

Global Loss of Coastal Habitats Rates, Causes and Consequences

Carlos M. Duarte (ed.)

Offprint of Chapter

2. LOSS OF SEAGRASS MEADOWS FROM THE SPANISH COAST: RESULTS OF THE *PRADERAS* PROJECT

by

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2.1. INTRODUCTION

SEAGRASS MEADOWS CONSTITUTE the dominant ecosystem of shallow sandy seabeds in all seas, the polar zones excepted, where they fulfill important trophic and structural functions. Since the 1980s, the area of an increasing number of the planet's seagrass meadows has diminished partially or completely. Strong and intense meteorological perturbations, like hurricanes, and the spread of infections are responsible for some of this decline. However, the main cause of the loss of meadows on a global scale is attributed to perturbations of anthropogenic origin, such as coastal eutrophication, arising from the growth and development of the human population. Climate change, as reflected in the increased frequency and intensity of storms and the global warming the planet has experienced in recent decades, may contribute to accelerating seagrass meadow loss. At present, it is difficult to quantify the scale of this loss accurately because the global area occupied by seagrass meadows and the status of most of them are not known.

In 2006, the BBVA Foundation funded a three-year project as part of its Second Call for Research Proposals in Conservation Biology titled "Conservation of underwater meadows: the causes of their decreasing size and the effects on ecosystem functions", known as the *Praderas* (meadows) project for short. The ultimate aim of this project was to evaluate the conservation status of seagrass meadows, particularly those of the Spanish littoral zone, to identify the main threats to their conservation, evaluate the relationship between their conservation status and their roles in the ecosystem, and develop management guidelines for their conservation. This chapter presents the results obtained regarding the conservation status of *Posidonia oceanica* meadows, describes the principal factors that threaten them, and discusses the future of seagrasses in the light of the global change scenarios predicted for the 21st century.

◀ **Photo 2.1: Spreading rhizomes of *Posidonia oceanica* colonized by epiphytic organisms**

2.2. SEAGRASS MEADOWS: *POSIDONIA OCEANICA*

Seagrass meadows are made up of angiosperms, plants with flowers and fruits that can only complete their life cycles in the sea. Four species occur on the Spanish coast: *Posidonia oceanica*, *Cymodocea nodosa*, *Zostera marina*, and *Z. noltii*. While *C. nodosa*, *Z. marina*, and *Z. noltii* form meadows on the Mediterranean and Atlantic coasts, *P. oceanica* is endemic to the Mediterranean Sea. *P. oceanica* meadows occupy some 2,800 km² of the Spanish Mediterranean coast at depths between 0 and 45 m, and account for more than 90% of the total area of seagrass meadows along the Spanish coast.

Seagrass landscapes may be continuous or patchy but are usually extensive, composed of apparently identical shoots of a small number of genetically differentiated individuals, the clones or genets (photo 2.2). Marine angiosperms are clonal plants, whose stems, called rhizomes, spread and ramify across the sediment surface and keep neighboring shoots physiologically connected. Unlike non-clonal plants, in which new individuals arise exclusively by sexual reproduction through the germination of seeds, clonal plants produce most of their new individuals vegetatively by means of rhizomatous spread. This



Photo 2.2: Seagrass meadow of *P. oceanica*, Formentera, Balearic Islands. Declared a World Heritage Site by UNESCO.

form of growth allows marine angiosperms to occupy space with little investment in sexual reproduction. Although sexual reproduction does not contribute significantly to the increase or maintenance of shoot abundance in clonal plant populations, it is essential for initiating the formation of new clones and so is also necessary for the development and maintenance of seagrass beds.

The architectural pattern and growth forms of marine angiosperms are very similar. All species have shoots that are connected to a rhizome fragment from which roots are produced. The flowers or inflorescences sprout from the shoot (photo 2.3.A), and in most marine angiosperm species, including *P. oceanica*, they do it laterally, allowing the shoots to survive and grow after flowering. With the exception of one genus (*Halophila*), all marine angiosperm species have strap-like leaves, with basal meristems. Their great architectural uniformity contrasts with their wide range of sizes and growth rates, which are inversely scaled to species size (Duarte 1991) as a consequence of the greater cost (i.e., carbon and nutrient requirements) of producing bigger modules. *P. oceanica* is one of the planet's biggest marine angiosperms, with leaves measuring more than 1 m in length and woody rhizomes of 10 mm diameter (Duarte 1991). The

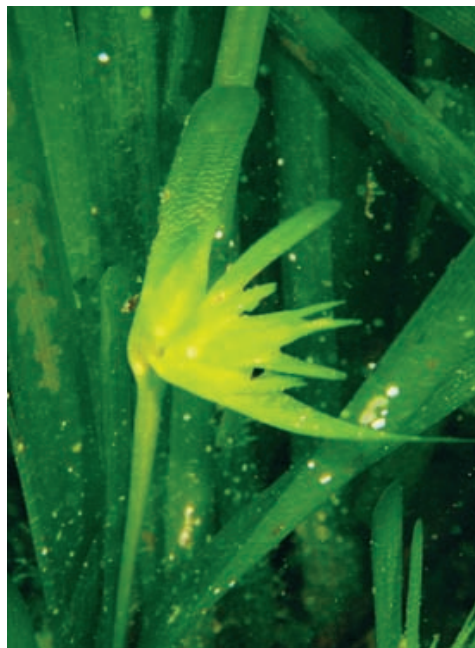


Photo 2.3.A: Inflorescence of *P. oceanica*



Photo 2.3.B: Fruits of *P. oceanica*, also known as sea olives.

horizontal rhizomes of *P. oceanica* grow between 1 and 6 cm annually and ramify once every 25 years on average (Marbà and Duarte 1998). The slow growth of *P. oceanica* rhizomes causes a slow radial expansion of its clones. *P. oceanica*, like the rest of its congeneric species growing on the southwest coast of Australia, flowers in the autumn. *P. oceanica* meadows exhibit scant flowering compared to other marine angiosperm species. Between 1957 and 2004, on average only 17% of *P. oceanica* meadows in the western Mediterranean flowered in any single year (Díaz-Almela, Marbà, and Duarte 2007a), and in the meadows that did flower an average of only 11% of shoots bore inflorescences. Due to this low flowering intensity and losses of 90% of fruit set (Díaz-Almela, pers. comm.), the rate of formation of new *P. oceanica* clones is very low, ranging from 0.004 to 0.02 m⁻² year⁻¹ in years of elevated reproduction (Díaz-Almela et al. 2008a). The low formation rate of *P. oceanica* clones is reflected in the genetic structure of seagrass meadows. The genetic study of *P. oceanica* meadows demonstrates that genetic diversity, calculated as the number of clones identified with respect to the number of shoots sampled, is fairly poor: in an area of 1,600 m² it may vary between 0.1 and 0.75 (Rozenfeld et al. 2007), depending on the meadow. Other genetic research on seagrass meadows shows that *P. oceanica* clones can reach a huge size, and it is not unusual to find genetically identical shoots at locations more than one kilometer apart (Díaz-Almela et al. 2007b). In the seagrass bed of the Es Freus–Ses Salines Marine Reserve (Ibiza–Formentera), a UNESCO World Heritage Site, identical genotypes have even been found in locations 15 km apart (Arnaud-Haond et al., in review).

P. oceanica optimizes its greater investment of resources (carbon and nutrients) by producing large modules with very long-lived shoots and clones. *P. oceanica* has the longest-living shoots of all marine angiosperms on the planet, reaching up to 60 years on average (Marbà et al. 2005). The detection, using molecular techniques, of *P. oceanica* clones spreading over dozens of meters and several kilometers of coastline, indicates that they may live for thousands of years. Based on the clonal growth rate of the species and its size, the large *P. oceanica* clone found in Formentera would be between 80,000 and 200,000 years old, making it the oldest organism on the planet (Arnaud-Haond et al., in review). Thousands-of-years-old *P. oceanica* meadows have also been identified by measuring the remains of rhizomes and roots in their deepest strata for the quantity of carbon-14 isotope remaining in the tissues (Mateo et al. 1997). Their long life allows the components of *P. oceanica* meadows to endure and spread over large areas, despite the species' low rates of clonal growth and new clone formation.



Photo 2.4: Painted comber (*Serranus scriba*) in a *P. oceanica* meadow

Due to the slow colonization and growth of *P. oceanica* clones, their meadows take centuries to form. Indeed *P. oceanica* colonization times can only be calculated using simulation models. From the rules governing the plant's clonal growth (rate of elongation of the horizontal rhizome, rate and angle of ramification, length of the section of rhizome connecting neighboring shoots), it is possible to simulate the spread of individual clones. This exercise reveals that a circular clone of *P. oceanica* would take 100 years to attain a diameter of 8 m (Sintes, Marbà, and Duarte 2006). Models simulating the development of a *P. oceanica* meadow composed of several clones growing in accordance with the species' growth rules indicate that *P. oceanica* would take 600 years to occupy 60% of the available space (Kendrick, Marbà, and Duarte 2005). The rate of seagrass meadow spread would vary throughout the colonization process. Its coverage would increase much more rapidly during the first 400 years of the meadow's life than in later years (Kendrick, Marbà, and Duarte 2005), when individuals would have to compete for space. The colonization time of *P. oceanica* is extremely long and thus its recolonization time in disturbed areas, to the extent that the loss of areas of *P. oceanica* is irrecoverable over a human timescale.

2.3. ECOLOGICAL FUNCTIONS OF *POSIDONIA OCEANICA* MEADOWS

P. oceanica meadows perform important ecological functions in the coastal area and on a global scale, over both short and long time periods. The roles of marine angiosperm meadows are described in detail in chapter 3 of this book (Dennison), and I will confine myself here to describing the long-term importance of *P. oceanica* beds, for the invaluable services they provide to the Mediterranean coastal area. *P. oceanica* meadows sustain a considerable biomass: on average, the leaf biomass of the meadow is 390 g dry weight m⁻², and the living biomass of rhizomes and roots is 1,700 g dry weight m⁻² (Duarte and Chiscano 1999). The biomass of *P. oceanica* meadows per unit area is similar to that of coral reefs, which ranks them among the marine plant communities that sustain the greatest biomass by area on the planet (Duarte and Chiscano 1999). *P. oceanica* meadows have a three-dimensional structure, forming terraces, channels and barrier reefs that can reach a height of 3-4 m (photo 2.5). *P. oceanica* meadows accordingly modify the seabed topography. This three-dimensional structure arises from the growth of vertical rhizomes and from the fact that spread rates are similar in an upward and sideways direction (Kendrick, Marbà, and Duarte 2005) and that meadow rhizomes decompose only slowly.

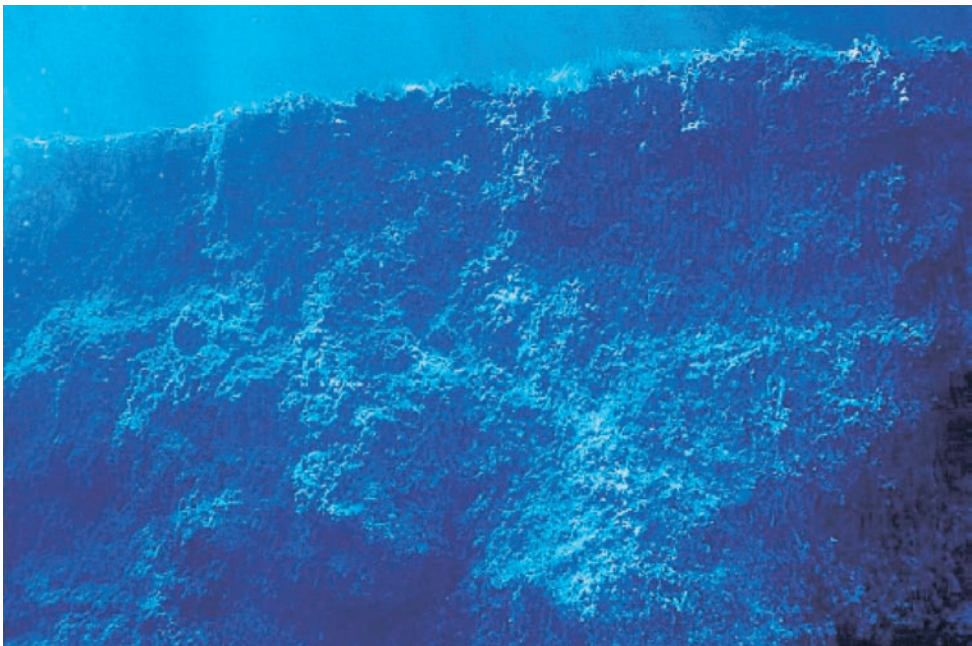


Photo 2.5: Thousand-year-old *P. oceanica* reef, Formentera, Balearic Islands

P. oceanica meadows are highly productive systems, fixing 400 g C m^{-2} annually (Barrón et al. 2006). Although most (80%) of the fixed carbon is respired by the community itself, the net annual production of seagrass meadows is about 72 g C m^{-2} , representing a net carbon fixation 60 times that measured in coastal marine sediments devoid of vegetation (Barrón et al. 2006). The high productivity of seagrass meadows alters CO_2 and O_2 flow rates in the water column. For example, during daytime, the partial pressure of CO_2 at the sea-atmosphere interface of Palma Bay (Balearic Islands) is lower in areas with seabeds colonized by seagrass meadows than in areas with seabeds without vegetation (Gazeau et al. 2005).

A large part (42%-62%) of the net carbon fixed in *P. oceanica* meadows is retained and buried there (Larkum, Orth, and Duarte 2006; photo 2.5). Considering that they occupy an area of $50,000 \text{ km}^2$ in the Mediterranean Sea, these meadows bury some 2 Tg C year^{-1} . There are no estimates of the amount of carbon sequestered in other Mediterranean coastal and oceanic habitats, so it is hard to get an accurate handle on the importance of seagrass meadows as carbon sinks on a basin-wide scale. It must be substantial, however, considering that almost half the carbon sequestered globally in the oceans is buried in coastal plant habitats, and that seagrass species together account for 15% of



Photo 2.6: *P. oceanica* detritus accumulated on a beach

the total carbon buried in the ocean (Duarte, Middelburg, and Caraco 2005). Hence *P. oceanica* meadows absorb and bury a portion of atmospheric CO₂, helping with the regulation of the planet's climate.

P. oceanica meadows prevent coastal erosion. The relief and foliar canopy of the meadows reduce current velocity and, in shallow beds, help calm the swell (Larkum, Orth, and Duarte 2006). *P. oceanica* barrier reefs, located several meters from the shore, act as a break so the waves reaching the beach are of low intensity. The foliar canopy stimulates the deposition of particles suspended in the water through a number of mechanisms. The reduction of water current speed near the foliar canopy enables some suspended particles to be sedimented. Seagrass leaves are surfaces that interrupt the trajectories of suspended particles, which consequently end up deposited on top of the sediments (Hendriks et al. 2008). Part of the fauna associated with the meadow, particularly filtering organisms that live on the plant's leaves, actively trap suspended particles. Seagrass meadows retain the deposited particles and sediments that they colonize because the canopy prevents their resuspension, and because they are fixed by the network of rhizomes and roots that form the meadow's rhizosphere, to a depth of several meters. The effect of seagrass meadows on particle deposition and retention also increases the settling rate of larvae and propagules in this ecosystem. Seagrass meadows, as such, also help to increase marine biodiversity.

Part of a meadow's net annual production is exported to adjacent systems, among which are emerged beaches and dune systems. After heavy storms in the autumn, when *P. oceanica* renews its leaves, leaf litter and rhizome fragments pile up on the shore, forming what are known as "banquettes" (photo 2.6). On beaches adjacent to extensive seagrass meadows, these deposits can comprise up to 400 kg dry weight m⁻¹ of coastline and amount to 50% of the material produced annually by the adjacent seagrass meadow (Larkum, Orth, and Duarte 2006). This biomass, produced in the meadow, supplies significant quantities of sediment and nutrients to the beach and associated dune system, particularly in regions where sediment production is of biogenic origin, as in the Balearic Islands. Considering that these islands have 100 km of beaches, seagrass meadows provide their sand dune systems with some 100,000 tonnes of biogenic material annually. Furthermore, 10% by weight of the biogenic material deposited on beaches is calcium carbonate originating from the structures of the epiphytic organisms that colonize the leaves and rhizomes of *P. oceanica*, plus the calcium carbonate precipitated on the leaves (Larkum, Orth, and Duarte 2006; photo 2.7). This suggests that *P. oceanica* meadows



Photo 2.7: *P. oceanica* leaves colonized by epiphytic organisms with calcium carbonate structures

may provide a substantial amount of the sand on the beaches. Moreover, this *P. oceanica* detritus covers the sand of the emerged beach, protecting it from erosion during heavy storms. Some of the *P. oceanica* detritus that accumulates on the shore stays in the water, increasing its viscosity and, thereby, reducing the intensity of the swell and also the risk of coastline erosion.

P. oceanica meadows are accordingly a key ecosystem for the functioning of and provision of services to the coastal zone and the Mediterranean basin. Prominent among these services are the burial of atmospheric CO₂ and maintenance of beaches, the latter being a vital element for the tourist industry. Conserving these functions and services depends on successfully conserving seagrass meadows.

2.4. THE STATE OF SPANISH COASTAL SEAGRASS MEADOWS: HOW BIG IS THE DECLINE?

Seagrass meadows are extremely vulnerable. Proof is that, since the 1980s, 102 of a total of 176 *P. oceanica* meadows reported in the Mediterranean basin have suffered a decline in the expanse and/or abundance of shoots. More than 50%

of the area of 17% of *P. oceanica* meadows has been lost over this period (Díaz-Almela, unpublished results).

The decline of *P. oceanica* meadows tends to be a gradual process. The cause of shrinkage is a progressive loss of shoots, so to prevent losses on a major scale, which are often irretrievable over human timescales, it is crucial to detect the problem at its initial stages. To achieve this means monitoring the state of seagrass meadows, using indicators that can quantify their current status and allow declines to be detected in time. The decline of long-lived seagrass meadows, like those of *P. oceanica*, can be detected early (on a yearly scale) by examining the demographic dynamics of their shoots in permanent plots (Short and Duarte 2001). An annual census of shoots in plots permanently installed in seagrass meadows (photo 2.8) allows to estimate the survival, birth, and death rates of a given population, and thereby its net growth rate, equivalent to the difference between birth and death rates. The net growth rate of the population indicates whether the meadow is declining (negative net growth), growing (positive net growth), or stable (net growth = 0).

Since the year 2000, the annual demographic balance has been quantified in 46 *P. oceanica* meadows growing at depths of between 5 and 25 m, 40 of them along the Spanish coast (figure 2.1). The density of their shoots at the beginning of the

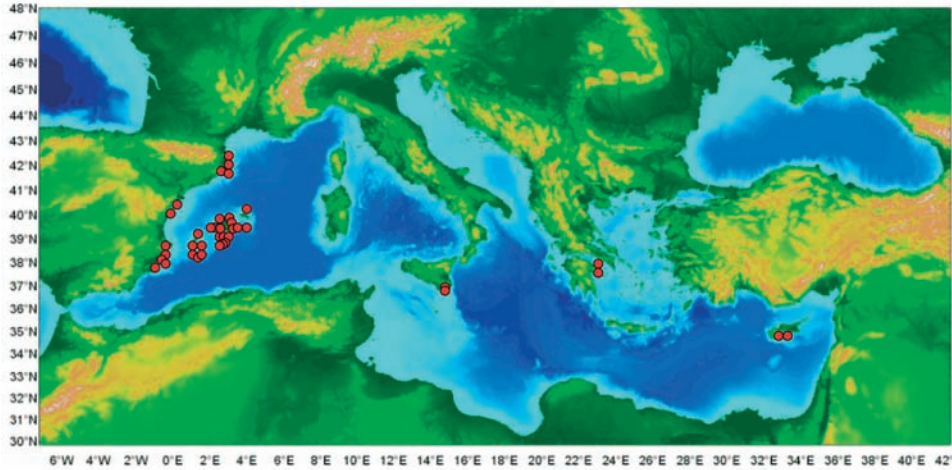


Photo 2.8.A: Permanent plots established in a *P. oceanica* seagrass meadow to evaluate the demographic balance of shoots



Photo 2.8.B: Detail of tagged shoots in a *P. oceanica* test plot

Figure 2.1: Distribution of Mediterranean *P. oceanica* meadows whose demographic status has been evaluated over the past seven years



Source: <http://www.chesapeakebay.net/info/wqcriteriapv/modeling.cfm>.

study varied between 60 and 1,725 shoots m^{-2} . In the last seven years, 67% of the meadows studied have suffered net losses of shoot density, exceeding 20% in 47% of cases. These losses were observed in seagrass meadows situated not only in coastal areas experiencing strong anthropogenic pressure, but also in protected areas (figure 2.2) like the Cabrera Archipelago National Park (Balearic

Figure 2.2: Density of shoots in the seagrass meadow of Es Castell, at a depth of 15 m, Cabrera Archipelago National Park, since the year 2000

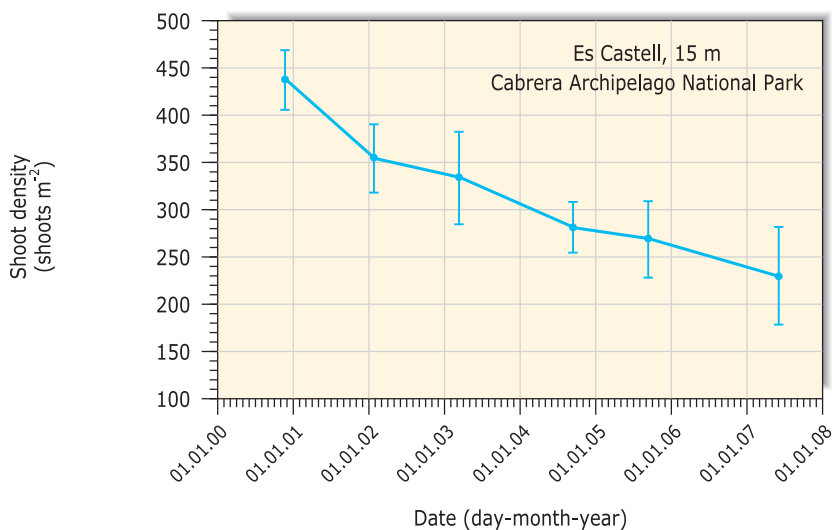




Photo 2.9: *P. oceanica* meadow growing on the coastal sea floor along the north coast of Ibiza, Balearic Islands

Islands), where measures to conserve the marine and terrestrial ecosystems have been in force since 1991. During this period, *P. oceanica* meadows experienced shoot mortality rates varying between less than 1% year⁻¹ (e.g., Es Castell 20 m, Cabrera) and 84% year⁻¹ (Pollença Bay, Mallorca), equivalent to absolute shoot mortality rates between 4 and 320 dead shoots m⁻² year⁻¹ (e.g., Es Castell 10 m, Cabrera and La Fossa, Alicante respectively). The mean annual mortality rate in seagrass meadows during the current decade stands at 11%, equivalent to 46 dead shoots m⁻² year⁻¹. The observed mortality rates indicate that *P. oceanica* shoot half-life (i.e., the age to which 50% of a population's shoots survive) is greater than six years in most meadows, and may even reach 20 years in some sites like Formentera. On the other hand, the annual birth rate of shoots since 2000 has varied from less than 1% (e.g., Es Castell 20 m, Cabrera) to 48% (Pollença Bay, Mallorca), resulting in absolute birth rates of less than 2 new shoots m⁻² year⁻¹ (e.g., Es Castell 15 m, Cabrera) and 200 new shoots m⁻² year⁻¹ (Santa María Bay 7 m, Cabrera). In 50% of the seagrass meadows studied, the annual birth rate of shoots during the current decade has been lower than 6% or 25 new shoots m⁻² year⁻¹. These low shoot birth rates indicate that most *P. oceanica* populations would take more than a decade to renew their shoots, and more than a century in the case of some off the island of Cabrera. Over the past ten

years, shoot birth rates have lagged mortality rates in most seagrass meadows. Their annual net growth since 2000 has varied between -43% (Pollença Bay, Mallorca) and 46% (e.g., Es Castell 10 m, Cabrera), though most meadows have recorded under -5% annually, equivalent to a net loss of 12 shoots $\text{m}^{-2} \text{year}^{-1}$. Net loss rates also suggest that, if the current environmental conditions persist, seagrass meadows that are in decline will see their shoot density half in less than a decade. In fact, since 2000, some (Pollença Bay, Mallorca; La Fossa, Alicante) have already lost 40% of their shoot density.

These results show that most Spanish coastal seagrass meadows have been declining over the present decade. The rate of decline of *P. oceanica* meadows is currently 5% per year, slightly lower than that of corals—the marine ecosystem undergoing the fastest decline—and higher than the global loss rate of marshes and mangrove forests (Duarte et al. 2008). This places *P. oceanica* meadows among the most threatened marine ecosystems on the planet. The general decline observed recently in Spanish coastal seagrass meadows may not have begun so recently, however. A retrospective demographic analysis of 27 *P. oceanica* meadows on the Spanish coast showed that 80% of them were already declining between 1967 and 1992 (Marbà et al. 1996). And the scale of their decline in the present decade is similar to in the past. This suggests that, over the last four decades, either (1) the same pressures have continued bearing down on seagrass meadows, or (2) a succession of different pressures have brought about a comparable rate of decline.

2.5. CAUSES OF THE DECLINE IN MEDITERRANEAN SEAGRASS MEADOWS

The current decline of seagrass meadows is due to multiple pressures, principally of anthropogenic origin, that act, frequently simultaneously, on the coastal zone. Most of these pressures also set in train synergistic processes that accelerate the decline when they interact (Duarte 1995). Eutrophication, disturbance of sedimentary dynamics, the mechanical destruction of the coastal area, climatic changes such as global warming, and biological perturbations are the main pressures threatening Spanish coastal seagrass meadows.

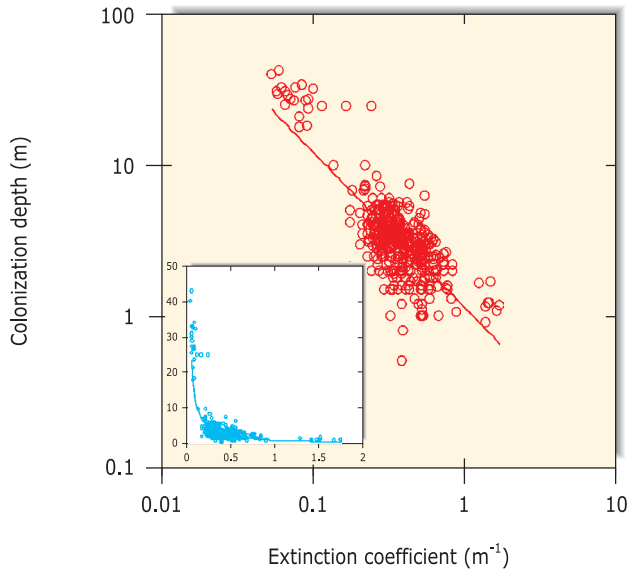
2.5.1. Eutrophication

The main cause of seagrass meadow decline is eutrophication of the coastal area. This originates from the discharges of agricultural nutrients and organ-

ic matter, waste water from the human population, and aquaculture. Dumping nutrients and organic matter into the sea degrades water quality, principally reducing the amount of light reaching the seagrass meadows. Their survival, like that of all aquatic photosynthetic organisms, is conditioned by the amount of light penetrating the water column. Seagrass meadows grow rooted in the sediment, and have their photosynthetic structures (leaves) on the seabed. They thus exhibit the greatest light requirements of all marine photosynthetic organisms (Duarte 1995). The leaves of marine angiosperms absorb three times as much light as do phytoplankton, but the light they absorb per unit weight and their photosynthetic capacity are considerably less (Duarte 1995; Enríquez et al. 1996). In addition, they require far more light to grow than the phytoplankton, because of the high respiration rate needed to maintain their non-photosynthetic parts (roots and rhizomes) (Duarte 1995). Seagrass meadows require environments that receive at least 11% of the surface irradiation in order to survive, while other benthic marine photosynthetic organisms, like corals and macroalgae, can grow on seabeds that receive only 0.02% or 0.0005% respectively (Gattuso et al. 2006). The position of seagrass meadows in the water column and their high demand for light make them extremely vulnerable to any deterioration of water transparency (Duarte 1995). Nutrient supply stimulates the proliferation of phytoplankton in the water column and of macroalgae on the seagrass meadow's foliar canopy. The proliferation of both groups of organisms reduces the amount of light that the seagrass meadows receive. Seagrass meadows are most vulnerable to increased water turbidity at their depth limit, and this close relationship allows us to develop predictive models for their lower depth limit based on rates of light extinction in the water column (Duarte et al. 2007; figure 2.3), and therefore to predict the magnitude of meadow depletion as water transparency diminishes.

Eutrophication also causes excessive sediment enrichment by nutrients and organic matter. *P. oceanica* meadows are very sensitive to deteriorating sediment quality, and their decline accelerates when the amounts of organic matter and phosphorus reaching the sediment exceed 1-2 g dry weight m⁻² d⁻¹ and 0.04 g P m⁻² d⁻¹ respectively (Díaz-Almela et al. 2008b). The excess nutrients and organic matter in the sediment stimulate bacterial activity, and consequently increase anoxia and the production and concentration of hydrogen sulfide. When the concentration of hydrogen sulfide in the sediment is high and that of oxygen in the plant is low, the hydrogen sulfide in the interstitial water penetrates the seagrass tissues and damages their meristems, thereby reducing their growth and survival (Borum et al. 2005). Hydrogen sulfide

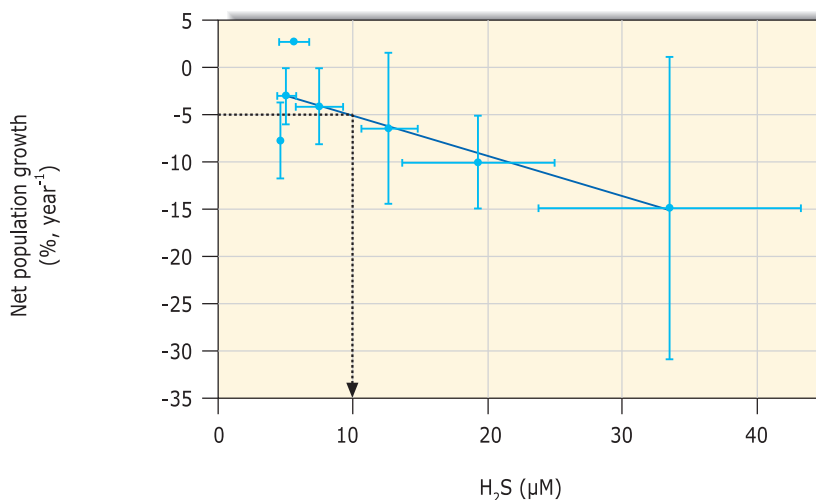
Figure 2.3: Relationship between maximum colonization depth of seagrass meadows of different species and the light extinction coefficient



Source: Duarte et al. 2007.

toxicity may be attenuated by the presence of labile iron in the sediment, which can remove hydrogen sulfide from the interstitial water, precipitating it in the form of iron sulfides. Sediments in which little iron is available—a characteristic of the carbonate-rich sediments (Bernier 1984) common throughout the Mediterranean—have a very limited capacity to attenuate the toxicity of hydrogen sulfide, making seagrasses more vulnerable to their organic enrichment. In the Balearic Islands, where the labile iron content of sediments is extremely low (Holmer, Duarte, and Marbà 2003), the state of seagrass meadows is conditioned by the supply of iron from external sources. The risk of decline in *P. oceanica* meadows increases when they receive less than $43 \text{ mg Fe m}^{-2} \text{ d}^{-1}$ (Marbà et al. 2008). Moreover, *P. oceanica* meadows are acutely sensitive to hydrogen sulfide. While many species of marine angiosperms can grow and survive in sediments with hydrogen sulfide concentrations up to $100 \text{ } \mu\text{M}$ (Terrados et al. 1999), *P. oceanica* meadows decline more rapidly when its concentration in the interstitial water is greater than $10 \text{ } \mu\text{M}$ (Calleja, Marbà, and Duarte 2007; figure 2.4). Once sediments have become contaminated it is very difficult for them to recover, and *P. oceanica* meadows continue to decline for years after the input of organic matter has ceased (Delgado et al. 1999).

Figure 2.4: Relationship between the net growth rate of the population of *P. oceanica* shoots in seagrass meadows and the concentration of hydrogen sulfide in the sediment. Negative net population growth rates represent rates of decline. The dotted line indicates the threshold concentration of hydrogen sulfide above which a meadow's decline is significant.



Source: Calleja, Marbà, and Duarte 2007.

2.5.2. Alteration of coastal sediment balance and mechanical perturbations

The disruption of the sediment balance in the coastal area increases the mortality of seagrass shoots. *P. oceanica* shoots have their meristems on the sediment surface, and their survival depends on maintaining that position throughout their life. *P. oceanica* meadows can survive burial rates of up to 4-5 cm year⁻¹, on account of the growth of their vertical rhizomes (Manzanera, Pérez, and Romero 1998). When sediment deposition exceeds this threshold, meadow decline accelerates, and depositions of 14 cm produce 100% shoot mortality. Sediment erosion is another cause of greater shoot mortality.

The transformation of our coastline due to the runaway construction of buildings and seafronts and the damming of rivers diminishes sediment supply to seagrass meadows. In the last 50 years, the amount of sediment reaching the Mediterranean coast has fallen by 90%, and a large part of the area is suffering erosion (Benoit and Comeau 2005). Coastal constructions like breakwaters and ports destroy the adjoining marine communities and can alter local sediment dynamics, increasing erosion and deposition of sediments in some zones. Dredging works on the seabed near seagrass meadows can easily destroy areas of meadow by directly pulling up fragments or eroding or bury-

ing them. These impacts principally affect the upper limit of seagrass meadows. Indeed recent studies show that some *P. oceanica* meadows have retreated 25 meters in 20 years (Besterrechea et al., unpublished results).

Trawling is an important cause of large-scale seagrass meadow destruction, with deep communities the worst affected. Trawling with nets above meadows tears out the shoots and rhizomes at rates between 100,000 and 360,000 per hour⁻¹ (González-Correa et al. 2005), while at the same time resuspending sediment and increasing water turbidity. The slow seagrass meadow recolonization rate means that the impact of trawling can persist for decades (González-Correa et al. 2005).

In coastal areas that receive large numbers of visitors, the anchoring of pleasure craft above seagrass meadows causes a significant reduction in shoot density. It is estimated that an average of 34 shoots anchor⁻¹ (Francour et al. 1999) are torn up during an anchoring cycle (lock-in and retrieval).

2.5.3. Rising sea temperature

Recent studies indicate that *P. oceanica* meadows are vulnerable to Mediterranean warming. Surface water temperature increased by 0.04°C year⁻¹ between 1980 and 2006 (Díaz-Almela et al. 2007a), and the highest value recorded was in summer 2003. Global warming affects biological processes like reproduction and may alter the stability of plant communities (e.g., Parmesan and Yohe 2003).

In the last 40 years, it has been observed that the number of *P. oceanica* meadows that flower each year and their flowering intensity (the fraction of a meadow's shoots that flower) vary interannually, with reproductive peaks every 9-11 years (Díaz-Almela, Marbà, and Duarte 2007a). Temporal fluctuations in seagrass meadow reproduction are coupled with sea temperature variations, such that reproduction increases as the temperature climbs. In autumn 2003, one month after the warmest recorded surface temperature in the Mediterranean of the last four decades, there was an episode of mass flowering throughout the western Mediterranean that extended to over 90% of seagrass meadows, representing a flowering intensity twice as high on average as during earlier reproduction peaks (Díaz-Almela, Marbà, and Duarte 2007a; photos 2.10 and 2.11). The relation between increased flowering of seagrass meadows and Mediterranean warming might reflect the plant's response to thermal stress, as occurs in some terrestrial plant communities (e.g., Peñuelas et al. 2002).



Photo 2.10: Seagrass meadow with inflorescences



Photo 2.11: Raft of *P. oceanica* fruits floating on the sea after the mass flowering episode of 2003

The mortality rate of *P. oceanica* meadows has varied interannually in the last seven years, with the highest shoot mortality recorded after very hot summers (Díaz-Almela et al., in review). This annual variability is related to sea water temperature, whereby the mortality rate rises 3% per year⁻¹ for each degree of increase in maximum annual temperature (Marbà et al., unpublished results). These observations also suggest that *P. oceanica* meadows may decline more rapidly when Mediterranean warming produces temperatures in excess of 28°C, since above this threshold the birth rate through clonal growth and sexual reproduction (Díaz-Almela et al., in review) is insufficient to compensate for the increased death rate (Marbà et al., unpublished results).

The greater mortality of *P. oceanica* meadows as a result of the warming occurring in the Mediterranean Sea may not only reflect the effect of temperature on the plant's physiology. The rise in sea temperature may stimulate other biological processes in the ecosystem, such as community respiration and microbial activity in sediments, which, acting synergistically, could hasten their decline.

2.5.4. Biological invasions

An increased number of marine species are growing beyond their original biogeographic distribution limits (Williams 2007). Some introduced species settle and behave as invasive species, causing a deterioration of native habitats. Maritime traffic, aquaculture, and the opening of sea-to-sea canals like the Suez Canal are the main vectors of species introduction (e.g., Gollasch 2005). The Mediterranean has the greatest number of exotic species of all European seas and the fastest rate of introductions in the whole of Europe. It is estimated to have 662 exotic taxa, of which 325 can be considered established, while the rate of introduction of new species has been reckoned at one every six weeks since the year 1950. This rate, moreover, has been accelerating since the late 1990s, mainly as a result of increased introductions of benthic macroalgal species (Gollasch 2005). Currently, the Mediterranean is home to around 100 species of introduced macroalgae, six of which live in seagrass meadows (Williams 2007), and 10% of which exhibit invasive behavior (Ballesteros, Cebrián, and Alcoverro 2007).

The impact of biological invasions on seagrass meadow stability has been examined for some species of invasive macroalgae. The best-studied of these exotic species are the macroalgae *Caulerpa taxifolia* and *C. racemosa* (pho-

tos 2.12 and 2.13). *C. taxifolia* was introduced into the Mediterranean from the Monaco aquarium in 1984, while *C. racemosa* var. *turbinata-uvifera*, originally from the Red Sea, was introduced in the 1920s, and *C. racemosa* var. *cylindracea*, which comes from Australia, was introduced in the 1990s. Both species are clonal green algae, can grow on *P. oceanica* rhizomes and sediment, and are between six and ten times smaller than its leaves. *Caulerpa* species accordingly find it hard to compete for light with *P. oceanica* and do not seem to penetrate dense and healthy seagrass meadows. However, these species grow in organic matter-rich sediments with high hydrogen sulfide concentrations and stimulate the rate of sulfate reduction in the colonized sediment. The proliferation of *Caulerpa* species in seagrass meadows could degrade sediment quality (Holmer et al., in press) and, in conjunction with other disruptions (e.g., eutrophication, Chisholm et al. 1997), accelerate seagrass decline.

In the last decade, the red macroalga *Lophocladia lallemandii*, which originates from the Indo-Pacific and entered the Mediterranean Sea through the Suez Canal, has rapidly invaded western Mediterranean seagrass meadows. Its development is seasonal, and it grows forming patches on the leaves and rhizomes of *P. oceanica* (photo 2.14). The proliferation of *L. lallemandii* in seagrass meadows increases shoot mortality and halves the density and size of surviving *P. oceanica* shoots in comparison to non-invaded areas (Ballesteros, Cebrián, and Alcoverro 2007). The amount of light that *P. oceanica* receives during the invasion of *L. lallemandii* is probably insufficient to sustain its metabolic balance.

The red macroalga *Acrothamnion preissii*, a species native to the Indo-Pacific region and observed in the Mediterranean since 1969 (Williams 2007), is another invader of *P. oceanica* meadows. Invasion by this species does not seem to alter meadow stability, but it displaces most of the epiphytic macroalgae on plant rhizomes, reducing species diversity and habitat complexity (Piazzi and Cinelli 2003).

2.5.5. Pathogenic organisms

Although microorganisms abound in the ocean (e.g., 10^6 bacteria cells ml^{-1} and 10^7 virus particles ml^{-1} ; Fuhrman 1999; Marie et al. 1999; Azam and Worden 2004), little information exists about their role as agents potentially pathogenic to marine plants. However, there is evidence of massive seagrass meadow mortality caused by pathogenic marine organisms. The decline of *Zostera*

Photo 2.12: The alga *Caulerpa taxifolia* growing in a *P. oceanica* meadow



Photo 2.13: *Caulerpa racemosa* growing on a community of native macroalgae in Portals Vells, Mallorca



Photo 2.14: Sponge (*Sarcotragus foetidus*) between a *Posidonia oceanica* bed and the invasive alga *Lophocladia lallemandi*. Cala Galiota, Cabrera, Balearic Islands.



marina and *Thalassia testudinum* meadows respectively along the Atlantic coast (1930s) and in Florida Bay (1980s) is associated with infection by marine protists of the genus *Labyrinthula* (Muehlstein et al. 1988; Robblee et al. 1991), when these act in combination with other environmental factors causing meadow deterioration (e.g., temperature increase, hypoxia, raised concentration of hydrogen sulfide in the sediment).

Recent studies have shown the presence in *P. oceanica* tissues of bacteria of the genera *Vibrio*, *Marinomonas*, and *Pseudoalteromonas*, and of the protist *Labyrinthula* (Marco-Noales et al. 2006; Vergeer and Den Hartog 1994). *Pseudoalteromonas* spp. bacteria are more abundant in seagrass meadows with high shoot mortality rates, which suggests that they may be contributing to *P. oceanica*'s decline (Marco-Noales et al. 2006). *Labyrinthula* is a widely distributed organism in Spanish coastal seagrass meadows and is observed in more than 70% of those bordering the Balearic coast (18 meadows examined in total, Garcias-Bonet et al. 2008). Experiments infecting healthy *P. oceanica* shoots with different *Labyrinthula* strains suggest that the virulence of this protist varies from one strain to another. However, the majority (71%) of those tested are capable of producing lesions in *P. oceanica*'s leaves (Garcias-Bonet et al. 2008). Although the presence of pathogenic organisms has not been shown to increase seagrass meadow mortality in the Mediterranean, they could increase the risk of ecosystem decline under conditions of environmental deterioration.

2.6. THE FUTURE OF SEAGRASS MEADOWS

The general decline affecting Mediterranean seagrass meadows is the result of isolated impacts that are hard to pin down, deriving from human population growth along the coast and on a global scale. Currently 40% of the Mediterranean coastline is built-up area. In 2000, it had more than 400 million residents, 70 million of them living in cities of over 100,000 inhabitants, and visitor numbers exceeding 200 million (Benoit and Comeau 2005). Predictions of human population growth suggest that by 2025, 50% of the coast will be built-up area, Mediterranean coastal cities with more than 100,000 inhabitants will be home to 90 million residents, and the coastal strip will receive more than 300 million tourists (Benoit and Comeau 2005). Not only that, aquacultural production in the Mediterranean is expected to double in the next 25 years, maritime freight traffic to almost quadruple, and passenger traffic to likewise double (Benoit and Comeau 2005). Assuming this scale of growth of



Photo 2.15: *P. oceanica* meadow near Tabarca Island, Alicante, Spain

human activity, the risk of deterioration of the coastal area, as exemplified by problems of eutrophication, erosion, proliferation of invasive species, and seabed destruction, and, therefore, the risk of seagrass meadow decline, can only increase in the years to come.

The climate change augured for the 21st century, arising from the increased concentration of greenhouse gases in the atmosphere, is a further threat to seagrass meadow conservation. The climate change scenarios managed by the IPCC point to an increase in sea level of between 0.09 and 0.88 m between 1990 and 2100 and an increase of 4°C in the temperature of the Mediterranean (IPPC 2001). Such a rise in sea level would cause coastal erosion and, therefore, hasten the decline of seagrass meadows' upper limit. According to the predictions of climatic warming and *P. oceanica*'s sensitivity to sea temperature increases, the seagrass meadow mortality rate could be three times its current level by 2100. Although the increased temperature would also stimulate sexual reproduction, and thus the formation of new clones, this would not be enough to offset death losses of meadows, so the rate of decline could well accelerate.

Reversing the trend of decline in seagrass meadows and conserving them in future will call for the implementation of management measures to minimize

the deterioration of coastal areas. We currently have a European, national, and regional legal framework that, effectively implemented, would facilitate conservation of *P. oceanica* meadows. The European Union, through Agenda 21, requires member states to protect up to 12.2% of their entire territory, which in Mediterranean countries with long coastlines is largely made up of *P. oceanica* meadows, and its fishing regulations prohibit trawling on seagrass meadows (Regulation (EC) 1626/94). Likewise, the EU Habitat Directive (Council Directive 92/43 of May 21, 1992) sets forth measures to guarantee biodiversity through the conservation of natural habitats, including seagrass meadows. In Spain, some autonomous communities, such as Valencia and Catalonia, also have regulations in place to protect seagrass meadows, and the Law of Coasts regulates the protection and use of the coastal area. However, measures to control the dumping of urban, industrial, and aquacultural waste in the Mediterranean Sea have still to be fully enforced: in 2002, 60% of urban waste water was still being dumped into the sea untreated, particularly in its south and eastern reaches (Benoit and Comeau 2005). Since 1997, the Mediterranean Action Plan under the direction of UNEP, with 16 countries affiliated, has included a protocol on pollution from land-based sources and a strategic plan to combat it. The European Union's Water Framework Directive, in force since 2000, defines a set of ambitious objectives to protect the quality of European water bodies, including those of the coasts. The United Nations Framework Convention on Climate Change, known as the Kyoto Protocol, has the goal of stabilizing greenhouse gas emissions at a level that impedes anthropogenic interference in the climate system.

But the conservation of seagrass meadows, their functions, and the services they provide does not just depend on an effective legal framework. It also requires advances in scientific knowledge, the development of technologies to reverse the decline and mitigate impacts, more social awareness around environmental issues, and coordinated action on a global scale. Only with the collaboration of science, technology, the legislator and society at large will it be possible to preserve these millennia-old and immensely valuable Mediterranean ecosystems.

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