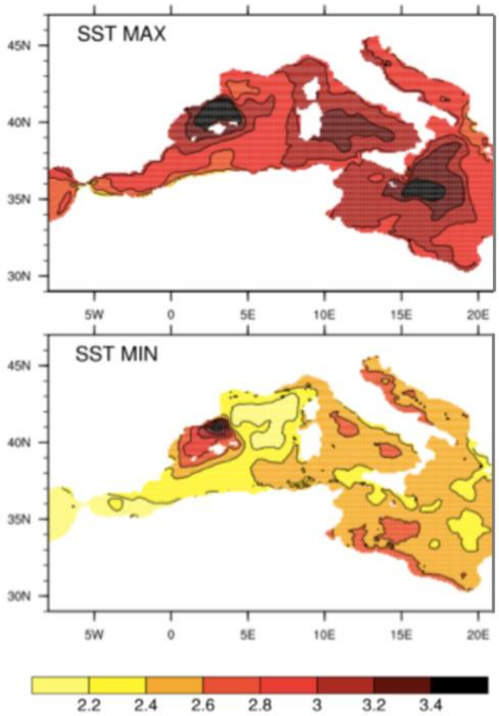

Figure 7. Expected minimum and maximum changes in sea surface temperature for the 2070–2099 period (vs. 1961–1990) based on a 6-member ensemble covering various sources of uncertain (°C). The Balearic Islands, the northwest Ionian, the Aegean and Levantine Seas have been identified as the regions with maximum increase of sea surface. Adapted from "*Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. Climate Dynamics*", by A. Adloff et al., 2015, Climate Dynamics, *45 (9-10), 2775-2802*.

in order to favour genetic variation; therefore, switching from clonal to sexual reproduction may enhance specie's adaptive potential and survival. In a strongly clonal species such as *P. oceanica*, epigenetic modifications accumulated during the clonal life in response to environmental stress are likely to be transmitted during sexual reproduction and seed dispersal (Ruiz et al., 2017). Additionally, seed dispersal is involved in sexual reproduction, which also confers an advantage providing a dispersal mode towards more suitable regions and seeds may tide over severe disturbances that living plants may not (e.g extreme weather events, mechanical degradation caused by trawling) (Ruiz et al., 2017; Diaz-Almela et al., 2007). This, may suggest that the response of *P. oceanica* to warming might be more plastic, more complex and potentially more resilient than previously thought (Ruiz et al., 2017).

4.2. Eutrophication

Eutrophication or over-enrichment of nitrogen and phosphorus in the water column has become one of the main causes of seagrass decline (Pazzaglia *et al.,* 2020). This abnormal amount of nutrients in the water column is often derived from human activities such as the aquaculture, the increasing use of fertilizers and direct sewage discharge and industrial waste. Eutrophication have indirect and direct consequences on seagrass' physiology (Pazzaglia *et al.,* 2020). For instance, excessive inorganic nitrogen (Ni, as $NO3-$ and $NH4+$) concentrations can stimulate an overgrowth of phytoplankton, macroalgae and epiphytes, reducing light availability hence, inhibiting seagrass growth and survival (Touchette & Burkholder, 2000). Additionally, Ni enrichment can directly affect growth in several seagrass species by altering their cellular function and generating a negative physiological response (Burkholder *et al.,* 2007). Seagrasses appear to be particularly vulnerable to the direct effects of eutrophication, since some studies suggest that feedback inhibitory mechanisms for Ni uptake are missing in seagrasses as a result of an evolutionary adaptation to oligotrophic habitats (Burkholder et al., 1992; Touchette and Burkholder, 2000). For instance, a study with *Zostera marina* (Burkholder et al., 1992) observed an uncontrolled uptake of Ni even during dark periods when exposed to nitrate-rich environment. This continuous uptake of Ni generates metabolic imbalances due to the high energetic-demand of N assimilation process (Touchette *et al.,* 2003). In a study by Pazzaglia *et al.,* (2020) they collected *Posidonia oceanica* plants from two environments with different nutrients load history: eutrophic environment and oligotrophic environment. The plants were

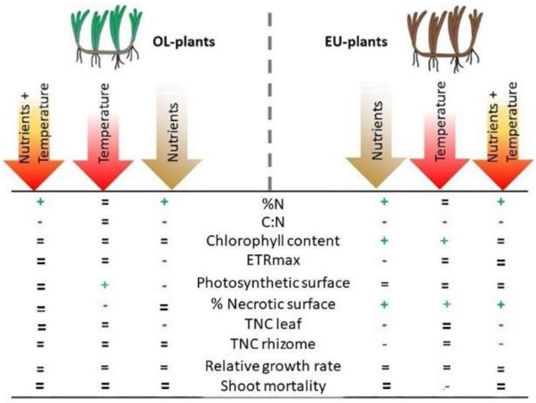

Figure 7. Summary of the overall physiological responses of *P. oceanica* from oligotrophic (OL) and eutrophic (EU) environments to nutrient excess, temperature increase and their combination. Signs (+, −, =) reflect statistical significance and direction of the difference in respect to the control. Reprinted from "*Does Warming Enhance the Effects of Eutrophication in the Seagrass Posidonia oceanica?*", by J. Pazzaglia et al., 2020, Frontiers in Marine science, (Vol. 7, p. 1067).

exposed in controlled conditions to high nutrient concentrations and increased temperature and their combination for 5 weeks in order to assess the effect of the single stressors and their interaction. Their results revealed that plants belonging to the eutrophic habitats were more sensitive to further exposure to multiple stressors than plants growing in oligotrophic habitats. Additionally, the plants appeared to be weaker during the treatments, showing the greatest percentage of mortality, particularly under increased temperature. Both groups of plants (eutrophic and oligotrophic) showed different morphological traits and physiological performances (Fig.7) suggesting a certain degree of plasticity in response to changes of environmental conditions (Pazzaglia *et al.,* 2020). However, the activation of high energy demanding physiological strategies to cope with excess of nutrients and other stressors, could affect plants present and future persistence, particularly under eutrophic conditions (Pazzaglia *et al.,* 2020).

4.3. Sea level rise

Light is a prerequisite for angiosperm growth and many types of temperate seagrass, including *P. oceanica* (Dennison & Alberte, 1985). Sea level is projected to rise 0.45-0.98 meters worldwide by 2100 (Church *et al.*, 2013). This means that the pastures of *P. oceanica* will be in deeper waters what traduces in a reduction of light penetration. (Church *et al.,* 2013). *P.oceanica* populations have survived past sea level increases, but the current rate of sea level rise is unprecedented (Collins *et al.,* 2013). Additionally, *P. oceanica* is one of the slowest growing plants with a low natural rate of sexual reproduction what may hinder the ability of the plant to adapt to these sudden light changes (Collins *et al.,* 2013; Short & Neckles, 1999). In a study by Short & Neckles, (1999), they exposed *P. oceanica* plants to high and low light environments and they observed that when plants were submitted to light reduction treatments, concurrent reductions in shoot density, leaf width, number of shoots, and overall growth rates. As a consequence of sea level rise, a phenomenon called self-shading is likely to occur. Self-shading occurs when an individual grows above the leaves of an adjacent plant to obtain light (e.g. algae) resulting in less light available to the underlying plant. As sea level rises and there is a shortage of light, competition for light intensifies, resulting in increased self-shading (Hemminga & Duarte, 2000). In contrast to the effects of ocean warming, the reduced availability of light reduces the prevalence of sexual reproduction in the pastures of *P. oceanica* due to lack of available energy (Diaz-Almela *et al.,* 2006).

4.4. Extreme weather events

Climate models indicate increases in the frequency and intensity of extreme whether events in the Mediterranean region during the 21st century (Collins et al., 2013). Heat waves, for instance, are harmful because they can cause thermal stress on the plants. Storm surges imply diverse negative impacts for *P. oceanica* meadows. First, increased turbidity of water may reduce light availability to the plants, hampering photosynthesis. Secondly, cyclonic winds, hurricanes and storms can induce intense sedimentary dynamics which may cause large-scale alteration in *P. oceanica* meadows by burying partially or totally the shoots. In a study from Manzanares et al., (2011), they experimentally induced different levels of burial intensity, frequency, timing and duration. They found a strong population decline with increasing sedimentation. When the burial level was 4 cm they recorded a 65% of shoot disappearance and undergoing 100% mortality with 9 cm burial. Nevertheless, at 4 cm burial, they detected some response capacity of plants to burial, consisting of rhizome elongation and rhizome branching. Rhizome vertical annual growth and internode length increased by 34% in the 4 cm treatment.

On the other hand, other authors add that with the alteration of tidal circulation and flow patterns, sea beds may be eroded in some areas or create new depositional areas where beds can colonize (Harlin *et al.,* 1982).

5. REGULATION AND CONSERVATION MEASURES

Posidonia oceanica meadows have been degrading very rapidly throughout the last century, to a large extent, caused by anthropogenic pressures such as water pollution, spillage, proliferation of coastal constructions, trawling fishing, free anchoring and the presence of invasive species (e.g. Boudouresque *et al.,* 2012). During the last decades several conservation measures have been implemented in order to protect and preserve *P. oceanica* from humans impact (Díaz-Almela E & Duarte., 2008). At an international level, one of the firsts agreements to protect marine environments from anthropogenic impact took place during the Bern Convention (Conservation of European wildlife and Natural habitats), signed in 1979. Marine plants were initially not mentioned, but the Annexes were modified in 1996 and finally included *P. oceanica* (Díaz-Almela E & Duarte., 2008). The Barcelona Convention, or Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean (1975) adopted the Mediterranean Action Plan (MAP), the first-ever Regional Seas Programme under UNEP's (United Nations Environment Programme) umbrella which aim was to protect the environment and to foster sustainable development in the Mediterranean basin (European Commission). The Annex II includes *P. oceanica* among the most endangered species in the Mediterranean sea (RAC/SPA, 1992) and since 1997 *P. oceanica* meadows have been protected at European level as a priority habitat (Díaz-Almela E & Duarte., 2008). The Common Fisheries Policy of the European Union for the Mediterranean (Council Regulation EC No. 1626/1994, as amended by Council Regulation EC No. 1967/2006) prohibits trawling on marine angiosperm seagrasses (Díaz-Almela E & Duarte., 2008). Mediterranean countries also adopted legal regulations in order to prevent the decline of *P. oceanica* (Boudouresque et al., 2012). In 1976, the governments of France, Italy and Monaco, founded RAMOGE committee (RAMOGE agreement signed in 1976) which urges for the prevention and combat against pollution in the marine environment and the littoral of the PACA Region. Outside the RAMOGE area, several countries (Algeria, Croatia, Spain, Libyia, Malta, Slovenia and Turkey) have implemented specific laws about meadows (Boudouresque et al., 2012).
Additionally, up to 1,215 areas Marine protected areas (MPAs) have been implemented in order to preserve and restore the health of marine ecosystems. In the Mediterranean there are 1,215 MPAs and Other Effective area-based Conservation Measures (OECMs) covering 171,362 km2 which places a surface of 6.81% under a legal designation (over 72.77% is located in the Western

Mediterranean). According to MedPAN, (2016), 39.77% of *Posidonia Oceanica* meadows are covered (*Gabrié et al.,* 2012).

Despite the efforts of governments and institutions combating anthropogenic pressures, scant attention to the ocean has been devoted from a climate change perspective until the Paris Agreement at the 21st Conference of the Parties (COP) on 12 December 2015 (Gallo et al., 2017). The ocean is being disproportionately impacted by increasing carbon dioxide (CO_2) and other greenhouse gas emissions that affect marine ecosystems (Gallo et al., 2017). Although the 1992 UNFCCC formally recognized the importance of marine ecosystems as sinks and reservoirs of greenhouse gases, ocean, marine, and coastal ecosystems were largely left out of subsequent COP negotiations. Hence, The Paris Agreement marked a historic turning point for recognition of the oceans within the climate negotiations, evidenced by an increase in ocean-related side events, greater participation of ocean scientists and non-governmental organizations, and the signing of the 'Because the Ocean' declaration by 22 Parties (Gallo et al., 2017). The Paris Agreement, adopted through Decision 1/CP.21, addresses crucial areas necessary to combat climate change and some of the key aspects directly concerning the preservation of marine ecosystems agreed for the parties were: First, the long-term temperature goal (Art.2) which reaffirms the goal of limiting global temperature increase to well below 2 degrees Celsius, while pursuing efforts to limit the increase to 1.5 degrees. Indeed, this has a direct consequence on the ocean's temperature since, oceans have absorbed more than 90% of the heat gained by the planet between 1971 and 2010, with around 290 ZJ (1 ZJ = 1021 J) contained in the top 2,000 m (Zanna et al., 2018). Secondly, the Paris Agreement also encourages Parties to conserve and enhance, as appropriate, sinks and reservoirs of greenhouse gases (Art.5) (Delbeke., et al 2019). Therefore, the preservation of coastal ecosystems like mangroves, salt marshes and seagrasses is essential since they play a vital role in carbon storage and sequestration (Vassallo et al., 2013).

6. DISCUSSION AND CONCLUSIONS

Posidonia oceanica gives life to the Mediterranean Sea. It constitutes one of the most valuable submerged ecosystems on the Earth providing biomass, oxygenating the oceans and providing suitable habitat for hundreds of species (Boudouresque et al., 2012). Many governments and institutions are implementing active management to combat disturbances derived from human activities. For instance, restrictions on trawling over *P.oceanica* meadows have been reinforced in the last decade. Many countries such France, Italy and Spain have opted for the deployment of protective artificial reefs. These protective reefs consist on heavy cubic or pyramidal concrete structures, in which any trawling gear passing over them gets entangled and breaks (Díaz-Almela E & Duarte., 2008). Protective reefs are usually installed in Marine Protected Areas (MPA), but, given the special protection status of *P. oceanica* habitats, they could also be installed in any area with *P. oceanica* meadows that suffers from illegal trawling. A practical example of the implementation of protective reefs occurred in Campello and Villajoyosa (Alicante, SE Spain, SW Mediterranean Sea). In 1992, 358 artificial reefs were placed in an area altered by illegal otter trawling: 40% of the *P. oceanica* beds between depths of 14 and 28 m (290 ha, over 7 km of shoreline) were damaged. Reef installation was complemented by a follow-up research program. Eight years later, partial meadow recovery through rhizome growth could be observed. However, rhizome growth was 5 times slower than in adjacent non-impacted meadows at the same depth because the light intensity in the impacted meadows was still 4 times lower than in non-impacted areas due to the altered sediment structure (Díaz-Almela E & Duarte., 2008). Such low rates of vegetative growth may prolong the time needed for recovery up to 100 years (González-Correa et al., 2005).

Climate change has brought new threats and challenges that are adding extra pressure on *P. oceanica* ecosystems. Seagrass areas along coastlines that are already affected by human activities (causing e.g. sedimentation, nutrient enrichment, eutrophication and other environmental destruction) are most vulnerable to climate change impacts (Boudouresque et al., 2012; Díaz-Almela E & Duarte., 2008). Therefore, mitigating strategies (e.g. limiting greenhouse gas emissions) that affect the rate and extent of climate change impacts should be coupled with resilience-building adaptation strategies (Johnson and Marshall 2007). For instance, by promoting policies that protect and conserve *P. oceanica* meadows, while also assisting in mitigation efforts by raising awareness about the vulnerability of seagrass habitats to coastal impacts (Johnson & Marshall, 2007).

Posidonia oceanica role as natural carbon sink may be severely compromised if the overall observed trend towards ecosystem loss is not halted. This, translates into a major concern in terms of climate change mitigation. Accordingly, at present, P. oceanica in the Mediterranean basin would be sequestering annually between 20 and 27 Tg CO2, representing between 62% and 87% of that sequestered before 1960. Meditarranian population is estimated to be about 180 million people (Benoit & Comeau, 2005) and it was estimated that the annual CO2 emission is 3.3 tons per capita (Boisgibault & Mozas, 2012). For instance, the loss of 12 Tg CO2 of annual carbon sink capacity of *P. oceanica* meadows represents 2% of the total emissions by Mediterranean countries. This is, however, a conservative estimate, as the loss of *P. oceanica* vegetation may potentially trigger CO2 emissions from the erosion of the thick organic carbon deposits accumulated over millennia in the sediment once the vegetation is lost (Fourqurean *et al.,* 2012). Conservation measures effective in reducing the current loss rate and possibly recovering some of the area lost would, therefore, contribute to climate change mitigation (Duarte *et al.,* 2013).

Ruiz *et al.,* (2017) described the effects of climate change on organisms as “a global experiment in adaptive capacity, as species tolerate, adapt, or die with changing conditions”. The term adaptation implies adjustments to long-term continuous changes in the environment such as caused by global change (Björk *et al.,* 2008). Under changing environments, genetically diverse seagrass populations may have higher chance of success than do genetically conserved ones. A study by Ehlers *et al.,* (2008) showed that genetic diversity in the temperate *Zostera marina* could help the plants to cope better with high summer temperatures (Ehlers *et al.* 2008). It has been shown that evolutionary change in a species can occur within a few generations (Rice & Emery, 2003), thus making it possible for seagrasses to cope if the changes occur at a slow enough rate to allow for adaptation (Björk *et al.,* 2008).

Despite the effects of ocean warming, eutrophication and ocean acidification on *P. oceanica* are relatively well studied, the consequences of extreme weather events, for instance, remain unclear. Extreme weather events are likely to increase and it has been observed damages caused on *P. oceanica* meadows as well as reductions in biodiversity within the ecosystem (Ruiz et al., 2017). However, how these events will progress in the 21st century is uncertain (Collins *et al.*, 2013). Climatic models do not seem favourable for *P. oceanica* persistence in the Mediterranean Sea (Giorgi, 2006). Sexual reproduction might be essential for the long-term survival of this species providing a way to resist these changing environments, by genetic mutations. However, while the normal response of organisms to warming involves northward migration (colder regions) the endemism of Posidonia in the Mediterranean and its low connectivity restricts dispersal of *P. oceanica* to other regions (Collins *et al.*, 2013).

To conclude, some climate change is inevitable, even if global greenhouse gas emissions are significantly reduced in the coming decades (Donner et al., 2005). There is, therefore, an urgent need for managers to implement and reinforce practical and immediate effective actions to ensure the persistence of *P. Oceanica* in the Mediterranean (Marshall & Johnson, 2007).

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