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Modelling leaf dynamics and assessing the carbon storage capacity of a *Posidonia oceanica*'s meadow

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To Gabriele and my family

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Abstract

Many human activities are regularly carried out in marine environments, to take advantage of the several benefits provided by these ecosystems. Consequently the management of marine resources should be achieved within a comprehensive governance. Seagrass meadows play an important ecological role in marine environment and *Posidonia oceanica* is the dominant seagrass in the Mediterranean Sea. This species forms large meadows providing ecosystem service with great value such us protection against coastal erosion, contribution to fishery supporting food webs and high biodiversity, absorption of pollutants by filtrating water, nursery for species of commercial interest. In addition *P. oceanica* is characterised by its capacity to absorb and store considerable amount of carbon in its carbon rich-sediments. Despite their protection, meadows of P. oceanica are regressing at fast rates, which represents the loss of an important carbon sink. Modelling seagrasses dynamics can help to formulate the necessary protocols to ensure the accountability of mitigation actions involving the conservation and restoration of *P. oceanica* meadows. The work presents a stochastic non-linear model, spatially explicit with seasonal dynamics, consisting of a cellular automaton describing the main processes involved in the growth of a *Posidonia oceanica* meadow. In particular, the model simulates the seasonal dynamics of expansion, longevity and senescence of leaves and the joint effects of multiple stressors acting on these dynamics. The purpose of the study is to develop modelling approaches to be used as efficient tools to assess factors regulating and affecting growth dynamics of P. oceanica to predict the approach of the system to critical situations. Its goal is thus to provide a valuable support to the definition of management actions on the coast. More in detail, the basic model implemented is a spatially explicit cellular automaton with annual dynamics (52 weeks). The base is an I × J matrix where each cell contains an automaton that simulates a *Posidonia oceanica* bundle with a maximum number of 7 leaves. The development and the seasonal dynamics of each leaf is described, according to a law of growth determined by the following drivers:

- light absorption, depending on the season and the depth at which the meadow is located;
- shadowing neighbouring beams, the size of which depends on the (i,j) position of each single bundle in the matrix;

- availability of nutrients, increasing growth to a certain threshold;
- presence of epibionta, calculated as percentage of leaf surface, varying according to the leaf length and age, as well as to the availability of nutrients.

In the model the main factor reducing biomass is the death of leaves occurring at an average age of 46 weeks. The model returns values of biomass produced by meadow. Then it is possible to calculate the carbon value stored by the meadow as proportional to its total biomass, based on the percentages suitably estimated in the literature: the purpose is to assign an economic value to the *P. oceanica* carbon storage. The model is running under simulation scenarios in order to highlight how biotic and abiotic stressors can affect the conservation state of the simulated meadow. For each scenario the model gives different value of biomass production and different amounts of stored carbon. The results of the simulations, compared with values from the literature, shows that the model can reproduce a realistic pattern of the seasonal growth and production dynamics of a *Posidonia oceanica* meadow. The final aim is using model results to estimate the loss or benefit in economic terms, associated with anthropic interventions and specific management of coastal systems. Once model uncertainties are defined and the model is validated, it will provide an essential tool to explore the effects of management choices on *Posidonia oceanica* ecosystem.

Contents

Chapter 1

Introduction

This study investigates the use of dynamical system modelling in describing and analysing the dynamical characteristics of *Posidonia oceanica* habitat, the dominant seagrass habitat in the Mediterranean Sea and the most important coastal shallow water habitat in the region. The main aims of this research study are:

- to integrate knowledge about *P. oceanica* habitat and synthesise current data about seagrass community structure into a working model for a generic *P. oceanica* meadow;
- to describe and test the preliminary model for the seagrass *P. oceanica* and to consider the influence of changes in exogenous variables such as light and nutrient availability in scenario analysis.

Posidonia oceanica (L.) Delile is an endemic seagrass in the Mediterranean Sea, where it covers about 50.000 km^2 from near the surface down to 40 m depth [14], [198]. It assembles extended meadows giving rise to key ecosystems for the coastal strip [112]. The ecological community supported by *Posidonia oceanica* modulates important biogeochemical processes like oxygen and carbon cycles [53] and plays an important role in the nutrient budget of the coastal marine ecosystems [180]. Moreover this seagrass stabilizes the processes of sedimentation and coastal erosion ensuring the conservation of geomorphology balance in the coast. With its high rates of primary production, *Posidonia oceanica* supports a diversity of trophic interactions [235] providing a preferential habitat and nursery areas for many fish and invertebrate species [141]. The *Posidonia oceanica* habitat offers varied and highly valuable ecosystem services, so it is essential to preserve its resilience, the ability to tolerate perturbations without suffering drastic changes in order to protect the coastal environment. In the last years the *Posidonia oceanica*'s meadows have experienced a rapid and worrying decline due to the runaway increase of coastal infrastructures and the consequent intensification of human impact. The most widely factor is the anthropogenic nutrient enrichment [120], [55], [51]: nutrient loading stimulates an overgrowth of algae and epiphytes covering *Posidonia oceanica*'s leaves, limiting the quantity of light available to photosynthetic processes. In this work a dynamical system approach is identified to help addressing and understanding the complex dynamics between anthropogenic stressors and natural systems in the coastal zone. The information needed by resource managers to exercise adequate environmental stewardship is not available through data monitoring alone. The capacity to anticipate the behaviour of the ecosystem is greatly advantageous to policy-makers dealing with such complex systems. At present it is commonly recognized the importance of mathematical models in predicting the behaviour of a natural ecosystem and in exploring future policy measures for the management of this ecosystems. The aim of our research is to develop a specific model for the ecosystem of interest and its population-level properties. This is here strongly justified by the management application of this study. In order to develop tools useful to predict whole ecosystem dynamics it is appropriate to use scales coarser than the individual scale of the plant, which is more appropriate for evolutionary and eco-physiological studies. In this research, we construct a mathematical model able to describe the main growth processes of a *Posidonia oceanica* meadow; the model includes the seasonal dynamics of the expansion, longevity and senescence phases of its leaves. The basic model, turned into a numerical one via a Fortran 90 code, is a spatially explicit cellular model with annual dynamics (52 weeks): the base is a matrix, where each cell matches an automaton simulating a *Posidonia oceanica*'s bundle. The model strength is the possibility to simulate different natural scenarios of human-environment interaction, then making quantitative evaluation of the results obtained so, in order to predict the behaviour of a *P. oceanica* meadow undergoing different stressors such as pollution. The purpose is develop and apply modelling approaches to be used as efficient tools to achieve a better understanding of the functional state of *Posidonia oceanica*'s meadows and consequently provide a valiant support to refining management actions on the coastal band. The final goal will be evidencing bifurcations and regime shifts which may be observable at different temporal and spatial scales. In particular, at a more advanced stage of the model, one will aim at studying the stability portrait in general. That will mean investigating the stability or instability of possible equilibria, depending on the stressors, hence improving our knowledge of the properties characterizing critical conditions of the environment. Early warning of critical transitions in the ecosystem will be possibly deduced from the simulated time series; finally it should be possible mitigate the impacts of global changes. This model, at the stage presented here, represents the first attempt to provide a general theoretical analysis of the combined effects of light, nutrients and other factors on the growth of *Posidonia oceanica* in a wide variety of habitats. Thus, the general predictions of this model should apply to *Posidonia oceanica* populations with widely differential morphologies in dramatically different environments. Future objectives are to validate the model with real biological parameters, to introduce new important biological functions and to investigate the effects of other stressors on the health state of the *Posidonia oceanica* habitats. The present work provides a platform upon which further model development will be made, and constitutes an important step towards creating a useful management tool for valuable *P. oceanica* resources in the Mediterranean.

In addition to its key role as highly productive ecosystem [79] supporting high biodiversity [111], *Posidonia oceanica* is characterised by its capacity to sequester and store considerable amounts of Carbon in its carbon-sink sediments. Reducing carbon (C) emission is a necessary step in the fight against climate change. Moreover, because greenhouse gases will linger in our atmosphere for another hundred years, there is also a need to find ways to remove C from the atmosphere. Biosequestration is one promising option that capitalises on natural CO_2 capture and storage by photosynthetic organisms and soil microbes. Although much of the attention on biosequestration has centred on terrestrial forests, world's greatest C storage potential may be in our coastal ecosystems. Seagrasses meadows bury C at a rate that is 35 times faster than tropical rainforests, and their sediments never become saturated [160]. Furthermore, while terrestrial forests bind C for decades, seagrasses meadows can bind C for millennia [142], [152]. *Posidonia oceanica* is an exceptionally effective long-term carbon sink thanks to its significant low input and loss rate [189]. The rate of carbon sequestration in the long-term performed by *P. oceanica* is estimated between 6 and 175 g C m^{-2}

y^{-1}, which represents 10-25% of the its net primary production [189]. This is an important service for the Mediterranean Sea and the Mediterranean Countries. The current decrease of *P. oceanica*'s meadows heralds the loss of an important long-term C sink, and raises concern that degraded meadows could leak vast amounts of ancient C back out into the atmosphere, thus shifting the*P. oceanica* from C sink to C sources, and potentially accelerating climate change. Realisation of the important carbon sink capacity of the seagrasses meadows has recently led to the proposal that seagrasses, along with salt-marshes and mangrove forests, could be used to support strategies to mitigate climate change. These strategies would be based on both the conservation and reforestation of seagrass meadows. However, the development of management schemes based on the role of seagrasses as intense carbon sinks has been precluded by limitations in current knowledge on the mechanism conducive to their high carbon sink capacity and the rates of carbon burial they do support. It is therefore necessary to conduct a comprehensive and rigorous assessment of seagrasses C budgets using the most up-to-date technologies, and to use this information to model the sequestration capacity for different conditions. The model presented here supplies the ability to estimate the amount of carbon stored from a *P. oceanica*'s meadow and to assign to it an economic value. The Carbon value associated with meadows is obtained as a percentage of the total biomass based on the percentages estimated in the literature relative to the dry weight per unit of surface. The purpose is to use the different values of biomass production and carbon uptake provided by the different simulation scenarios, in order to be able to estimate the loss or gain in economic terms, associated with anthropic interventions and specific management of coastal systems, causing variations that are easy to model. The model allows to predict the cumulative carbon sink associated with meadows restoration projects and to evaluate their cost efficiency. The final aim is to provide a practical list of research priorities that will lead to policy changes, with the introduction of effective measures to protect vulnerable meadows's carbon stocks, as well as restore and improve the C sequestration capacity of their ecosystems.

In order to set the scene for the present work, a background to seagrasses and the seagrass species *Posidonia oceanica*is given in the next section. The stressors relevant to the habitat and the current management initiatives towards reducing and/or eliminating these stressors are also discussed. Another section provides a summary of the main production models about

Posidonia oceanica. A review follows of key techniques and methodologies that can be used in research towards developing C budgets, and an analysis of methods to put a price on carbon. Then the model is described in detail and the result of simulations discussed.

Chapter 2

The seagrass *Posidonia oceanica*

In this first chapter a description of the species Posidonia oceanica, analysed by this study, is provided. Knowing the biological features of a species improves the awareness of how it is potentially adaptable, but it is also useful to realize how fragile it can be and how a variation of one environmental variable can be harmful and lead to a great loss. Only by recognizing the factors determining the photosynthetic processes of each plant, it's possible simulate the growth dynamics of a meadow. After the systematic classification of the species, a description of the ecological factors affecting the distribution, the morphological structure and the reproductive mechanisms, is supplied.

2.1 Scientific classification

Posidonia oceanica (L.) Delile is an endemic seagrass of the Mediterranean Sea. Seagrasses are monocotyledonian angiosperms (flowering plants) with terrestrial ancestors which, about 120 million years ago, have recolonized the marine environment. Despite their terrestrial origin, seagrasses are well adapted to life in the marine environment, in shallow water at water depths less than 50 m [76], and grow close to the shore. Seagrasses have an anchoring system that allows to withstand the energy of the wave motion; they are rhizomatous, clonal plants that occupy space via the repeated production of shoots, leaves and roots as a result of their rhizome extension [147]. Asexual propagation generally constitutes the main proliferation mechanism for seagrasses, although some species such as *Zostera marina* have a high rate of sexual reproduction: seagrasses complete their life cycle in water and use an hydrophilic pollination mechanism that allows them to colonize large areas especially on sandy substrates [106], [129]. Many of them are considered as engineering species, which are able to modify the substrate to make it suitable for the colonization of other species and they are therefore key species of their ecosystems [30]. Seagrasses are some of the most important ecosystems, both ecologically and economically [128], [66]: it has been estimated that the average annual seagrass production is 1012 g DW m^{-2} per year [79]. Marine species are a very small number compared to land monocotyledons: about 60 species are known with over 300,000 species of angiosperms. This is by no means proportional to their abundance or their ecological and economic importance. Seagrasses are present in temperate and tropical regions Fig. (2.1): the temperate boreal regions are dominated by the Zostera genus, the Australian by the genus Posidonia. They usually have long leaves and live very close to each other forming meadows which look like grassland, this is why they are called “seagrasses”. In tropical areas multi-species meadows are common, while in temperate areas meadows are usually monospecific or oligospecific.

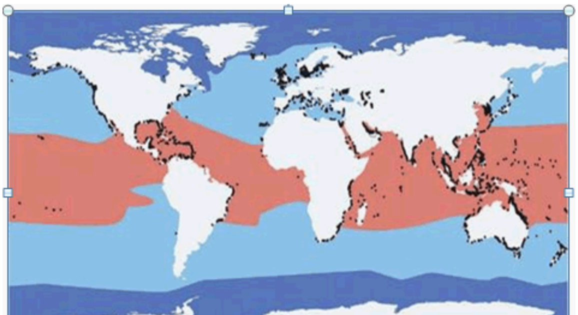


Figure 2.1: Current global distribution of seagrasses in relation to mean ocean temperature (from [106].

There are 60 described species of seagrasses worldwide, within 12 genera, 4 families and 2 orders: four species are native to the Mediterranean, *Zostera marina*, *Zostera noltii*, *Cymodocea nodosa* and *Posidonia oceanica*. The family Posidoniaceae has only one genus, Posidonia, which includes 9 species: 8 of them are widespread in the Australian coasts, while one of them, *Posidonia oceanica*, is endemic to the Mediterranean Sea.

2.2 Distribution and ecology

The *Posidonia oceanica* has a distribution limited to the Mediterranean Sea and it disappears in the extreme western area where the Mediterranean waters mix with the waters coming from the Atlantic Ocean Fig. (2.2). Its presence is found on almost all the coasts of the basin: it is missing only in confined regions (on the coasts of Egypt, Palestine, Israel and Lebanon) and the Black Sea [30].

Figure 2.2: Distribution of *Posidonia oceanica* (red line) along the coast of the Mediterranean Sea. From [222]

In the Mediterranean basin about 50.000 Km^2 are covered by *P. oceanica* from near the surface down to 40 m depth [14], [198], [208]. Irradiance, nutrient availability and temperature are the main factors regulating primary production of marine vascular plants [240], [238], [107], [4]. Light availability is one of the most important factors regulating the depth distribution, abundance and productivity of Posidonia oceanica [238], [87]. The maximum depth that can be reached by *P. oceanica* depends on the cleaness of the water column; the maximum limit, of 45-48 m, was observed in Corsica [9], [31].

Posidonia oceanica is particularly sensitive to low salinity values, while it seems to be better resistant to high levels of salinity, although some studies have shown that 41% is its maximum tolerance limit. It needs a constant salinity level, so it is not common in estuaries or lagoons. Temperature can significantly affect the rates of physiological processes such as photosynthesis and respirations, and influences flowering and fruiting events. The temperature range in which the plant lives and reproduces successfully is from 9° C to 29° C. High hydrodynamism tear portions of meadows: for this reason, in areas exposed to wave movement, *P. oceanica* does not appear more than 2 meters in depth; under favorable hydrodynamic conditions, in sheltered areas, the plant colonizes very shallow bottom. It grows healthier in waters free from pollution, and for this reason its presence is an indicator of water cleanness. The main habitats of the plant are generally incoherent substrates with sandy granulometry on which it can form dense and extensive monospecific meadows. On rocky substrates, *P. oceanica* usually develops matte of moderate size and meadows are little extended [30]. While 5% of the *Posidonia oceanica* stands may occur in patches of various sizes or in continuous meadows [23], [65], other growth patterns characteristic of this species of seagrass include “collines” (hillock-like stands generally surrounded by sand) and barrier reefs [30], [202]. Long persistence, slow vegetative growth, infrequent sexual reproduction and low genetic variability are all typical characteristics of *P. oceanica* meadows [152].

2.3 Morphology and structure

The plant is organized in roots, rhizomes and leaves Fig. (2.3). Adventitious roots usually develop from the lower side of the rhizome, generally at the nodal zones; they are thin, soft and very often branched. Roots, in addition to ensuring anchoring and absorption of nutrients, act as a reserve of oxygen, produced by photosynthesis from the leaves. The rhizomes, which constitutes a modified underground stem similar to a root but with leaves, have the function of transporting water and mineral salts to the leaves, storing the reserve material and, together with the roots, anchoring the plant to the substrate. Rhizome may increase by stolonization horizontally (plagiotropic rhizome) and perpendicular to the substrate (orthotropic rhizome), [159].

The first one allows the plant to colonize large areas of the substrate, anchoring through the roots that are formed on the lower side. The latter,

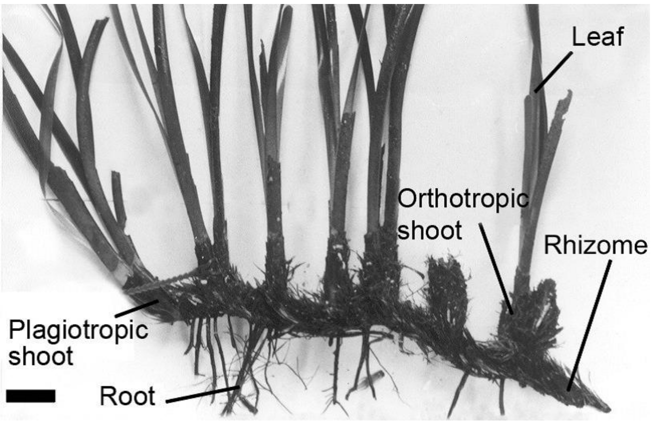


Figure 2.3: Components of *Posidonia oceanica* (from [103].

through vertical growth, allows the plant to escape from progressive calving and competition for the light [33]. Depending on the available substrate and environmental conditions, a rhizome may change its growth orientation from orthotropic to plagiotropic, and conversely [98]. Rhizomes' growth is very slow: plagiotropic rhizomes stretch by about 5-12 cm per year, while the orthotropic grows from 0.3 to 7 cm per year; speed varies according to season, while it does not seem to be influenced by the depth where plants are located, and the density of leaves. The factor that determines the elongation of rhizomes on the substrate or perpendicular to it is mainly sedimentation rate: if excess sediment accumulation occurs, rhizome reacts by increasing its orthotropic growth. Beyond a certain treshold, however, its vegetative portion remains too sunken and perishes [58]. The plagiotropic and orthotropic growth of the Posidonia oceanica leads to the formation of terraced structures consisting of rhizomes, roots and sediment. The progressive burial of roots, rhizomes and leaf sheaths leads to the accumulation of large quantities of organic debris beneath *P. oceanica* meadows. The network of living and dead rhizomes with sediment filled interstices is commonly termed “matte” Fig. (2.4) and is a characteristic unique to *P. oceanica* meadows [188]. The comparison of batimetric cards [166] [152] and dating techniques with the C^{14} allowed estimate the matte growth rate around 1 m/century [29].

At the top of the rhizome there is the vegetative apex from which leaves arise: the leaves are the carbon fixing center, and they are also important for the absorption of nutrients. The leaves look like thin ribbons, with a

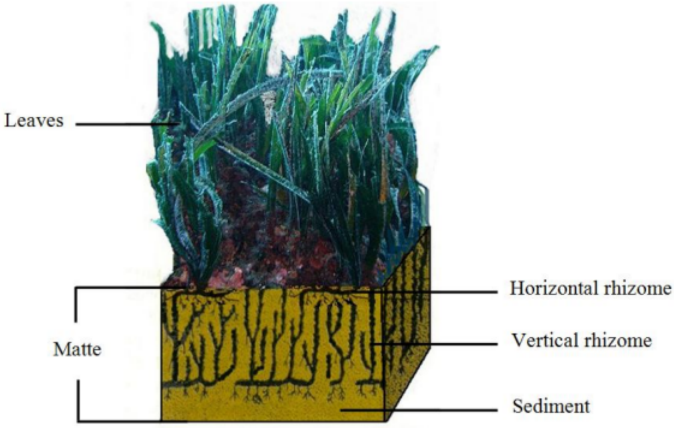


Figure 2.4: *Posidonia oceanica* matte (from $https://it.wikipedia.org/wiki/Posidonia_oceanica$).

rounded apex; they have a width between 0.6 and 1.2 cm that can exceed one meter in length [102]. They are composed of two parts: the base, present only in those that have reached a certain development, and the flap, which represents the photosynthetic part; the boundary between the base and the flap is marked by a concave line called ligule. All leaves have a basal meristem that increase the formation of new tissue at the base. This creates an aging gradient into the leaf in the longitudinal direction so the apex, the oldest part of the leaf, first meets degenerative events producing the appearance of a brown tissue. The leaves are arranged in tufts of 4-8 elements [182], typically fan-shaped, with the younger leaves in the tuft, while the older are more external Fig. (2.5). Depending on the degree of maturity, there are 3 categories of leaves:

- juvenile leaves: less than 5 cm length;
- intermediate leaves: the length is greater than 5 cm still they don' t show the presence of the ligule;
- adult leaves: the typical structure with base and flap is shown;
- old leaves: brown and photosynthetically inactive.

P. oceanica, like other seagrasses species of the genera, tends to develop very high above-ground (about 500 g DW m^{-2}) biomass. On the other

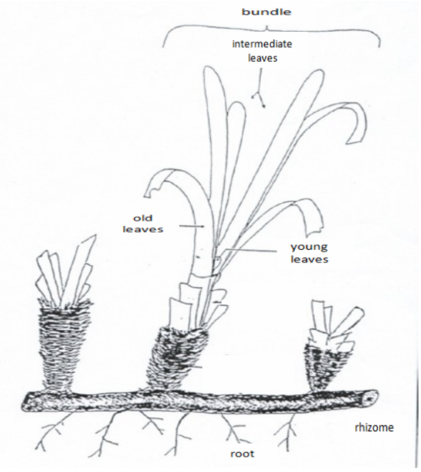


Figure 2.5: Classification of *P. oceanica*'s leaves (adapted from [182]).

hand, below-ground biomass developed by *Posidonia* exceeds by far (about 1000 g DW m^{-2}) those developed by other seagrasses [80]. The *P. oceanica* average ratio of below to above-ground biomass varies between 4.5 and 19.3. The production of new leaves is continuous but their growth rate changes with the season, minimum in summer and maximum in spring [181]. In the summer the meadows are rich in very long leaves and densely covered by epiphytes. Between September and December there is a renewal of the leaf bundle with the appearance of juvenile and intermediate leaves and the fall of the older leaves. Towards the end of August many leaves are dead and autumn storms cause their detachment; epiphytic population is drastically reduced by decrease in temperature. The first leaf of the annual growth cycle appear between the end of August and the beginning of September and successively they continue to appear until the end of May. The growth rate of plants is increasing until it reaches its peak at the end of spring, then it decreases again in the following period. Summarizing the growth of a new leaf is observed at least once a month (for an annual average of 10 leaves) and the fall of at least one adult leaf throughout the seasons, although it has a peak in autumn. Seagrass production that is buried in the matte is rather noteworthy (25-35%) and, due to high resistance to decay, may furthermore persist for thousands of years [152]. Observation of the oldest materials by Mateo et al. [152] indicates that plant parts that last the longest are the leaf sheaths (their external morphology is left intact after 3000 years) and roots, which are usually found in a fragmented state. Rhizomes are less resilient to decay, and no identifiable remains are found in the oldest (>1000 year) samples. Various studies identify this large reservoir of belowground detritus as an important and substantial sink for various biogenic elements [59] [192] [153]. The augmentation of the matte is a delicate process that depends on the fastness of sediment accretion: intuitively, the quicker the accretion is, the bigger the matte becomes. However, if sedimentation is too fast, rhizomes risk to be stifled by the excess of sediments. On the other side, if sedimentation is too slow, the meadow risks regression.

2.4 Reproduction

Posidonia oceanica reproduces both vegetatively and sexually. The main propagation mechanism is the vegetative one, and it is achieved by the separation of last rhizomes from parental rhizome [166], and by division and elongation of rhizomes. Another breeding strategy, observed for the first time in 2004 along the coasts of the Balearic Islands [12], involves the formation of seedlings directly from the inflorescences. The frequency and the evolutionary meaning of these reproductive events are not known: probably is a useful strategy for dispersion on short distances and for the maintenance of a species that can persist for thousands of years and whose ability to colonize new spaces is very slow [12]. In the *Posidonia oceanica* sexual reproduction occurs through the fertilization of hermaphrodite flowers Fig. (2.6), grouped in inflorescences and produced at the beginning of autumn. Bearing fruit is finished in the spring, through the production of a drupe called “sea olive” Fig. (2.7) which, after falling from the plant, is scattered by the currents. The seeds fall to the ground and, with favorable conditions, germinate in June, without getting into quiescence. The relationship between flowering and water temperature is based on the observation of this phenomenon occurs after a summer with high temperatures [101] and the fact that flowers appear usually one month after reaching the maximum annual temperature [44]. In particular, it has been noted that meadows in shallow waters flower in September-October, while meadows in deep waters bloom in November-December. The flowering and fruiting of *P. oceanica* are uncommon events [166] and few informations are available on them.

The asexual mode of propagation is therefore predominant for *P. ocean-*

Figure 2.6: Flower of *Posidonia oceanica* (from $http://www.naturamediterraneo.com$).

Figure 2.7: Fruit of *Posidonia oceanica* (from $http://www.biologiamarina.org/posidonia - olive/$).

ica. Clonal growth is the main mechanism by which *P. oceanica* occupies space, during the colonisation of new habitat for example, or in recovering from disturbance. Such means of vegetative propagation is common to all clonal plants, and is a key trait in understanding and modelling the dynamics of seagrass populations [81] [111]. The growth of *P. oceanica* rhizomes regulates the rate at which shoots are formed within a meadow as well as their spatial distribution [147]. Rhizome growth is a tightly regulated process with rules that govern the rate at which rhizome internodes are added, the size of rhizome internodes, the frequency at which rhizomes branch, the angle at which branching takes place, and the rhizome length in between consecutive shoots [54]. Knowledge on the dynamics of *P. oceanica* rhizome growth makes it possible to predict and understand the extent and density of a population.

Chapter 3

Ecosystem of *Posidonia oceanica*

The P. oceanica forms widespread meadows constituting one of the most important habitats in the Mediterranean basin. The P. oceanica ecosystem plays a major role in benthic primary production [48], with a contribution ranging between 0.4 and 2.5 kg DW/m^2/y [28] [59]. The P. oceanica meadows provide services, illustrated in the next sections, that are essential to the functioning of coastal zone systems involving the high ecological and economical values of this natural resource. As P. oceanica habitat declines in the Mediterranean, fundamental consequences are to be felt in the social, economic and biological activities in the region. Given the importance of seagrasses to humans [66] [131], the preservation of P. oceanica meadows and their ecosystem services should be a worldwide priority, an effort that would provide benefits to all aspects of coastal ecosystems. The considerable resources required for restoration, where possible, and the long time periods required for meadow recolonisation and recovery, in contrast to the rapid dynamics that bring about reduction, highlight the need for proactive management of this valuable habitat.

3.1 The *Posidonia oceanica* habitat and the associated species

Posidonia oceanica develops highly productive meadows, sometimes in association with other phanerogams. The extension and morphology of the meadows depends on the biological characteristics of the plant and also on the environmental characteristics, such as nature of the substrate, the ground geomorphology, hydrodynamism, depth and brightness, sedimentation rate and water turbidity [47]. The inferior limit of a meadow can be due to four different factors Fig. (3.1):

- if the available sunlight is not enough, leaf density decreases and the rhizomes do not go beyond a certain threshold. This is the climatic or progressive limit;
- if the substrate under a certain level changes in another kind of substrate that is not suited to these plants, there is a clean or edaphic limit, with a high leaf density and no matte;
- if hydrodynamics is too strong, the meadow cannot expand. It is called erosive limit, and in this case there are matte and a high leaf density;
- if water becomes too polluted there is no available sunlight in the deep, in this case there are only dead mattes and the limit is called regressive.

The *P. oceanica* ecosystem is a complex and structured system with a leaf biomass of about 1 kg m^{-2} in dry weight, like ground forestry. The structure of *Posidonia oceanica* habitat makes available several resources that are vital to the survival of other organisms: offers a substratum for attachment and growth of various organisms [134]. *Posidonia oceanica* is considered a structuring species, constituting life habitats for other species because its meadows are characterized by a high biological variability of plant and animal communities constituting an ecosystem very complex in terms of specific wealth and biotic interactions [46]. Some authors prefer to stress a separation between the community associated with leaves and with rhizomes. Other authors [126] [40] [13] [156] consider the *P. oceanica* system as an integrated “stratocenosis” with all the associated communities, from the leaf to the rhizomes layer. *Posidonia oceanica* is the substrate for many organisms that play an essential role in the productivity and growth

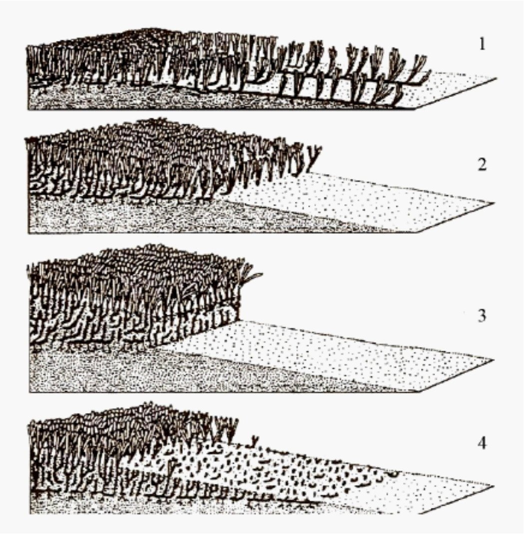


Figure 3.1: The inferior limit of *P. oceanica*'s meadows: 1)progressive limit; 2)clean limit; 3)erosive limit; 4)regressive limit. From [190].

patterns of the host plant in terms of competition for available light, energy and nutrients [157] [156] [192] [5]. These organisms can be classified in three categories: epiphytes, animals and detritivore organisms. Epiphytes are bacteria, algae or bryozoa that live attached to the leaves. The epiphytic vegetation community consists of photophilous species, predominantly colonizing the leaves, and shallow species populations that settle in the rhizomes where the brightness is reduced. Colonization of the leaves occurs with a definite temporal succession Fig. (3.2). The first are bacteria that can colonize very young tissues and are therefore found on leaves with 1 or 2 days of age. Already after a week of leaf life, unicellular algae reach the plant, the most common of which are Diatoms. Bacteria and Diatoms are a source of food for many animals and their presence preserves the leaf tissue from the grazing. In leaves with more advanced age, and therefore mainly on the apex level, it is possible to observe the first pluricellular algae. The epiphytic macroalgal flora of the leaves is distinguished by an overlaying layer and an erect layer. The first one is made by the incrusting macroalgae belonging to the Rhodophyceae class and to the Phaeophyceae class. The macro-algae with erect habitus are generally on the incrustant layer and, with their tubular and branched structure, can also rise above the leaf surface. They are mainly brown algae belonging to the genera Dictyota and Giraudia, and red algae, belonging to the Ceramium and Polysiphonia genera. The floristic richness and the coverage depend on seasonal, reaching a maximum in summer, between June and September, and a minimum in winter, between December and April.

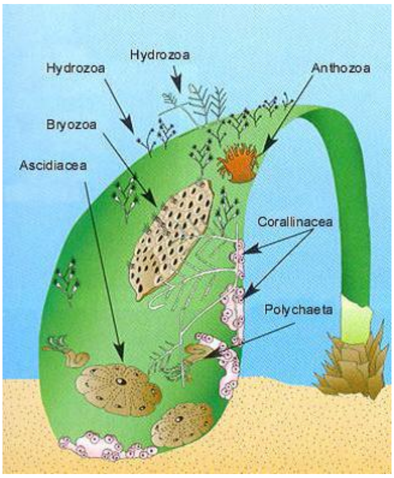


Figure 3.2: Leaf's colonization by epiphytes (from [206].

At the level of rhizomes, there is an epiphytic algal community consisting of shadowy species, common in environments where the light intensity and the movements of the water are reduced. We can observe, among the algae on rhizomes, the Peyssonnelia and Ceramium genera for red seaweeds, Halopteris and Dictyopteris for brown algae and Cladophora and Flabellia for green algae. Essentially, the epiphytic community on *P. oceanica* is itself dynamic, with numerous species growing over the first to settle. Consequently, a multi-layered stratum is present on *P. oceanica* leaves and rhizomes, where different species are mixed and whose composition varies with depth and other conditions that influence epiphytic dynamics such as the same abiotic factors which influence the seagrass host [158], the life cycle of the epiphyte species [177] or grazing by fauna [118]. These epiphytes can damage the plants: they contrast gas exchanges, reduce nutrient, are responsible for direct shading reducing the surface available for sunlight absorption, and their weight may become excessive and lead the leaves to a premature decay. As a result of their short generation times and rapid rates of growth, the epiphytes attached to seagrass leaves are extraordinarily productive, despite the small biomass they represent. While the average biomass of the autotrophic community growing on *P. oceanica* leaves and rhizomes ranges between 160 and 420 g DW/m^2/y [35], its contribution towards primary production lies between 500-900 g DW/m^2/y and it typically accounts for 20-60% of total seagrass aboveground productivity [111]. It is the sum of seagrass and epiphyte stocks, in shallow waters, that enable the *P. oceanica* habitat to achieve the highest values of net primary production observed not only in the marine but also the terrestrial realm [30]. The exchange of fixed nitrogen between epiphytic bacteria and *P. oceanica* is thought to partly explain the paradoxically high biomass and productivity of *P. oceanica* systems; this is unexpected given the oligotrophic conditions that characterise Mediterranean waters. Shading by excessive epiphyte growth is, on the other hand, an effect that often proves detrimental to the host plant and has been commonly listed among the causes of seagrass decline around the world [89] [169] [225]. The animal population of the meadow include sessile, sedentary and floating species, distributed in a lower population associated to the rhizomes and a higher one related with the leaves. The most abundant sessile population near rhizomes includes numerous species of Poriferan, Anthozoos, Crustaceans, Bivalves and colonial Tunicates. The sedentary fauna is represented by various species of decapod, gastropods and echinoderms, such as the *Astropecten spinolosus* sea star and the sea urchin *Sphaerechinus granularis*. These species take shelter during the day at the bottom of the meadow between the rhizomes of *P. oceanica* while at night they go back to the leaves chasing the oscillations of oxygen and carbon concentrations in water during the daily cycle. Floating fauna includes numerous species of scorpionfish and syngnathidae, among which seaneedles and seahorses fish. Similar to the canopies of other seagrass species, those of *P. oceanica* function to trap particulate matter and make for a favourable feeding environment for filter feeders such as the endangered fan mussel, *Pinna nobilis*, another protected species in EU Member States (EEC, 1992). This complex biocenosis is also a nursery for numerous species of larval or juvenile fish. *P. oceanica* and its epiphytes provide nutrition to organisms that consume them. Three species directly linked to *P. oceanica* habitat through their consumption of *P. oceanica* leaves are the fish *Sarpa salpa* [108], the sea urchin *Paracentrotus lividus* [191] and crustacean isopods *Idotea spp* [28]. When consuming seagrass leaves, these species additionally consume the epiphytic material growing on *P. oceanica.* Consumption by herbivores Fig. (3.3) is not considered to be a major route for *P. oceanica* material on the other hand, and less than 10% of the leaves are directly consumed [59]. The majority of leaves are consumed after being shed, as detritus in the litter, through the action of crustaceans, gastropods and microorganisms [192]. The low consumption of many seagrasses is often attributed to the poor nutritional quality of the plant material [219]. *P. oceanica* has a high C/N ratio [81] and its high cellulose content often makes the digestion process difficult for most invertebrate grazers [132]. The presence of chemical deterrents is said to further contribute to the unpalatabiliy of *P. oceanica* [1].

Figure 3.3: Grazed leaf of *P. oceanica* (from [171])

Despite these observations, a number of studies have reported considerable impacts of grazers on seagrass biomass and production herbivores have been known to defoliate vast areas of *P. oceanica* [127] [229] [219]. Trophic interactions are gaining recognition as critical structuring forces in seagrass systems [61] and hypothesised overfishing is often put forward to account for seagrass decline, through a mechanism of epiphytic overgrowth, similar to that of eutrophication [115]. Other than the loss of large herbivores, overfishing may also be responsible for a reduction in small invertebrate grazers of epiphytes via trophic cascade. Studies indicate that top-down control of plant biomass, as a result of indirect effects of predators on plants via shifts

CLASS	**N shoot/m^2**	**Kind**	**Description**
I	>700	very dense beds	meadows on matte and with prevailing vertical rhizomes
II	400-700	dense beds	meadows expression of degeneration or increasing and with prevailing vertical rhizomes
III	300-400	sparse beds	meadow expression of degeneration or dynamic equilibrium placed on any kind of substrate
IV	150-300	very sparse beds	meadows in regression or settlement with many dead shoots without leaves and horizontal rhizomes
V	50-150	semi or half-beds	meadows in regression mainly distinctive of the deep limit

Table 3.1: Meadows classification [101]

in herbivore abundance, is strongest in the marine environment [212]. Furthermore marine benthic species exhibit the strongest trophic cascades of any tested system, supporting assertions that grazers may be equally important in controlling the accumulation of algal biomass in seagrass habitats via top-down effects as are nutrient fluctuations via bottom-up effects [110].

3.2 Characterization and evaluation of the state of meadows

Physical, structural (density and coverage) and functional descriptors (biomass, growth and productivity) are used to describe, from a quantitative point of view, the state of meadows of *P. oceanica.* One of the main structural descriptors of the health status of seagrass is the density of vegetation, the number of foliar beams per square meter. The temporal analysis of this variable allows to evaluate the dynamics of the meadow over time and to identify key elements driving ecosystem evolution. The most common methods to classify meadows, based on the absolute density values, are two. The first [101] Table (3.1) classifies the meadows according to the number of beams per square meter, dividing them into 5 density classes.

The most recently method [190] Table (3.2), classifies the meadows taking into account not only the absolute density values of the beams, but also considering the sampling depth because density values decrease with the

Depth	**DA**	**DL**	**DN**	**DE**
1	<822	822-934	934-1158	>1158
5	<413	413-525	525-749	>749
10	<237	237-349	349-573	>573
15	<134	134-246	246-470	>470
20	<61	61-173	173-397	>397
25	<4	4-116	116-340	>340
30	0	0-70	70-294	>294
35	0	0-31	31-210	>210
40	0	0	0-165	>165

Table 3.2: Pergent classification

depth. The meadows are classified in 4 categories:

- "very disturbed meadows", with abnormal density (DA): these are critical situations, where the vitality of the meadow is extremely low;
- "disturbed meadows", with a low density (DL) corresponding to a reduction in the vitality of the meadows: this state should be taken as an alarm signal to begin rehabilitation actions;
- "balanced meadows" with normal density (DN), which corresponds to satisfactory vitality values, observable when there are no signs of anthropic pressure;
- "balanced meadows" with exceptional density (DE) that corresponds to very high values of plant vitality or batimetric extension of the meadow.

The estimate of the absolute density of a meadow must be associated with the estimate of the root percentage covered by the plant, to give a more accurate assessment of the structure; however the percentage of substrate occupied by the plant results from a subjective and seasonal valuation. Functional synthetic descriptors are the variables that depend on the biological characteristics of the species and are affected by environmental changes. Phenological analyses consist of the study of the anatomical structures of the plant, especially the morphometric parameters of the leaves, taking into account the sampling period. Lepidocronological analyses are carried out on the rhizome to indirectly evaluate the production, in terms of biomass, of the meadow and to determine the age of the sampled plant underlining any changes caused by environmental stresses over years. The derivative descriptors are obtained from the measurements and observations of the structural and functional synthetic descriptors and are: number of leaves per bundle, number and width of adult or intermediate leaves width, length of base, L.A.I. (Leaf Area Index) corresponding to leaf surface per beam or per square meter. These parameters contribute to describe the health of meadow and its variations with time, and to determine any sources of disturbance.

3.3 Ecological role

P. oceanica's meadows play an important role in coastal systems [84] Fig. (3.5). The belowground structures of the plant (root system and rhizomes) are essential for the stabilization of the seabed, holding the sediment and preventing its dispersion. In particular the meadow damps the swell and forms an obstacle to the movement of sediments on the bottom [42], and plays an active role in the sedimentary balance of the beach both supplying biogenic sand and trapping sediments in eventual offshore migrations. Moreover, the loss of leaves, especially in the autumn, produces the formation of massive accumulations of plant material along the coast, called banquettes Fig. (3.4), reducing the erosive action of the wavy motion on the beach. The hydrodynamic forces are reduced from 10% to 75% under the leaves [100], and of 20% few centimetres above the meadow. Different studies showed that the loss of one meter cube of meadow causes coast recession of about 20 m [34].

The presence of *P. oceanica* grasses contribute significantly to the nutrient budget and cycling in the coastal marine ecosystems [180]. The high rate of biomass production by seagrasses implies an equally high rate of oxygen production (1 m^2 of meadow produces 4-20 litres of oxygen per day, [15]), a photosynthetic by-product which, when released, becomes available for other marine life [25]. As the gross photosynthesis of seagrass leaves exceeds the respiratory demands of the plants by almost an order of magnitude [221], oxygen is often released to the water column and sediment. The largest release of oxygen from seagrasses is from the leaves to the water column, during periods of high light intensity and photosynthesis. Oxygen is, on the other hand, continuously released from roots and rhizomes to the anoxic sediment, during both light and dark phases [26]. The enhanced mineralization

Figure 3.4: *Posidonia oceanica*'s banquettes (from https://www.ilgiornaledeimarinai.it/posidonia-oceanica/).

of organic matter within sediments below a seagrass meadow, as a result of oxygen loss by seagrass roots and rhizomes, has been confirmed through research studies [205]. Other important implications of seagrass oxygen release to the sediments include enhanced redox processes such as sulphide reoxidation [133], and nitrification and denitrification [53]. Seagrasses therefore do more than oxygenate surrounding waters; they constantly modify the sediments they inhabit, enhancing their own production and that of sediment dwelling organisms, which are also linked to nutrient cycling. Nitrogen is another nutrient that enters significantly into marine sediments via seagrasses. In contrast to terrestrial plants, seagrasses have the ability to take up inorganic nitrogen through both leaf and root tissues which means they are able to exploit the water column as well as the sediments for nitrogen [133] [184] [218]. Besides taking up dissolved inorganic ammonium and nitrate, seagrasses also support microbial nitrogen fixation, a process that occurs on the leaves and in the sediment of seagrasses [19]. Nitrogen-fixing bacteria in the leaf canopy and sediments of seagrass beds form a diverse community, including photoautotrophic heterocystous cyanobacteria and heterotrophic nitrogen-fixing bacteria [185]. *P. oceanica* meadows are one of the most productive marine ecosystems, occupying 0.15% of the world's marine surface and contributing to 1% of world marine primary production. The ecosystem formed by *P. oceanica* is highly autotrophic over the year, with the annual P:R ranging from 1.5 at deep areas to 3.6 at shallow meadow limits, with the average probably around 3 (for the leaf compartment [155]). Net primary production amounts to an average of 420 g DW/m^2/year; the average biomass of *Posidonia oceanica* is about 2112 g DW/m^2 aboveground and 1611 g DW/m^2 belowground [30]. About 10% of the primary production is used by herbivores, especially *Sarpa salpa, Paracentrotus lividus* and the isopod crustacean *Idothe hectica* [233] [192] [41]. Most biomass produced (24-85%) is exported like dead leaves [192] [163]. The rest represents the support of the trophic network of detritives and decomposers to transmit energy to higher trophic levels: 24-44% is remineralized, the remaining 11-47% of the production is assumed to correspond to the indirect estimate of the potential flux to the short and long-term *P. oceanica* carbon sinks. *Posidonia oceanica* meadows provide shelter and food, reproduction and nursery sites for many species [177], also of great economic value: various fish communities, resident species and juveniles live on or are protected by *P. oceanica* leaves, or in the sediment where it stands. The meadows of *P. oceanica* support many plant and animal epiphytes, which can reach up 20-30% of the biomasses of the leaves [104]. Moreover the meadows host more than 400 different plant species and several thousand animal species, so they can be considered an hotspot of biodiversity [16] [17] [95] [38].

3.4 Decrease and conservation

Decrease is a phenomenon that involves all seagrasses in the world and an alarming decline of the *P. oceanica* meadows has been reported in the Mediterranean Sea and mainly in the north-western side of the basin [8] [37] [168], where many meadows have already been lost during last decades [20] [135] [167]. An examination of 39 studies in 135 sites in the Mediterranean indicates that 46% of the *P. oceanica* meadows investigated have experienced some form of decline, while 20% have severely regressed since the 1970s [74]. In order to appreciate the magnitude of the risks associated with the decline of *P. oceanica*, one may consider a common method of rating the severity of any impact on biodiversity. Using this measure involves evaluating the time that is needed for a decline to be reversed. While most pollution events, including oil spills, lie in the range of one to thirty years, and the near elimi-

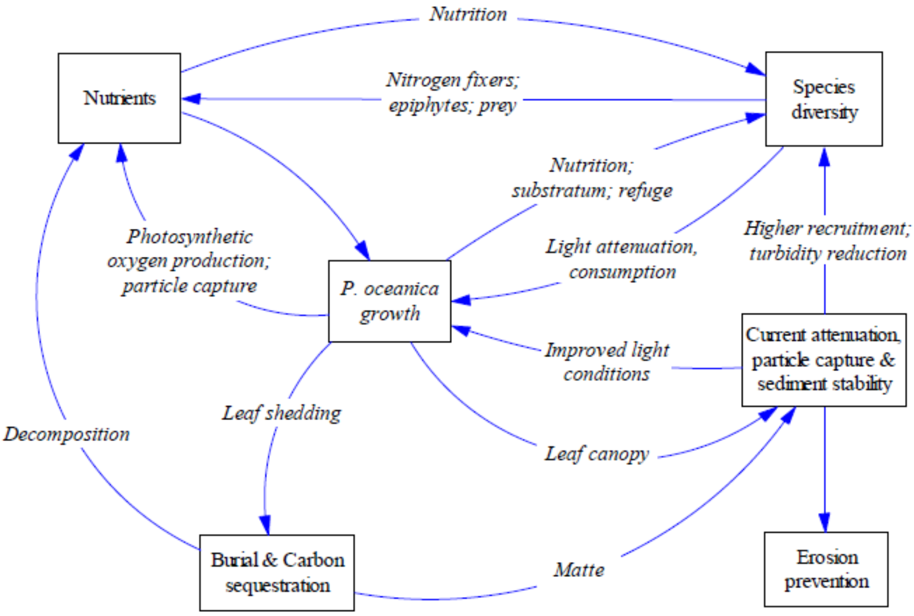


Figure 3.5: Some important links between *Posidonia oceanica* and the surrounding ecosystem (from [206])

nation of most long living species is in the range of ten years to one century, the destruction of *Posidonia oceanica* meadows in the Mediterranean sea would require one century to one millennium to be reversed [32]. While variability as a result of natural environmental factors does exist in such systems, multiple human stressors, including dredging, fishing and anchoring on seagrass beds, eutrophication, coastal development, hypersalinisation, siltation and poor water clarity, habitat conversion, and climate change are becoming a major source of change to seagrass habitats worldwide [84]. For *Posidonia oceanica*, the main cause of the regression and degradation is represented by the intense anthropic activities [135] [168] that inevitably affect its distribution, either directly by physical damages [162], or indirectly through the impact on the quality of waters and sediments. Coastal regions have been frequently identified as areas in which human activity is highly concentrated. This implies that coastal areas support a disproportionate amount of infrastructure supporting industry, transportation and trade, energy generation, tourism and more. Manufactures on coastal areas, modify the behaviour of waves and currents, and interact with sedimentation processes. Local increases in sedimentation may lead to seagrass burial, or erosion of the sediment under seagrass beds [193]. Seagrass burial may also derive from land-based erosion, a consequence of changes in land use leading to increased erosion rates and silt export from water sheds. Burial affects seagrasses negatively by reducing light availability to photosynthetic tissue, reducing oxygen diffusion to the roots and rhizomes, and preventing deeply buried meristems from producing new leaves [230]. Sedimentation may indeed serve as a positive stimulus if it brings with it new nutrients [151], and its magnitude does not exceed the survival capacity of the seagrass species. Large inputs of silt and sediment material to coastal waters typically result in increased light attenuation and a deterioration of the underwater light climate for seagrasses [111]. Since seagrasses are photosynthetic organisms, one of the main requirements for their growth is adequate light, usually an underwater irradiance of around 11% of that present at the water surface. Sedimentation events therefore, compromise seagrass ability to photosynthesise via reductions in light availability and water transparency [230]. Suspended material derived from disturbed soft sediment bottoms has also been shown to have harmful effects on seagrasses via this mechanism of light reduction. Light reduction features, once again, as the single most important mechanism leading to seagrass decline in waters subject to eutrophication. Most eutrophication in coastal environments is caused by increased nitrogen and phosphorus input. The problem stems mainly from the intense use of fertilisers in agriculture, and sewage contamination, which lead to heightened nutrient loads in runoff to the coast [172]. The most common means by which light is reduced, as a result of nutrient over-enrichment, is the stimulation of high biomass algal growth, specifically phytoplankton and more commonly epiphytes and macroalgae, that are considered superior competitors for light relative to seagrasses [24] [51] [73]. Light reduction due to attenuation in the water column and shadowing on seagrass blades limits seagrass ability to photosynthesize and in extreme cases may even lead to death of the plants that constitute the meadows altogether [210]. Urban discharges also introduce into the sea a high amount of chemical elements that cause alteration of the biosynthesis mechanisms of photosynthetic pigments [9]. Detergents can cause death of plant's tissues and alter growth processes, due to their toxicological properties. Moreover, the presence of hydrocarbons in water for naval traffic hinders the penetration of light and, when deposited on plant leaves, reduces gaseous exchanges. Another source of disturbance for *Posidonia oceanica* are the fish farms: they increase the organic loading in water and sediments, inducing degradation of meadows due to the increase in the epiphytic community present on the leaves, the attenuation of light radiation and the lack of oxygen [56] [113] [186]. The effect of such impacts can be reduced by the use of water treatment techniques [28]. Mechanical stress is also important: trawling activities and the indiscriminate anchorage of boats [62], lead to the removal of large portions of matte, making plants more susceptible to the mechanical action of waves. In places where small boats are numerous, the cumulative effect of boat moorings and propeller scars may result in a considerable loss of vegetation as shoots and rhizomes are damaged, or even completely removed from the substratum [231]. Fishing practices that disturb the bottom, such as trawling and dredging, similarly have direct, harmful effects. Dredging to deepen and maintain navigation routes and harbour entrances, as well as dredging for marine aggregates, have similar recognised effects. The introduction into the Mediterranean of aloft species, like Caulerpa spp., broke balance in coastal marine ecosystems. In fact, these species are competitive with the phanerogams for colonization of the substrate [70]. While healthy *Posidonia oceanica* meadows have been shown to act as barriers against Caulerpa spp. (namely C. racemosa and C. taxifolia), dead or dying *P. oceanica* beds leave vacant niches open for colonisation, enabling Caulerpa species to invade successfully [64]. This may essentially mean that, once lost, an area of *P. oceanica* meadow may not be naturally recovered [173]. The increase of water temperature in the Mediterranean Sea [165], causes a variation in normal reproductive plants cycles. The slow growth rate of the plant, low genetic diversity and sometimes small population sizes, can further compromise *P. oceanica*'s capacity for expansion and survival. MarbÃ et al. [148] made a research about *Posidonia oceanica* diffusion from 1842 to 2009, linking each human activity to the number of impacted meadows Fig. (3.6). The main causes pointed out by MarbÃ et al. are:

- the increase in the number of residents and tourists. This leads to a raise in urban wastewater discharge
- industrial activities, that need to discharge their wastewater too

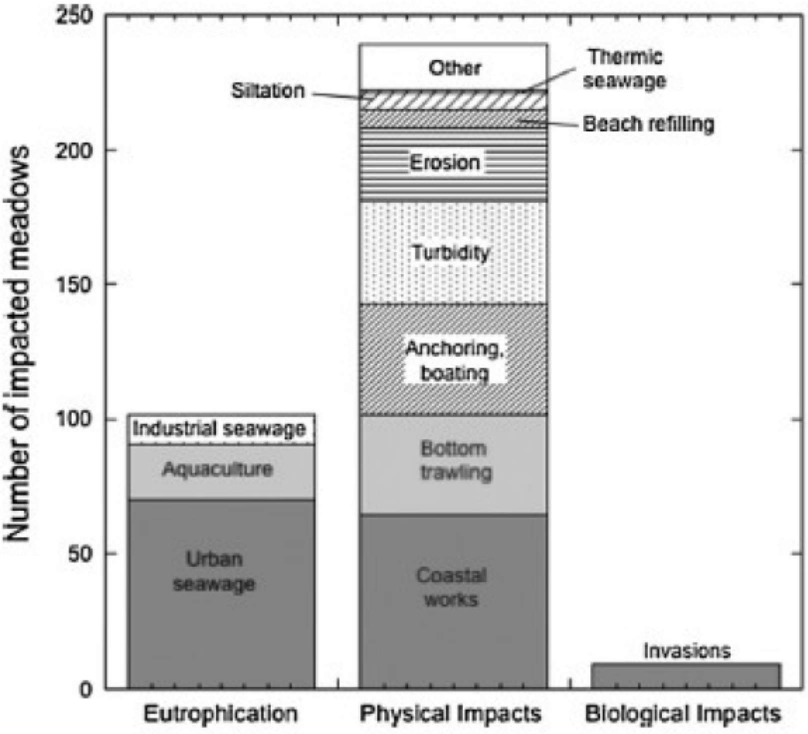


Figure 3.6: Loss and damage drivers and the number of meadows impacted in the sample considered by [148].

- progressive building over the coastline (about 40% built over by 2000)
- enhancement of aquaculture
- human activities over the sea: anchoring, boating and bottom trawling

These human facts have caused a few phenomena which in turn have endangered and damaged the meadows, as it was pointed out by MarbÃ̃ et al.:

- water turbidity: the light is filtered, and this does not let the seagrasses live in deep water
- water eutrophication, that helps antagonist species and increases water turbidity

- erosion and siltation: they augment hydrodynamism and make the shallow limit decrease
- invasion of alien species and excessive proliferation of antagonist species
- perturbations and mechanical stresses, especially in the shallow layers.

In conclusion, seagrass systems are being stretched thin, and predictions for the future of seagrass-dominated coastal systems are not hopeful as yet ([84] [178]. Ecosystem services, such as those provided by *P. oceanica* habitat in the Mediterranean, are often not given adequate weight in policy decisions. This is because it is particularly difficult to do so when such services are not marketable goods and their value is not quantified as economic services and manufactured capital are [66]. Furthermore, the impact of habitats such as *P. oceanica* meadows on human well-being is often "invisible" to policymakers partly because its effects are not immediate. Nevertheless the ecological and economic importance of *Posidonia oceanica* meadows and the considerable sensitivity of the plant to natural and/or artificial perturbations, has prompted national, European and international authorities protect them. In 1979, *Posidonia oceanica* was included in the list of protected species (Annex I) after Bern Convention. In 1990 it is included in the Red List of marine species of the Mediterranean at risk of extinction. In 1995 it was cited in Annex II (threatened species) of the Protocol of the Specially Protected Areas of the Barcelona Convention. The *P. oceanica* meadows are also considered priority habitats in Annex I to the EC Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and Wild Fauna and Flora. The Directive defines these priority habitats as Sites of Community Interest (SCI), whose conservation requires the designation of Special Conservation Areas (SCA). SCAs are identified by EU member states and collectively form the ecological network titled Natura 2000: SCAs must be maintained, or restored when necessary, at a status of favourable conservation. The monitoring of *P. oceanica* meadows has been given much emphasis as an important management tool [236]. Monitoring is useful in inventorying and detecting new seagrass habitat losses or gains, as well as evaluating the effects of policies and interventions. *P. oceanica* habitat may be monitored at a variety of scales, three in particular: the system scale, in which areal cover is estimated; the meadow scale, where limits of the meadow and shoot density may be estimated; and finally the shoot scale, where sediment properties, leaf epiphyte biomass, and other fine scale details such as genetic structure may be obtained [28]. *P. oceanica* monitoring in the Mediterranean was initiated in 1984 with the establishment of the "Resau de Surveillance Posidonies" in the French Riviera [36]. Monitoring of this habitat has subsequently expanded to other regions in the Mediterranean including France, Italy, Spain, Algeria, Tunisia and Malta [236]. Increasing *P. oceanica* habitat monitoring was much encouraged by the EU Water Framework Directive (WFD), adopted in 2000. Linking the status of coastal waters to economic benefits such as coastal fish populations, the WFD made legally binding the duty to monitor water quality and biological quality elements, including aquatic macrophytes such as *P. oceanica* (EC, The EU Water Framework Directive, 2000). Recent adoption of an ecosystem-based approach towards the management of marine waters has further emphasised the importance of seagrass monitoring (EC, 2008). The increasing loss of *P. oceanica* habitat and the species' slow rate of regeneration has prompted the development of methodologies for habitat restoration, rehabilitation and meadow creation. Restoration of *P. oceanica* meadows has focused on recruitment from seeds [18], laboratory seed germination and seedling development [11], and the transplantation of entire plants from donor beds to restoration sites [199]. The use of seeds and seedlings is advantageous as genetic diversity is sustained; a transplant would serve to simply propagate a clone. Furthermore, seagrass seed collection involves minimal damage to the donor bed, particularly if seeds are obtained from drifting fruit. Seagrass seed collection and plantlet management therefore constitute an additional and important route towards the conservation, propagation and restoration of *P. oceanica* habitat [179]. Other active areas in managing *P. oceanica* habitat include the installation of anti-trawling reefs [105], the installation of seagrass friendly moorings [96], and good practices in the management of beach cast *P. oceanica* material. The heavy impact of bottom trawling on sensitive habitats like *P. oceanica* has led to restrictions on trawling over seagrass meadows in places like Spain, Italy and France. In many cases, the deployment of protective artificial reefs has further reinforced such restrictions. Protective artificial reefs are heavy concrete constructions that are often armoured with protruding steel bars and cause any trawling gear passing over the structure to entangle and break. The low maintenance and high endurance of these structures has made them a popular solution to the discouragement of trawling in protected areas. Artificial reef initiatives have reported general success in curbing illegal trawling. Leaves that are shed from the *P. oceanica* leaf canopy are transported to the shore by currents and waves and are deposited along the coast. Material that is beach-cast in this way accumulates to form banks, termed "banquettes", that range from a few centimetres to several metres in height [69]. Removal of such banquettes may prove detrimental to beach stability as well as to nearby *P. oceanica* meadows [82]. For this reason, best management practises in this case involve the adoption of a no-removal policy. This may however prove difficult in beaches that are heavily used by bathers and tourists. In the latter case, a variety of policies are recommended, including the establishment of no-removal periods during off-peak seasons. While marine protected areas are both necessary and important in the mitigation of local threats to *P. oceanica* habitat, they do not provide sufficient protection alone as they are not isolated from all critical impacts [7]. Bearing in mind the spatial and temporal scales over which coastal development and other anthropogenic impacts occur, broad scale evaluation is necessary for the management of *P. oceanica* meadows in the Mediterranean, in line with the ecosystem-based approach [176]. A basin-wide monitoring initiative would see an integration of the different data sets in existence and establish a Mediterranean-wide inventory of the habitat, allowing for a comprehensive detection of changes. Developing a capacity for prediction as part of a comprehensive integrated management programme is then mandatory. An important advance in addressing a fundamental monitoring need to improve documentation of changes in seagrass meadows worldwide was recently achieved with the advent of Seagrass Net in 2001. Seagrass Net, the first program developed to monitor seagrasses on a global basis, uses a consistent protocol for both seagrass parameters and environmental parameters to assess change in seagrass habitat over relatively short periods (1- to 2-yr intervals), through quarterly monitoring of permanent transects and plots. At present, Seagrass Net has been established at 48 sites in 18 countries, with data collection by a team of trained local people, and maintenance of a central database. As it continues to develop and strengthen, this program should provide a powerful tool for coastal resource managers through improved tracking of seagrass populations over time. Such exemplary programs should be coupled with improved models to enable reliable, quantitative forecasts of the cumulative effects of eutrophication from adjacent watersheds and other stressors on seagrass growth and survival [176].

Chapter 4

Posidonia oceanica's ecosystem services

> *The importance of P. oceanica meadows, in addition to their biological value for biodiversity conservation, is linked to the ecosystem services they provide. Such services are important to the coastal ecosystem and to all the economic activities it supports. In this Chapter, the main ecosystem services are described, trying to give them an economic value in order to understand how Posidonia conservation is primary. Peculiar attention is given to the fact that Posidonia meadows play a main role in the carbon cycle because they accumulate and trap carbon in the sediment, hence representing a powerful tool in the control of climate change.*

4.1 Seagrass carbon sequestration

Seagrass meadows rank amongst the most productive ecosystem on Earth [79] and play a key role as habitats supporting high biodiversity [111]. "On average, net primary production per unit of area of seagrass populations, when considering that of leaves, rhizomes and roots, is about 1012 g DW m^{-2} $year^{-1}$, with a ratio above-ground: below-ground production of 16.4 ± 8.5" [79]. The biomass is largely consumed through respiration, especially by the photosynthetic epiphytes living on *P. oceanica* leaves; only a small part is consumed by herbivores. This means that a large portion of biomass is accumulated in the sediment and here remains for a long time due to lack of oxygen reducing decomposition rates of microbial metabolism. Sediment under *P. oceanica* meadows are very stable thanks to the strong anchoring system of rhizomes and roots, and also because *P. oceanica* is able to reduce the strength of currents and the wave motion, increasing sediment deposition and retention [99] and decreasing resuspension [138] [217]. The combination of all these factors allows the carbon sequestration in seagrass sediments, resulting in a tendency for seagrass ecosystems to be generally autotrophic communities acting as carbon sink [78]. A carbon sink is any natural or artificial stock where carbon can accumulate and reside for a time depending on the carbon inputs. Natural carbon sink can be terrestrial or marine: the carbon stored into these sinks is called green carbon in the former case, blue carbon in the latter. Typical green carbon sinks are rainforests and pastures, where carbon is sequestrated by photosynthesis and held in biomass and in the soil below. Mangrove forests, salt marshes and seagrass beds are the most relevant blue carbon sinks. Especially, seagrasses have a capacity to sequester carbon 35 times faster than tropical forests [143] and the carbon residence times in their sediments are very long: this makes seagrasses one of the most important carbon storage ecosystems. Terrestrial and marine carbon sinks have a different behaviour and a comparison is necessary, if we want to understand the mechanisms, make correct estimates and previsions and take the right decisions in managing them. First: the residence time. Thanks to the formation of sediments and to the longevity of some plants, marine ecosystems bury carbon for longer periods than the terrestrial ones: a rainforest can store carbon for decades or centuries, while a blue carbon sink can keep it for millennia; the residence time ranges from decades for the biomass to millennia for the sediments [152] [161] [93]. Second: carbon saturation. Unlike the terrestrial burying ecosystems, the marine ones do not become saturated with carbon, because sediments accumulate vertically, so there is a continuous creation of new storage space for the incoming carbon. Third, the marine plant biomass is much less than the terrestrial one, but it is more efficient: total marine biomass equals only 0.05% of the terrestrial one, but it stores the same amount of carbon per year. Fourth, marine ecosystems are more endangered than the terrestrial ones: they are disappearing four times faster than terrestrial habitats, and their rate of loss is even accelerating, from 0.9% per year until the '70s, to 7% per year in the last decades. Fifth, our consideration and valuation of the two categories of sinks is undeservedly different: in our society there is a relatively deep knowledge of green carbon sinks, the benefits they provide and the threats they are facing, while there is a lack of information about blue carbon sinks, maybe owing to their submerged location or their humble, unsightly appearance. Finally, another fact to be taken into account is that being underwater, seagrass sediments are free of fires, which are responsible for the emission as CO_2 of much of the organic carbon accumulated in forest soils on land. Seagrass meadows are responsible for 50-70% of the global carbon sequestration in marine sediments despite occupying 0.5% of the ocean surface [82]. The actual estimates of the CO_2 stored by seagrasses are about 586-681 g CO_2 m^{-2} $year^{-1}$. The behaviour of seagrass and the carbon fate Fig. (4.1) are closely related to the balance between gross primary production (GPP) and respiration (R). When GPP is greater than R (GPP>R), seagrasses bind carbon in their sediments and the carbon stock increases. When GPP and R are equal (GPP=R), the stock does not grow and the stable meadow is only a carbon store. Finally, if the carbon produced by respiration is more than one consumed by photosynthesis (GPP<R), seagrasses become a carbon source. Of course the health conditions of a meadow are important in determining whether it acts as a carbon sink or carbon source: a damaged or degraded meadow will give a bit of the stored carbon back to the atmosphere. “Seagrass meadows tend to be net autotrophic ecosystem when GPP exceeds 186 mmol O_2 m^{-2} day^{-1}, and seagrass meadow tend to act as CO_2 sink when average aboveground biomass exceeds 41 g DW m^{-2}”. C stored in seagrass meadows consists of C stored in the:

- above ground (minor component) and below ground biomasses (roots and rhizomes);
- sediment within organic (bacteria, microalgae, and detritus) and inorganic (carbonates) forms.

It is important underline that normally only the carbon stored as carbohydrate is considered, while carbonates are not included. Moreover we must take into account there are two types of carbon stock: a short-term stock and a long-term one, more important for C cycle and balance. The first type consists of the carbon into leaves tissues not buried in the sediments due to the leaves fall and are decomposed by bacteria; it is need to consider also the carbon produced by the epiphytes species living attached to the leaf surface: this is lost when the leaves are eaten by grazers [224]. The long-term stock is the carbon stored by roots and rhizomes into the matte, whose long residence time is linked to the low microbial activity and consequently slow decomposition rate [94]. It consists of the carbon produced by the seagrass, but also of the one produced by the benthic algae living in the meadows and, finally, from allochtonous one whose sedimentation is promised by the seagrass reducing water flow.

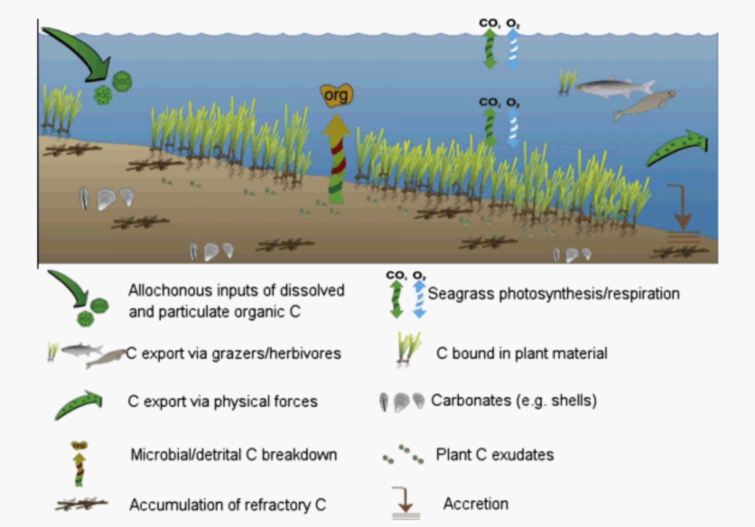


Figure 4.1: Conceptual diagram of the C stocks and fluxes in a seagrass meadow (from [144].

Unfortunately anthropic activities release large amounts of carbon into the atmosphere with drastic consequences as global warming and ocean acidification. The basic mechanisms of action for these impacts are the alteration of the amount and distribution patterns of energy and water, and the alteration of the functioning of the food webs of the ocean. These mechanism are intensified by human-mediated acceleration of the output fluxes from the massive natural carbon sinks turning them into sources to the atmosphere by means of an extremely efficient mineralization process: burning. The stocks of carbon slowly accumulated over millions to hundreds of millions years are being returned to the atmosphere and, concomitantly, to the oceans, in less than two centuries. Therefore, on the one hand we are releasing more greenhouse gases (GHGs) in the atmosphere, and on the other we are weakening the mechanisms by which these GHGs used to be naturally sequestered from the cycle. Reducing carbon emission is a necessary step in the fight against climate change. In addition, because GHGs will linger in our atmosphere for another hundred years, there is also a need to find ways to remove C from it. Bio-sequestration is one promising option that capitalises on natural CO_2 capture and storage by photosynthetic organisms: the oceans represent a unique resource for achieving this goal. A first input to the awareness of the significance of carbon sinks was in the Kyoto Protocol where seagrasses was not considered yet; since then many studies have been carried out in order to demonstrate the importance of the oceans in the carbon sequestration [82] [130]. It was estimated that coastal areas could contribute with about 10% to the needed carbon emission reduction: the seagrasses contribute for approximately 40% of this percentage. Unfortunately, seagrasses are suffering a rapid global decline, at a rate of about 5% per year [84] [161]. This is a risk to the environment conditions because it involves the release of large amounts of carbon in waters. From here carbon then returns to the atmosphere even it is unknown in which percentage. Is it possible that meadow C that is oxidised via disturbance, exposure, or diagenesis is retained, buried, or merely redistributed within the aquatic environment and not lost to the atmosphere. For example, if sedimentary organic C were to be mineralised into CO_2 and fluxed into the water column, it may then undergo two fates:

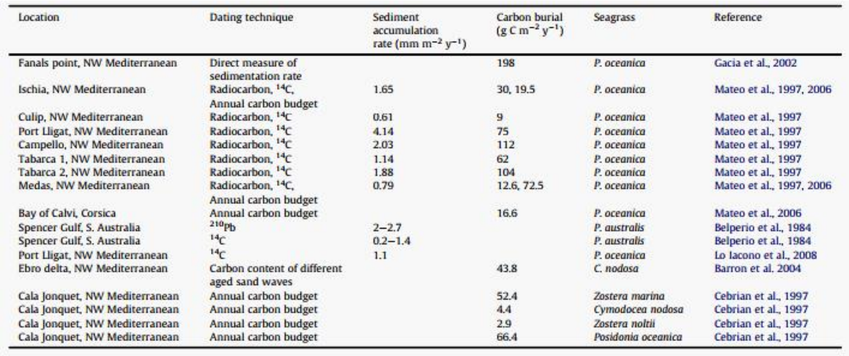
- it could exit the water column and pass into the overlying air, thereby contributing to atmospheric CO_2;
- it could be remain within the water column and undergo speciation to form carbonic acid (H_2CO_3), hydrogen carbonate (HCO_3^-), or carbonate (CO_3^{2-}).

In the latter case, there would be a carbon recycling, with a carbon sequestration by seagrass for one more time. In any case, there is a clear need to carry out further and more thorough studies on this issue. The seagrasses recovery can occur through planting programs but above all through the preservation of their habitat. It is therefore necessary to improve our knowledge on the seagrasses, filling the existing gaps in order to make right choices for their conservation and recovery. The actions require to address current uncertainties include improving estimates of global seagrass cover, reaching a more comprehensive knowledge of carbon stocks and burial rates over different time scales, and elucidation of the fate of the carbon exported from seagrass meadows because it can be buried in sediments at least tens of meters away. Seagrass meadows range greatly in their capacity to act as carbon sinks. Whereas this variability is partially associated with changes in the biomass and species composition of the meadows, it will be fundamental improve models (still lacking) able to predict the carbon sink capacity of seagrass meadows and identify the factors responsible for variability in seagrass carbon sink capacity. The models could be crucial to identify suitable areas to support seagrass growth, including light requirements, sediment characteristics and dynamics, wave and energy environment an even biotic requirements.

4.2 Carbon stocks estimation

In the last decades, several methods have been developed to calculate the amount of carbon stored by *Posidonia oceanica* meadows Fig. (4.2). Most of them are based on metabolic calculations: the difference between how much C is produced and how much C is consumed can be assumed as the stock potentially accumulated in the sediment. With this metod Duarte and CebriÃ n [78] estimated, "that, on average, 16% of seagrass primary production accumulates in sediment". However, these are indirect evaluation that do not take into account the differences between seagrasses species and provide information on short-term accumulation. A more direct method is based on sediment traps able to record the amount of sinking particles. Finally radioactive isotopes (lead, ^{210}Pb and carbon, ^{14}C) are used: being their decay time known, the age of a sediment layer can be derived from the amount of isotope that the layer contains; this method provides information of the long-term stock.

In Duarte (2013) [85] a model was developed to estimate long-term carbon stock, taking into account both the autochthonous carbon produced by the meadow and the allochthonous one derived from outside inputs. This model, used in restoration programmes, has been applied to five different seagrass species, but *P. oceanica* is not included. In the model, patches of 1 m^2 were used, with an internal shoot density equal to their steady-state value: shoots can extend radially at the same rate of rhizome growth. Duarte et al. have estimated an average carbon sequestration rate of 610 g CO_2 m^{-2} year^{-1}; interesting is the identification of the threshold 42 g DW m^{-2}, below which carbon is not stored [86]. Mateo and Serrano (2009) [139] calculated an indirect estimate of the carbon stored by the plant itself. According to their



Location	Dating technique	Sediment accumulation rate (mm m^{-2} y^{-1})	Carbon burial (g C m^{-2} y^{-1})	Seagrass	Reference
Fanals point, NW Mediterranean	Direct measure of sedimentation rate		198	*P. oceanica*	Gacia et al., 2002
Ischia, NW Mediterranean	Radiocarbon, ^{14}C, Annual carbon budget	1.65	30, 19.5	*P. oceanica*	Mateo et al., 1997, 2006
Culip, NW Mediterranean	Radiocarbon, ^{14}C	0.61	9	*P. oceanica*	Mateo et al., 1997
Port Lligat, NW Mediterranean	Radiocarbon, ^{14}C	4.14	75	*P. oceanica*	Mateo et al., 1997
Campello, NW Mediterranean	Radiocarbon, ^{14}C	2.03	112	*P. oceanica*	Mateo et al., 1997
Tabarca 1, NW Mediterranean	Radiocarbon, ^{14}C	1.14	62	*P. oceanica*	Mateo et al., 1997
Tabarca 2, NW Mediterranean	Radiocarbon, ^{14}C	1.88	104	*P. oceanica*	Mateo et al., 1997
Medas, NW Mediterranean	Radiocarbon, ^{14}C, Annual carbon budget	0.79	12.6, 72.5	*P. oceanica*	Mateo et al., 1997, 2006
Bay of Calvi, Corsica	Annual carbon budget		16.6	*P. oceanica*	Mateo et al., 2006
Spencer Gulf, S. Australia	^{210}Pb	2–2.7		*P. australis*	Belperio et al., 1984
Spencer Gulf, S. Australia	^{14}C	0.2–1.4		*P. australis*	Belperio et al., 1984
Port Lligat, NW Mediterranean	^{14}C	1.1		*P. oceanica*	Lo Iacono et al., 2008
Ebro delta, NW Mediterranean	Carbon content of different aged sand waves		43.8	*C. nodosa*	Barron et al. 2004
Cala Jonquet, NW Mediterranean	Annual carbon budget		52.4	*Zostera marina*	Cebrian et al., 1997
Cala Jonquet, NW Mediterranean	Annual carbon budget		4.4	*Cymodocea nodosa*	Cebrian et al., 1997
Cala Jonquet, NW Mediterranean	Annual carbon budget		2.9	*Zostera noltii*	Cebrian et al., 1997
Cala Jonquet, NW Mediterranean	Annual carbon budget		66.4	*Posidonia oceanica*	Cebrian et al., 1997

Figure 4.2: Summary of estimates of sediment accumulation and carbon burial rate in seagrass meadows (from [85]

study, the leaf net production ranges between 45 and 542 g C/m^2 per year, while the production made by rhizomes and roots corresponds to about 30% of this amount, so the resulting overall production ranges between 60 and 705 g C/m^2 per year. Their indirect estimation of the stored carbon is calculated subtracting to this amount the quantities which are spent in some ways, and considering what remains as the probable quantity of stored carbon. Considering that 24-44% of the carbon is remineralized, 6-50% is exported and 6-20% is grazed, the remaining 11-47% is assumed to be sequestrated for short-term and long-term collectively. This percentage corresponds to a range between 7 and 331 g C/m^2 per year. They also estimate the amount of organic carbon flux which has a long residence time, that is about 6-175 g C/m^2 per year. Another way to analyse the storage process is to distinguish the contribution of the different parts of the plant. Let us start with a distinction between plant and epiphythes. Carbon sequestration is proportional to primary production, so we can use a quantification of this process to get an overview: the plant has a primary production ranging between 400 and 2500 g DW/m^2 per year, while the production made by the epiphytes ranges between 500 and 900 g DW/m^2 per year, for an overall estimated production ranging between 2000 and 3000 g DW/m^2 per year [28]. We should note that these global estimations only concern seagrasses living in shallow layers and that productivity decreases with depth because of the decreasing sunlight availability. Now, a more accurate distinction can be drawn among the parts of the plant. In their research Romero et al. (1995) [4]

noted down carbon concentration in different parts of the plant at different depths: the highest carbon percentage belongs to the roots. The research made by Romero et al. leads us to the third way to analyse the carbon storage process, that is variability: some exogenous variables have an influence and some studies about these effects are available. Romero et al. focused on the depth variable and pointed out that the plant, globally, has a higher C content when it lives in the shallow layer. Alcoverro et al. (2001) [3] instead studied the seasonality of carbon storage. In fact, this process is affected by seasonal changes in variables such as sunlight availability, water turbidity, photosynthetic parameters, respiratory rates, plant growth and distribution of its parts at different ages. Their results show that the overall C balance is negative from September to June and positive from July to August (at least in their sample), and that the annual C balance can be alternatively positive and negative in consecutive years. The purpose of this paper is to give a first input to a greater understanding of these mechanisms.

4.3 The *Posidonia oceanica*'s carbon sink

Because of its areal overwhelming dominance in the Mediterranean and because it is the only species for which some detailed and direct estimates of the sink are available, we will deal with the carbon sink associated to *P. oceanica.* The organic carbon buried in the sediments Fig. (4.3) is the main sink associated to *P. oceanica.* The source is the excess of organic carbon production of the highly productive ecosystem this species supports which, ultimately, is derived from the atmosphere.

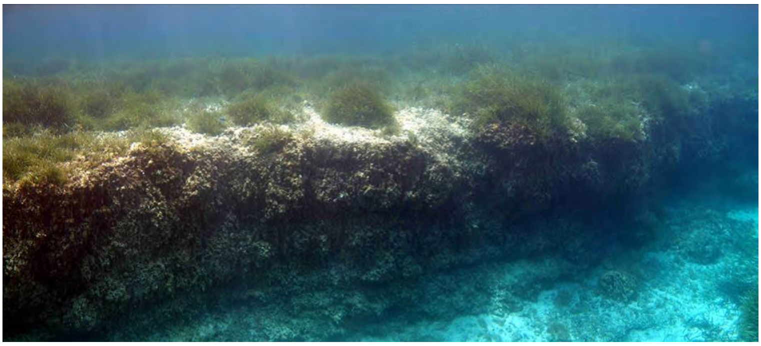


Figure 4.3: *Posidonia oceanica* sediments (from [140])

Our interest in the *Posidonia oceanica* seagrass is due to its ability to sequester carbon for a useful residence time. This process can be seen as a composition of three steps: taking it, storing it and not losing it. The whole mechanism can be analysed in different ways. First, basically, the input and output fluxes Fig. (4.4). Boudouresque et al. (2006) [28] pointed out two main organic carbon inputs and three carbon outputs in *Posidonia oceanica* ecosystems. The inputs are:

- heterotrophic plankton and particulate organic matter coming from the pelagic ecosystem;
- fishes that during the day eat zooplankton in a pelagic ecosystem and then are harboured by seagrass meadows at night.

These inputs represent a potential first step: the carbon they bring may be sequestrated. The outputs are:

- the so-called outwelling, that is the exportation of dead leaves, which causes the loss of a large part of the leaf production. This is an example of the failure: the carbon previously stored in these leaves is lost;
- fishes that, after growing up in the so-called seagrass nurseries, go away. This reduces the potential carbon input listed above;
- the organic carbon sequestrated in the matte for millennia. Actually, this is not a real output because it is not causing any carbon leakage: on the contrary, it is the successful realization of the photosynthesis processes.

The refractory nature of the *P. oceanica* rhizomes and roots tissues, fixing matter and sediment particulates, makes this seagrass an excellent long-term carbon sink. The carbon stored by *Posidonia oceanica* meadows it is estimate with the relationship between GPP and R, and thus with the balance between the carbon produced and the consumed one. The estimation corresponds to a range between 7 and 331 g C/m^2 per year ([14] [194] [152] [60] [155] [125] [**?**]): several researches come to an average value of around 83 g C m^{-2} y^{-1}. Other studies have investigated *Posidonia*'s health conditions along the coasts of the Mediterranean, in Spain, Italy and Malta ([204] [152] [69] [140]). These estimates show that, approximately, 10-25% of the net carbon fixed by the plant enters into the long-term stock with a rate of 47-138 g of C m^{-2} or 6-175 g C m^{-2} per year (average 90.5 g C m^{-2} per year). This amount, which can

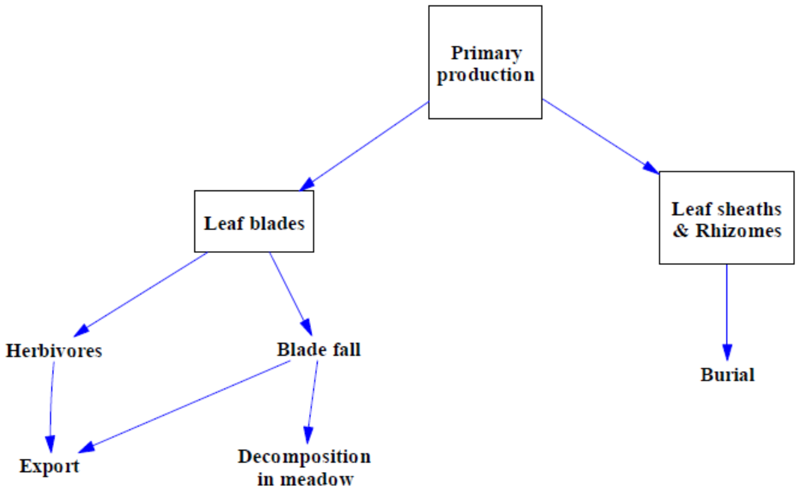


Figure 4.4: Fate of *P. oceanica* primary production. From [206]

represent 33-62% of the C stock [124], must be considered with the allocthon C giving a large contribution to the stocks, especially in the more superficial bathimetric levels: "at levels greater than 1 m in sediment, carbon stocks reach 5000 g C m^{-2} [153].". Considering the entire Mediterranean, *Posidonia*'s contribution to C-related seagrass in worldwide is between 0.5 and 20%. The research made by Romero et al. (1995) [4] leads to another way to analyse the carbon storage process, that is variability: some exogenous variables have an influence and some studies about these effects are available. Romero et al. (1995) [4] focused on the depth variable and pointed out that productivity decreases with depth because of the decreasing sunlight availability. Therefore the plant, globally, has a higher C content when stays in the shallow layer. In [3] instead studied the seasonality of carbon storage. In fact, this process is affected by seasonal changes in variables such as sunlight availability, water turbidity, photosynthetic parameters, respiratory rates, plant growth and distribution of its parts at different ages. Their results show that the overall C balance is negative from September to June and positive from July to August (at least in their sample), and that the annual C balance can be alternatively positive and negative in consecutive years. P. oceanica have been shown to be a C source (GPP<R) over winter

and a C sink (GPP>R) for the remainder of the year [97]. This model tries to explore, measure and predict how this delicate system changes and alters its mechanisms while dealing with human activities.

4.4 Economic evaluation of Carbon sink

Our model required a conversion of photosynthesis production values to carbon sequestration values so it is important to know the available possibilities to estimate the C storage and its economic value. In this section we describe the existing evaluation model, in order to find out which methods and prices are most popular. A similar review has been made in Jerath et al., [117] aimed at evaluating the environmental service provided by a mangrove forest in Florida. The main methods are:

- damage cost assessment, called SCC;
- damage avoidance method, very close to the Marginal Abatement Cost (MAC) curve evaluation method;
- market price analysis, that is the price of emission allowances and similar market products;
- stated preference approach, which reflects people's willingness to pay for emission reduction;
- shadow price of carbon, that is the carbon price adopted by governments.

Being *Posidonia oceanica* an endemic species of the Mediterranean Sea, it is better to consider the European Union Emission Trading Scheme (EU ETS). In this market the currency of exchange is the EUA (European Union Allowance): 1 EUA equals 1 Assigned Amount Units (AAU) and 1 AAU means 1 ton of CO_2 emitted. If the verified emission amount caused by a facility is lower than the allowed amount, this facility can sell some of its allowances to a facility whose emissions are exceeding the established threshold. In the end, each facility has to owe enough AAUs (or equivalent credits) to justify its emission amount, or it will have to pay a penalty.The determinants of price trends in the EU ETS market have been the object of extensive econometric enquiry. Alberola et al. [2] studied four main price drivers: policy issues, energy prices, temperature events and economic activity. As the allowance price is too variable [63] and too dependent on external factors to be a reliable approximation of the real value of 1 ton of CO_2, other evaluation methods should be considered. The answer may be found in the Marginal Abatement Cost (MAC) curves, that show for each sector how much the reduction of an additional ton of carbon costs; there are few studies, and each one models its own MAC curve(s). Now we focus on the social side of the issue and study the Social Cost of Carbon (SCC). MAC and SCC are just both sides of the same medal: the former quantifies the cost of abating 1 more ton of carbon, the latter the cost we will bear if we do not abate it. The Social Cost of Carbon represents the cost of not reducing the GHG amount in the atmosphere, and it is calculated as the net present value of the long-term impacts of 1 ton of carbon emitted today. It can be practically used to value the benefits of a policy or aimed at GHG reduction, for example protection activities on *Posidonia oceanica* meadows. Most of the existing studies calculate the SCC through an Integrated Assessment Model (IAM), that combines environmental and economic data and processes in order to predict the future Gross Domestic Product (GDP) along with the damages brought by climate change. The forecasted GDP is then discounted and compared to the present one (Sustainable Property, 2011). Since 1982 over 200 SCCs have been estimated, whose variability is due to the choice of four key parameters involved. First, the discount rate; the second parameter is the different areas; third, the chosen time horizon (it must be analysed in a long-term frame) and fourth, the choice to use either the median or the mean value. The variability in the estimates also depends on what matters according to the researchers. Some models only consider economic costs and benefits, while some others include also non-material factors such as welfare, biodiversity and sustainability. Resuming we can see that a ton of carbon dioxide in Europe is paid at around € 15 in the carbon market ([213] Point Carbon, 2011). This means that the organic carbon retained in *P. oceanica* sediments in the Mediterranean is woth € 6-23 m^{-2}. This is 9-35 times more than one square metre of tropical forest soil (€ 0.66 m^{-2} [130] or 5-17 times when considering both the above and the belowground compartments in tropical forests. So good and benefit (GB) provided by long-term sequestration of carbon achieved by *P. oceanica* in 2014 are thus estimated between 7.7 and 230 €/ha/year.

4.5 Economic evaluation of other ecosystem services

Seagrass meadow perform important functions for marine environment and for its use by humans Fig. (4.5), as protection against coastal erosion, supporting fish species with high commercial value, maintaining the sediment, absorption of pollutants and filtrating water [209]. In the Mediterranean basin *Posidonia oceanica* is the most common seagrass providing those services, but still today, its importance and the primary need of its conservation are poorly known [137] [67]). This is mainly because citizens, stakeholders but also policy makers, don't evaluate properly what, as ecosystem services, lacking of a specific economic value. So it Is important, for guide-lines policies, the identification and economic assessment of the ES provided by *P.oceanica* meadows in order to calculate the economic losses associated with environmental changes affecting dynamics of these ecosystems [66] [119]. The traditional ES and GB assessment pays specific attention to human and his interests and assigns a value to ecosystem services based on their actual use by populations. Recently, a new approach has been developed: it evaluates ES independently from the benefits that users could derive from them and from the public consideration of these ES [201]. Vassallo et al. [227] identified 25 ecosystem services through a review of available literature in order to evaluate the economic value of the species *P. oceanica*; their method was applied to a specific context, in the Marine Protected Area “Isola di Bergeggi” (Ligurian Sea, NW Mediterranean). They have taken into account the GB derived from the linked ES according to the Common International Classification of Ecosystem Services (CICES), which is the latest classification of ES approved by the European Commission (2013). This economic evaluation uses the GB market prices or the damage costs avoided, the costs that the authorities will not have to support thanks to the services provided by *P. oceanica.*

Posidonia oceanica leaves have been used since prehistory throughout the Mediterranean, especially as building insulation, but also to reduce the pollution of the waters. The dead leaves, dragged by wave motion, accumulate on the beaches, forming banquettes that often spoil the landscape of some seaside resorts. The use of these banquettes is regulated in a different way in each country: in general, they must not be kept in protected areas while they may be removed in other areas, subject to appropriate dero-

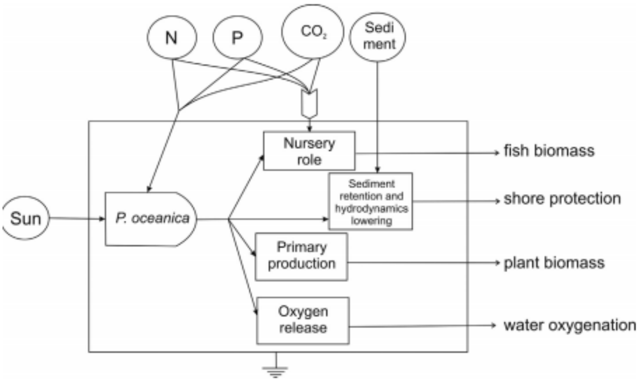


Figure 4.5: System diagram of *Posidonia oceanica* services (from [227]

gation. In this last case, it is possible obtain capitals or refunds for costs associated with banquettes removal. So the cost linked with the use of *Posidonia oceanica* as a material can be considered null. Other important role of *P. oceanica* is the protection from coastal erosion due to its ability to modify and control the hydrodynamics of waves and currents, the ability to stabilize sediments with its root and rhizomes [100] [68] and due to the banquettes developed by dead material accumulated on the beaches [154] [214]). Mangos et al. [146] estimated that such protection would cost around 150 €/ha/year, a cost that *P. oceanica* allows to break down. *P. oceanica*, being representative of the Mediterranean Sea, participates in the resilience of marine waters and wastewater treatment, decreasing water pollution and turbidity: Costanza et al. (1997) [66] calculated that this service is worth 4.8×10^6 €/year. Moreover *Posidonia oceanica* contributes to the maintaining water quality, with the oxygen production (more than 14 litres of oxygen per day per m^2 for [15]), making the Mediterranean Sea a hospitable environment for many fish species. The *P. oceanica* meadows constitute a very high biodiversity habitat, so their contribution to fishery improvement is essential: considering only adult fishes, Mangos et al. [146] have calculated that the economic value of this resourecs ranges between 27 and 35 €/ha/year. All estimated ecosystem services contribute to the maintenance of seaside tourism activities [39]. Finally, due to its important features, its sensitivity to environmental changes and its ability to accumulate heavy metals, *Posidonia oceanica* is considered an efficient bioindicator: studying it improves our knowledge of the dynamics and health conditions of coastal systems. Pugh and Skinner [200] calculated the value of this service through the cost of research projects: considering only LIFE and national projects the value is about 0.33 €/ha/year. The total economic value of the most important ecosystem services provided by *P. oceanica* ranges between 284 and 514 €/ha/year, it is about 22500 €/ha/year for Costanza et al. (1997), and about 172 €/m^2/year for [227]: the different values, often under-estimated, are due to the considered services and the use of economical evaluation method. Taking into account the current regression of *P. oceanica* and the difficult reversibility of the destruction of its meadows [167], those values allows to quantify the annual loss of this specie about € 1.11-2.00$\times 10^6$ for Mediterranean countries [227] .

Chapter 5

Review of relevant modelling efforts

This Chapter provides a brief overview of the previous models simulating the growth and production patterns of the seagrass Posidonia oceanica. Several biological studies have provided a big amount of qualitative and quantitative information and data on the characteristics of the Posidonia ecosystem and on the abiotic and biotic factors regulating and affecting it. Other studies have formulate mathematical models with descriptive and predictive purposes. An overview of the models known, with the biological information provided in the previous Chapters, can help to better understand the underlying premises of our model, and also provide suggestions for improvements in the next steps of this work.

5.1 Models of growth dynamics in seagrasses

Natural phenomena are characterized by extreme complexity in which operate numerous variables all intrinsically connected in a non-linear way. Mathematical models are important tools to create an idealized representation of reality that is expressed through a quantitative relationships between the system's characteristic variables. Modelling of seagrasses can be an effective tool to assess factors regulating their growth, to understand and predict the evolution of the system itself, and to understand the consequences of different actions, before employ them directly in nature. In the last decades an increasing interest in using computer models for developing such predictive capacity and exploring future options for natural resource management is evident [49]; there is plenty of literature about mathematical modelling of trophic networks in marine ecosystems using different approaches [203]. Over the last 30 years, part of the literature on seagrasses, not only in the Mediterranean Sea, had the aim to develop model simulations of the seasonal dynamics of the growth patterns of plant biomass, the time evolution of growth rates, and the flows of nutrients ([211] [239] [10] [145] [21] [88]). Most of these models are made for phanerogams [22] [237] also diffused in lagoon environments (*Zostera marina, Zostera noltii, Cymodocea nodosa*) that know worrying regressive processes in recent years. The models currently developed have been concentrated mainly on temperate species and especially on Zostera marina [106]; [228]; [169]; [10]; [21]. There are also studies on the biomass processes responsible of other species such as *Zostera noltii* [197], *Potamogeton pectinuatus* [114], *Potamogeton perfoliatus* [145], *Ruppia marittima* and *Halodule wrightii* [90]; [50]. Many models describing seagrasses are based on carbon, few are based on nitrogen, they do not make the distinction between nitrate and ammonium, and in general the models do not take into account the biomass of the rhizomes. Some of these models have been implemented to understand the effects of the macrophytic plants on the environment and vice-versa [57]; sometimes they have been implemented to describe seagrasses like an only one species without taking into account the specific differences, but in other cases, have been focused on individual species. The studies mentioned above employ a variety of methods to model and simulate seagrass communities. Since seagrasses, like *P. oceanica*, are connected to and influenced by other systems in the coastal zone, linking individual component models together enables the evaluation of a larger interacting set of dynamics, improving guidance for coastal management. An important point in seagrass research is their response to the presence or absence of a certain amount of nutrients; the models trying to investigate these mechanisms have remained at the level of physiological or quantitative models. These models often use the classic Michaelis-Menten and Monod equations to simulate, respectively, the nutrients uptake and the growth rate of marine plants in relation to the nutrient concentration in the substrate and in the water column . In other models the Droop equation or Cell-Quota Model is used, developed by Michael Droop, in 1968, to describe the growth and utilization of nutrients (especially organic nutrients) by algal cells. Zimmerman et al. [?, 240] developed a mathematical model on *Zostera marina* to simulate its response to nitrogen and radiation availability. The model was applied to make steady-state predictions about the relative effects of light and Ni availability on Ni absorption and partitioning between above and belowground tissues. It was also applied to estimate the Ni concentrations in the sediment and water column that would be required to saturate growth. A more complex model was developed to simulate photosynthesis and growth of *Z. marina* in lower Chesapeake Bay [232]. The model was based upon theoretical non-linear functions to simulate biologically controlled processes, and empirical or statistical relationships to include physical/chemical interactions and environmental forcing functions. Models that reliably predict population response to cultural eutrophication are lacking for most seagrass species, or limited to localized areas [220]; [92]; [109]. Seagrass response to nutrient loadings has proven difficult to quantify beyond localized areas because long-term data consistent in quality are generally lacking, an seagrass abundance and productivity in natural habitats are often highly variable from year to year because of stochastic meteorological and hydrographic conditions [225]; [220]; [52]. Early empirical models by Nielsen et al. [170] and Duarte [83] enabled simple predictions of areal loss of seagrass meadows following reduced water transparency from eutrophication. In consideration of future efforts to improve protection of remaining seagrass meadows and reduce nutrient loading, Duarte [83] noted that reversing the eutrophication process suggests replacement of rapidly growing algal species by more slowly growing seagrasses, with the expectation of increased lag periods between nutrient reductions and seagrass recovery. Duarte developed a simulation model for seagrass recovery from eutrophication as a non-linear process best represented by a logistic growth curve. This model projects that seagrass recovery will be more rapid with increasing rate of patch elongation than with increasing rate of patch formation. It predicts that the time scale needed for meadow re-formation (95% cover) would range from less than 1 years (small, rapidly growing species, e.g. Cymodocea nodosa) to about four centuries (large, slowly growing species, e.g. *P. oceanica*). Thus, although seagrass loss can be rapid, the ecosystem consequences may last for decades or centuries after nutrient reductions are imposed [83]. The analysis of literature available on the seagrasses shows a common approach to the system, about choice of model components (status variables, forcing functions, parameters) and mathematical formalization (predominantly differential equation systems). The structure of these mathematical models is mainly based on two state variables: the biomass of the above-ground system, and the biomass of below-ground system (rhizomes and roots), and sometimes the epiphites of each compartment. The seasonal evolution of these biomasses is considered predominantly due to two forcing functions: the water temperature and the light irradiance, both considered to be key factors in regulating the growth of the seagrasses [187]. Modellers may also want to account for socio-economic factors or behavioural patterns at the coast given that humans are an integral component of coastal ecosystems.

5.2 *Posidonia oceanica*'s growth patterns: modelling approaches

In the previous paragraph we have summarized the models about seagrasses as a big group of marine plants, and about seagrasses species different from *Posidonia oceanica*. There are many studies on the simulation of seagrasses growth dynamics, instead the available literature for *P. oceanica* is reduced. In addition to this lack of modelling on the *Posidonia oceanica*, it is necessary to note that this plant is different from the other seagrasses as far as its growth and physiology is concerned. This difference makes difficult the application to it of models made on other species and other areas. The existing models about *P. oceanica* are different from each other: much of the studies carried out since 1960 focused on the analysis of the growth dynamics of the *P. oceanica* meadows [75]; [182]; [45] at two different levels of investigation: the leaf (growth of single leaf) and/or the beam (cyclic renewal of leaves in the tuft). Moreover the models are often concentrate on different aspect of the habitat's dynamics and on different drivers and stressors [122]; [88]; [149]; [241]. In the next pages a review of the bibliography will be carried out, only about the species of our interest. In the first section, the main models simulating spatial growth of *Posidonia oceanica* meadows and the complex structures of their matte are briefly explained. The aim of these models is to describe how *P. oceanica* increase its underground roots and rhizomes in order to occupy the surrounding space. Also factors affecting growth patterns and the speed with which the meadows can extend themselves colonizing the environment are investigated. Next, we examine those models, closest to our model, that simulate the biomass production of *P. oceanica* meadows, thus focusing on plant growth due to balancing between photosynthesis and respiration processes. To our knowledge for *P. oceanica* there are two important production models: one concerning growth of only above-ground biomass based only on the temperature, and the last one considering the physiology of the whole plant and the influence of change in forcing functions such as light.

5.2.1 Spatial model: Molenaar et al., (2000)

In the study of Molenaar et al. [164] in order to predict the growth pattern of transplanted cuttings, a mathematical model is developed, based on the analysis of the growth process, the branching process, the rate of transformation from plagiotropic to otrhotropic branches, and the mortality of plants. "The mathematical model is constructed in order to quantify the distribution of internodes within growth units from different morphological types of axes and branching orders" Fig. (5.1). Eighty samples are collected, at 6 m depth, from a *P. oceanica* meadow near Cannes, France. Finally the observed frequency distribution are compared to model ones; the result are compiled from 12 years. The order-1 axis is the principal plagiotropic rhizome of each sample, the order-2 axes are the lateral branches borne by an orde-1 axis, the order-3 axes are the branches borne by order-2 axes. The internode is the part of the rhizome produced between two successive leaves. The growth unit is the part of the rhizome produced during one lepidochronological year corresponding to about 12 months.

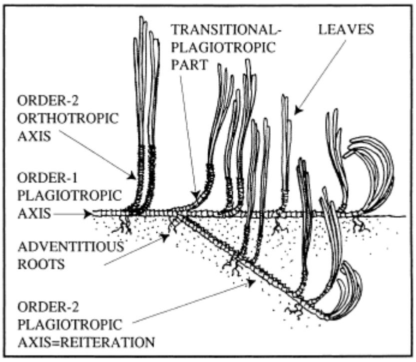


Figure 5.1: Axes differentiation in *Posidonia oceanica* (from [164])

In this model the growth process is described by frequency of the number of internodes produced per annual growth unit; the branching process is described by the frequency distributions of the internodes bearing a lateral axis in relation to their rank on the growth unit. To estimate the natural mortality rate as a function of age, the viability of the meristems is considered. The transformation process in the meristem is expressed by the probability of modification of the orientation of the axis during the following growth stage. Assuming that the transformation rate is constant from one growth unit to the next one, having chosen axes with a N growth units, the probability for a growth unit to become orthotropic after N plagiotropic growth units is Eq. 5.1:

$$1 - F(N) = C^N \tag{5.1}$$

where $F(N)$ is the percentage of plagiotropic growth units not transformed into orthotropic ones and C^N the probability of the rhizome to remain plagiotropic Eq. 5.1. The results reveal that the frequency distribution of internode formation per growth unit on plagiotropic axes changed according to branching order Fig. (5.2). It is governed by a Poisson distribution on order-1 axes, by a binomial distribution on order-3 axes and by any combination of the two laws on order-2 axes. The production of internodes per growth unit on orthotropic axes follows a binomial frequency distribution. The model shows that each year two series of branches occur in *P. oceanica* statistically, with different probabilities according to branching order.

5.2.2 Spatial model: Kendrik et al., (2005)

The study of Kendrick, MarbÃ and Duarte [123] investigates the role of slow horizontal and vertical growth of rhizomes in the formation of topographic complexity in *P. oceanica* matte using agent-based modelling. The simulated infilling of landscapes by *P. oceanica* is run over 600 iterations (years) for 10 random starts of 150 agents each. This modelling study focuses on seagrass clonal growth rules, while maintaining all other demographic and environmental variables fixed, to study the rates of spreading and expansion of *P. oceanica* meadows in three dimensions. The pattern of spread of agents was initially random in direction but, as the simulation time passes, larger patches were formed, and the canopy spreaded radially from these patches Fig. (5.3). The matte developed from growth of patches and its greatest

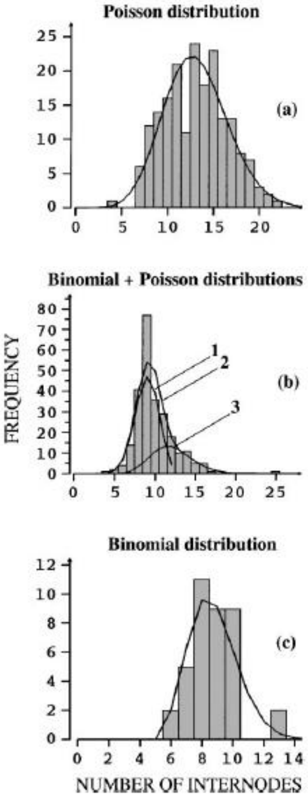


Figure 5.2: Frequency distribution of the number of internodes per growth unit. Bars:field data. Line:model. (a) in plagiotropic order-1 axes. (b) in plagiotropic order-2 axes: 1 is the model of the mixture of all data, 2 is a binomial model corresponding to short growth units and 3 is a Poisson model corresponding to long growth units. (c) in plagiotropic order-3 axes (from [164])

height occurred in more continuously occupied cells of the grid. The topography of the reef that occupied two-thirds of the landscape after six centuries of growth could be described as a pattern of channels between reef plateaus elevated 1 e 2 m above channels. These results demonstrate that development in *P. oceanica* meadows of three-dimensional structure, in the formation of biogenic reefs, can be explained by, and is an emergent property of, slow horizontal and vertical rhizome growth rates combined with the time it takes for the accumulation of rhizomes in any region of the landscape.

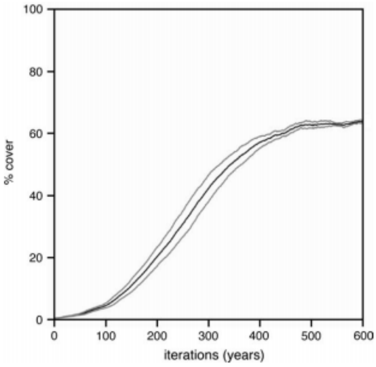


Figure 5.3: The simulated increase in mean % cover by seagrass agents with time (from [123]

The complexity of the simulated reefs developed by *P. oceanica* result from the slow horizontal spread of rhizomes of this species relative to the rate of vertical reef formation. It is precluded the ability to externally validate the outcomes through direct observations or experimental manipulations, as the time scales involved are of several centuries. Yet, the timespan for colonisation for the development of meadows derived from this modelling effort (more than 600 years) is in agreement with results derived from previous, independent models (600 years from [83]) and extrapolations from field. Previous models of patch extension and spatial occupation by seagrasses represent constant horizontal spreading rates [83] [147] [121], whereas the SWARM model simulates growth of individual agents and allows for local interactions between agents, consistent with such dynamics implicit in recent evidence of density dependence in seagrasses [150] [123] [215].

Forecasting capabilities about the future of species or habitats and their health conditions, are critical in defining the guidelines for environmental protection and conservation [226]. Making management decisions for seagrasses is always difficult because they are very complex systems, regulated by synergic interaction of different drivers and stressors. The same is true for *Posidonia oceanica*, a very long-lived species whose position in space is influenced, for example, by wave motion, but also by extreme events such as big storms [116]. Vacchi et al. [223] have developed an innovative predictive model that can accurately identify the seafloor portion where the meadow upper limit should lie in natural conditions Fig. (5.4) (conditions governed

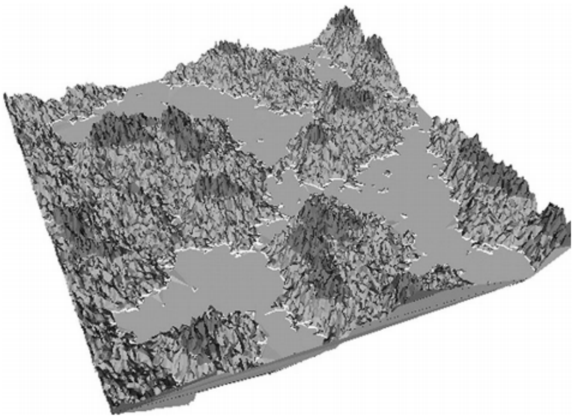
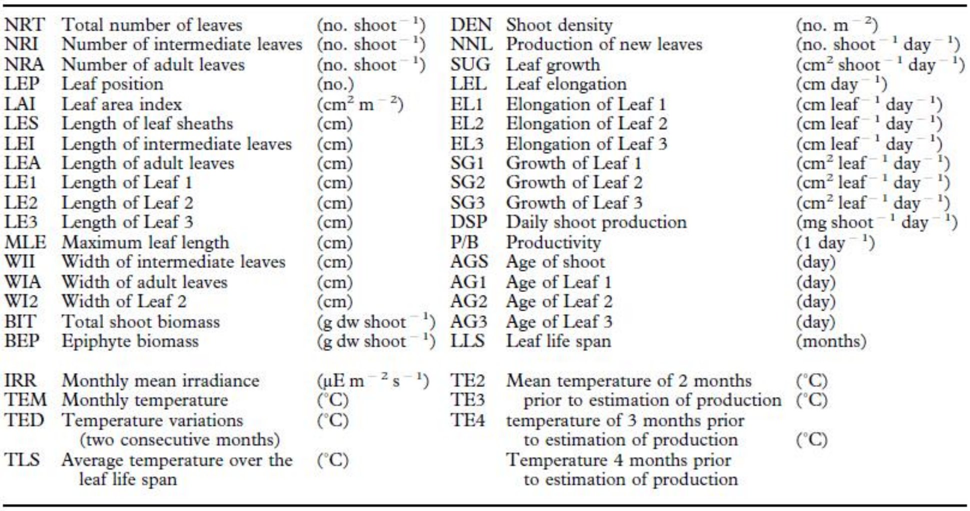


Figure 5.4: Three-dimensional representation of matte height after 300 years of growth. The light grey surface is 0-1 m in height and the dark grey is >1 m in height. This is a randomly chosen example from a single simulation (from [223])

only by hydrodynamics, in absence of significant anthropogenic impact), and that could provide the proper tool to define reference for healthy meadows.

5.2.3 Production model: Zupo et al., (1997)

The work of Zupo et al. [241] developed a mathematical model based on the dynamics of monthly production of new leaves of *P. oceanica*, on the growth of each leaf in a shoot and on the relative effects of temperature on these descriptors. The main aim of this research was to assess the influence of temperature on the spatial and temporal growth pattern of *P. oceanica* and also identify efficient descriptors of leaf primary production to achieve a simple method by which evaluate seasonal plant growth. It takes into account short-term (seasonal) and long-term (annual) production patterns, rate of leaf elongation and several phenological parameters like number and length of young, intermediate and adult leaves, shoot and epiphyte density and biomass. A continuous *P. oceanica* bed in Lacco Ameno (Island of Ischia, Gulf of Naples), were studied over 1 year: a shallow site at 5 m and a deep site at 22 m were chosen. Each month, 20 shoots were collected from both sites for phenological studies, and other 20 shoots were marked according to the Zieman method (1974) and used to obtain leaf production and length measurements, as described in Buia et al. (1992). Each leaf in the shoot was followed from the date of appearance to abscission. Irradiance and water temperature were monitored monthly, during the study period, at both sampling stations: for light each value represents the mean of three daily measurements obtained during the same day; for temperature data were collected on 1 day in each month. The relationships between biological and environmental factors were described using linear and non-linear equations. The significance of the correlation coefficients and regression analyses was tested by means of Analysis of variance (ANOVA), the analysis tool used in statistics to compare more than two groups at the same time, to determine whether a relationship exists between them. The best correlation obtained were applied to the production model.



NRT	Total number of leaves	(no. shoot^{-1})	DEN	Shoot density	(no. m^{-2})
NRI	Number of intermediate leaves	(no. shoot^{-1})	NNL	Production of new leaves	(no. shoot^{-1} day^{-1})
NRA	Number of adult leaves	(no. shoot^{-1})	SUG	Leaf growth	(cm^2 shoot^{-1} day^{-1})
LEP	Leaf position	(no.)	LEL	Leaf elongation	(cm day^{-1})
LAI	Leaf area index	(cm^2 m^{-2})	EL1	Elongation of Leaf 1	(cm leaf^{-1} day^{-1})
LES	Length of leaf sheaths	(cm)	EL2	Elongation of Leaf 2	(cm leaf^{-1} day^{-1})
LEI	Length of intermediate leaves	(cm)	EL3	Elongation of Leaf 3	(cm leaf^{-1} day^{-1})
LEA	Length of adult leaves	(cm)	SG1	Growth of Leaf 1	(cm^2 leaf^{-1} day^{-1})
LE1	Length of Leaf 1	(cm)	SG2	Growth of Leaf 2	(cm^2 leaf^{-1} day^{-1})
LE2	Length of Leaf 2	(cm)	SG3	Growth of Leaf 3	(cm^2 leaf^{-1} day^{-1})
LE3	Length of Leaf 3	(cm)	DSP	Daily shoot production	(mg shoot^{-1} day^{-1})
MLE	Maximum leaf length	(cm)	P/B	Productivity	(1 day^{-1})
WII	Width of intermediate leaves	(cm)	AGS	Age of shoot	(day)
WIA	Width of adult leaves	(cm)	AG1	Age of Leaf 1	(day)
WI2	Width of Leaf 2	(cm)	AG2	Age of Leaf 2	(day)
BIT	Total shoot biomass	(g dw shoot^{-1})	AG3	Age of Leaf 3	(day)
BEP	Epiphyte biomass	(g dw shoot^{-1})	LLS	Leaf life span	(months)
IRR	Monthly mean irradiance	(µE m^{-2} s^{-1})	TE2	Mean temperature of 2 months	(°C)
TEM	Monthly temperature	(°C)	TE3	prior to estimation of production	(°C)
TED	Temperature variations (two consecutive months)	(°C)	TE4	temperature of 3 months prior to estimation of production	(°C)
TLS	Average temperature over the leaf life span	(°C)		Temperature 4 months prior to estimation of production	

Figure 5.5: Main leaf features and environmental variables considered in the Zupo model (from [241])

The model, running by MS Excel software, consists mainly of differential equations whose general formulation is: $dX(t) = f(X(t))$, assuming that $dX(t) = X(t + dt) - X(t)$. The $X(t + dt)$ computed becomes the $X(t)$ for the next $X(t+dt)$ at each time step, as starting values are given for variables, and parameters are fixed. Posidonia production was computed over a 1-year period using a 1-day time step, while a check for the number of new leaves (NNL) that had appeared was simulated using a time step of 30 days. The model takes into account the date of appearance of each leaf and the water temperature to calculate the age and the daily elongation rates of leaves. The function Age_i Eq. 5.2 defines the age of each leaf in a shoot, according to its rank (from 1 to 7):

$$Age_{i(t)} = Age_{i(t-dt)} + (dt + Shift_{i-1} - Shift_i) \tag{5.2}$$

where i is the leaf rank and t is the time. The function $Shift$ rearranges the age of each leaf, taking into account the shift to higher ranks due to the appearance of a new leaf. The values assumed by these function, therefore, depend on the number of new leaves appearing (a maximum of two leaves per month is considered). To validate the model, simulations of production for several Mediterranean meadows were performed using the production and temperature data reported in the literature. The model, applied to a historical series (four years) of monthly temperature values measured in the prairie of Ischia (Tyrrhenian Sea - southern Italy), provides a long-term simulation of *Posidonia* leaf growth in the studied area.

5.2.4 Production models: Elkalay et al., 2003

A more complex approach is the one developed in Elkalay's study [88] based on a production model of *P. oceanica* occurring in the Bay of Calvi (Corsica, Ligurian Sea, NW Mediterranean). The model presented by Elkalay fills a gap in existing models in that it is a whole-plant approach: in particular changes in below-ground biomass are explicitly included. The model describes the development processes and variations in biomass and growth of *P. oceanica*, in relation to some forcing functions: irradiance, water temperature, availability of nutrients and space. The state variables are the belowground (roots, rhizomes) and aboveground (leaves, epiphytes) comparts, the epiphyte biomass and the internal nitrogen concentration of the whole plant. The state variables and the forcing variables considered in this model are schematically shown in the figure Fig. (5.6).

The growth is the result of the balance between productive and degenerative (consuming biomass) processes occurring in each of the different compartments considered (roots and rhizomes, leaves, epiphytes) and their interactions, under the influence of various physical factors (temperature, irradiance), chemical factors (nitrogen concentrations in water column, epiphytes, plant) and mechanic factors (grazing, hydrodynamism). A simple system of differential equations Eq. 5.3 describes, for each of the state variables

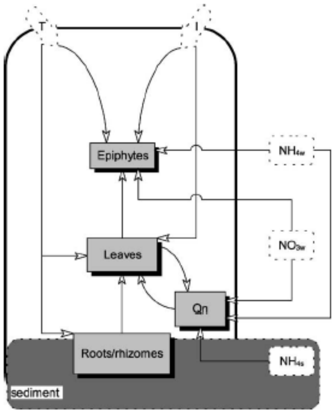


Figure 5.6: Diagrammatic representation of interactions between main ecological state variables. (T) temperature, (I) irradiance, (Q_n) nitrogen concentration in seagrass, ($NH4_w$) ammonium water column, ($NO3_w$) nitrate water column, ($NH4_s$) ammonium in sediment pore water (from [88])

considered (V_s), the variation of biomass and growth:

$$\frac{dV_s}{dt} = (GroV_s - transV_s - ResV_s) \times V_s \tag{5.3}$$

where $ResV_s$, the respiration rate coefficient for each state variable ($\text{day}^{-}1$), and $transV_s$, the translocation rate between different compartments (from leaves to epiphytes and from roots and rhizomes to leaves), are subtracted from the daily growth rate coefficient, $GroV_s$ Eq. 5.3. The influence of limiting factors is considered in a multiplicative formulation with the assumption that light, temperature, nutrient and space act independently on the growth. The shading effect is not introduced in this model, because this factor is related to space limitation mechanism (S) to control the carrying capacity of the system; the self-shading increases as a consequent of the increase in space limitation for leaves Eq. 5.4:

$$f(S) = 1 - \exp\left[-\left(\frac{V_s - sV_s}{k_sV_s}\right)^2\right] \tag{5.4}$$

where sV_s is the maximum V_s biomass, and k_sV_s is the V_s growth dependence on the space availability Eq. 5.4. The same equations are used for leaves, below-ground biomass and epiphytes, changing the specific coefficients. In the model the transport from below to above-ground material is also considered. The formulation used assumes that transport is proportional to below-ground biomass up-take rate by means of translocation coefficient k_{trans} estimated by model calibration. For the translocation from leaves to epiphytes they consider that part of the nutrients released by leaves are immediately consumed by epiphytes. In this model respiration is the only permanent mechanism of loss of leaf biomass, which is modelled as temperature dependent Eq. 5.5:

$$ResV_s = resV_s \times f(T) \tag{5.5}$$

where $resV_s$ is the maximum V_s respiration rate Eq. 5.5. The sensitivity of the model to altered light regimes is evaluated by varying the water depth (10, 20 and 30 m) and the average annual water column light attenuation. Finally the model predictions are compared with in situ measurements showing a good accordance, except for 30 m probably because the accuracy of the measured parameters would decrease with depth Fig. (5.7).

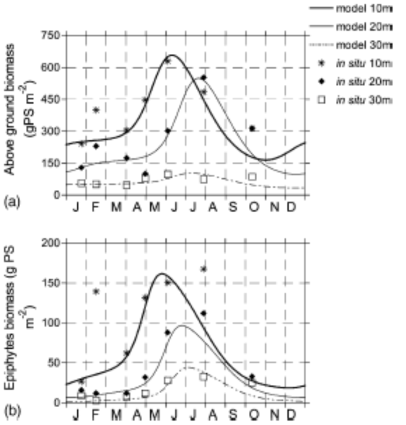


Figure 5.7: Simulated (lines) and measured (points) values for leaves (a) and epiphytes (b) biomass (g DW m^{-2}), at 10, 20, 30 m (from [88])

To evaluate the influence of light intensity changes, they create an artificial disturbance by increasing the attenuation coefficient by 10% and 20%. The same increase is applied at different periods in the year, and with different frequency and duration. Then they evaluate at each depth the percentage of mean annual biomass, losses for above and below-ground biomass. This percentage increases with time and depth and it is higher for leaf biomass. The biomass loss is higher at the beginning of the year, it increases with increased duration and it is positively correlate with frequency. Fig. (5.8)For the below-ground biomasses there are less measurements, limited at 10 m: the simulation indicate that the root biomass shows very small seasonal changes, in contrast to the leaves biomass.

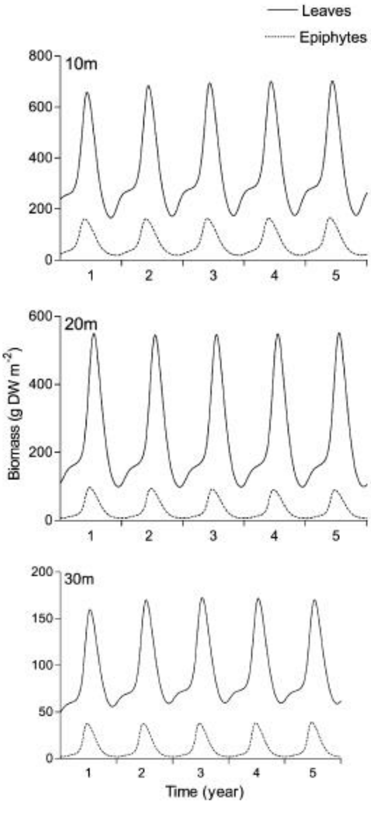


Figure 5.8: Biomass production of leaves and Epiphytes (from [88])

Chapter 6

Model development

A section explaining the premises of our model is fundamental. Posidonia oceanica's habitat is a very complex ecosystem where several internal and external components interact, hence determining the characteristics of each meadow. Environmental factors such as depth, light, nutrient abundance, and epiphyte pressure play a large role in altering meadow primary production and the resulting flux of matter and nutrients [191]. Understanding the relationship between photosynthetic capacity and the factors that regulate is important for estimating the productivity of P. oceanica habitat [3]. The purpose of this chapter is to describe the main drivers regulating the seasonal dynamics of leaf production of a P. oceanica's meadow and the way it is mathematically translated into the model. Therefore, in the next pages, a detailed description of our theoretical model is given, based on a thorough bibliographic research about the main biological mechanisms involved in the turnover of the aboveground biomass of Posidonia oceanica.

6.1 Conceptual model

The seagrasses systems behaviour is complex and difficult to predict. Orth et al. [176] and other authors [27] acknowledge the complex ways in which multiple stressors affecting seagrasses operate simultaneously, at different temporal and spatial scales, with interacting effects. A system dynamic is a powerful tool for a better understanding of the complexity inherent within a seagrass ecosystem, in order to guide resource management. Its advantage is that it allows a modelling method integrating “contrasting disciplines that are pertinent to the system being modelled, and avoids the need to couple multiple models” [216]. System dynamics was developed in the 1950s, by Jay Forrester at the Massachusetts Institute of Technology (MIT) to improve the understanding of strategic management problems in complex, dynamical systems [91]. A network of cause and effect relations between the elements within a given system is first con-structed. These causal links constitute the feedback processes that generate a system’s dynamics. Therefore we developed a conceptual model describing the hypothetical representation of critical state variables and processes occurring in a *Posidonia oceanica* meadow. First of all it was necessary a thorough bibliographic survey and a preliminary analysis of available data to evidence key elements (KE) driving ecosystem evolution. The definition of KEs characterise the ecosystem is of primary relevance: in order to write the equations representing the model, it is necessary to evaluate the strength of the interactions and dependencies among the various KEs, and towards the stressors, separating spurious correlations from actual causal relationships. System dynamics uses stocks and flows to capture the fundamental dynamics of a complex system [216]. Stocks represent sinks or reservoirs in a system and accumulate the difference between an inflow and an outflow to a process. Biomass produced by a *Posidonia oceanica* meadow can be considered a stock Fig. (6.1): then it is important identify inflow that “grow” this stock (e.g. photosynthesis) and outflow that “deplete” the stock (i.g. senescence and leaf shedding).

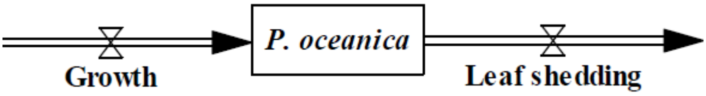


Figure 6.1: Example stocks and flows for *P. oceanica*

The current version of the model does not simulate belowground biomass stocks, and focuses on the material produced aboveground: this is a production model and, according to [87], we can suppose that 84% of the *P. oceanica* total production may be contributed by the above-ground biomass. The biomass stock of *P. oceanica* is estimated by the balance between the process increasing biomass, and processes that remove biomass. We suppose that our simulated meadow was a 1 m^2 patch of a *P. oceanica* meadow. This extention is not random: it has been chosen to manage the density and health conditions of our meadow, and it is performed setting the meadow shoot density, according to Pergent [190]. The area occupied by the canopy is fixed in our model, the dynamics by which the habitat patch may proliferate and increase their areal extension is not considered here. The number of active cells, containing a stolon able to develop leaves and produce biomass, is randomly selected at the beginning of the simulation and remains fixed throughout the simulation time. However, this number is generated by comparison with a fixed threshold read by the model from an external file. By varying the value of this threshold, it is possible to manage the number of beams active in the meadow and thus the potential density that it can reach. Seasonal conditions are simulated by different values of temperature (T) and surface irradiance (L). These values are derived from the web and referenced to the geographical area of the province of Livorno (Italy), where most of the studies on *Posidonia oceanica* in Tuscany are concentrated. Fifty-two values, one for each week of the year, have been selected (both for temperature and light) in order to simulate the observed seasonal changes and how it affects the dynamics of the meadow production: for light the maximum occurs in June and the minimum in December, for temperature the maximum in August and minimum in February. A conceptual diagram illustrates the core processes that control plant growth and abundance in the model. Forcing functions, indicated by rectangles, represent inputs of energy and materials from outside the system, such as temperature and light. The rhombus represents the main state variable, the leaf biomass, and arrows indicate flows of materials and energy between the state variable and the forcing variables within the system. A polarity is assegned to each link, positive (+) or negative (-) to indicate the way in which the dependant variables change in function of the independent variables [216]. Positive links imply that an increase (or decrease) in the cause will result in the affected variable being higher or lower than it would have been if that cause was held constant. Negative causal links, on the other hand, imply that an increase (or decrease) in the cause results in the affected variable being lower (or higher) than it would have otherwise been. The model, as shown in the conceptual diagram Fig. (6.2), focuses on a single state variable represented by the biomass of single leaf, while all the factors that we consider to control the growth processes are forcing functions: the light absorption and the contribution of nutrients increase the leaf biomass, while the epiphytes' attachment and the shadowing of nearby plants decreases the growth.

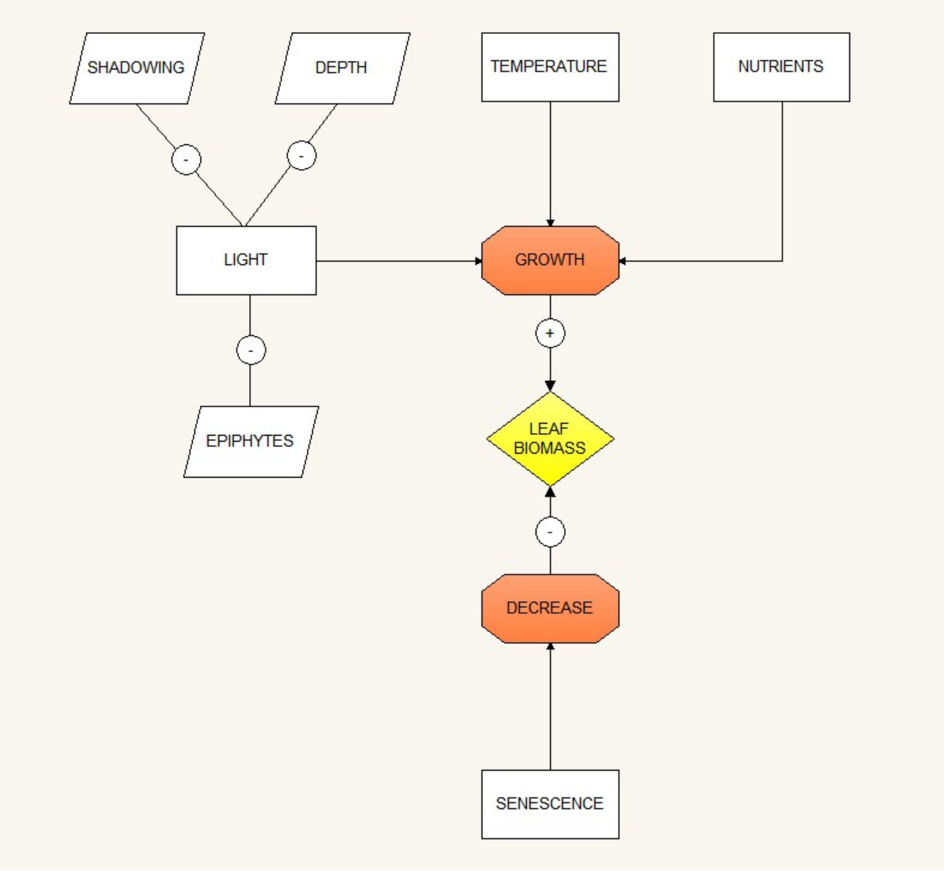


Figure 6.2: Conceptual diagram: the rectangles are the forcing functions; the rhombus represents the main state variable and arrows indicate flows of materials and energy.

6.2 Model structure and function

Posidonia oceanica habitat is a system showing a great diversity of complex patterns. This complexity, generated by the interactions of different components, can be investigated through "cellular automata" models. These models consist of main simple identical components that, interacting each other, generate complex systems. Therefore, in order to simulate the most important biological processes occurring in the growth dynamics of a *Posidonia oceanica*'s meadow, we chose to develop a non-linear, stochastic model, spatially explicit, that consists of a cellular automaton system. The model code is written in FORTRAN 90 and consists of a main program, reading input files with parameters values editable by the user through common editors, and of two subroutines developing some components of the model, the result of which is giving back to the main program with a suitable function calling the specific subroutine. The automaton system developed is a matrix of a specified shape that evolves, over time, according to a set of laws based on the state of the nearby cells. These laws are then applied iteratively for a number of discrete time steps. Cellular automata were studied, for the first time, around the 1950s, and their use in the implementation of biological models, was perfected in 1980 thanks to the work of S. Wolfram, who published his results in the book "A New Kind of Science" [234]. There are main types of cellular automata; a characterize feature is the grid shape that can be one or two-dimensional line. In our model the grid is square with the same number of rows and columns: it is exactly a grid 30 × 30. Each cell within the grid can assume a determinate number of states, 2 in the simplest case. In this model two states are possible for each cell: inactive cell without tuft, and active cell with a tuft on which a maximum of 7 leaves can grow, according to an initial random setting and to the dynamics of the model. In addition to the type of grid and the states the single cells may assume, it is also necessary to specify the dynamics with which cells interact each other. The simplest choice, the one we apply, is that each cell interacts only with its nearest neighbours, directly adjacent. In the full cells we imagine a tuft of seven leaves and for each leaf we follow its birth and development in a seasonal dynamic of 52 weeks, with a simulation time of 100 years and a time step of a week. A timer keeps track of the time in weeks, from the beginning of the simulation; the model uses weeks and years as time units since the intended purpose is to capture habitat dynamics that operate on time scales running across several years. Therefore the model is set to recalculate and update all system states 52 times per year in order to simulate growth patterns for a number of years. The mathematical construct consists of a growth equation Eq. **??** that predicts the expected increment in biomass over time of the f-th leave at the site [*i*,*j*]: at each site of indices [*i*,*j*], the increase undergone by the dynamical variable $B(\{i,j,f\},t)$, the f-th leave's biomass, from time t to time $t+1$, is some $\Delta B(\{i,j,f\},t)$ depending on the leaf configuration and on the forcing agents at time t Eq. **??** :

$$B(\{i,j,f\},t+1) = B(\{i,j,f\},t) + \Delta B(\{i,j,f\},t) \tag{6.1}$$

A relative growth rate $r(\{i,j,f\},t)$ is defined for the biomass $B(\{i,j,f\},t)$, such Eq. 6.2

$$\Delta B(\{i,j,f\},t) = B(\{i,j,f\},t) \cdot r(\{i,j,f\},t) \tag{6.2}$$

All leaf dynamics is encoded in the relative growth rate $r(\{i,j,f\},t)$ Eq. 6.2. The factor $r(\{i,j,f\},t)$ is the growth rate given by the positive contribution of photosynthesis affected by the presence of stressors and other driving forces, conditioning the leaf growth as we assumed to treat here. Four factors are considered, that are "factors" also in a mathematical sense, as r turns out to be their product. The agents composing r are:

- the sun light promoting photosynthesis, via a factor r_0, that is the same all over the meadow;
- the shadow of the nearby beams, via a reducing factor $\exp(-\alpha\cdot O(\{i,j\},t))$ depending on the position of the beam, being $O(\{i,j\},t)$ a proxy of the shadowing relative to the [*i*,*j*] cell, while α is a suitable positive constant;
- the bio-chemical effect of nutrients, that is the same all over the meadow, and is represented by a factor $F(N)$, being N a proxy of nutrient abundance;
- the shadowing effect of epiphytes, covering the single $\{i,j,f\}$-th leave, through a limiting factor $(1-\Psi(\{i,j,f\},t))$, being $\Psi(\{i,j,f\},t)$ a proxy of the epiphythe covering.

The most important factors in controlling the *Posidonia oceanica* growth are light, temperature [44] [241] and availability of nutrients [175] and space; in particular the light would affect the annual productivity [196] and temperature would condition the seasonality of growth patterns [241].

6.2.1 Light and photosynthesis

Light is the primary environmental factor affecting the *P. oceanica* photosynthesis. However, the photosynthetic radiation (PAR) is attenuated due to, penetrating underwater, it is partially absorbed and dispersed (the light penetrates water with three orders of magnitude less than it does in air), but also due to the presence of sediment particles present in the water column [77]. In addition to photosynthesis, light influences seasonality, vertical distribution, and spatial structure of Posidonia oceanica meadows [4] [71]). The relationship between the intensity of light and the rate of photosynthesis depends on the species and it is often described using photosynthesis-irradiance, or P-I curves, which indicate how efficiently light energy is used in the accumulation of plant biomass. Seagrass P-I curves Fig. (6.3) are similar to those of terrestrial plants and show an initial linear increase in photosynthetic rate with increasing light until the irradiance has become saturating, and the maximum rate of photosynthesis is achieved.

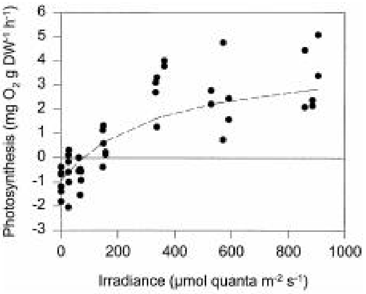


Figure 6.3: Photosynthesis-irradiance curve (from [6].

In this model light has been considered as positive contribution to growth: the increase of available light allow *P. oceanica* to photosynthesise more efficiently and be even more productive. It is important to remember that irradiance decreases exponentially with increasing depth Fig. (6.4).

This relationship is captured in the model and is determined as follows. The light factor $r_0(t; z)$ is the rate of growth of the leaf due to sun light. It will depend on the depth z of the canopy according to the relationship

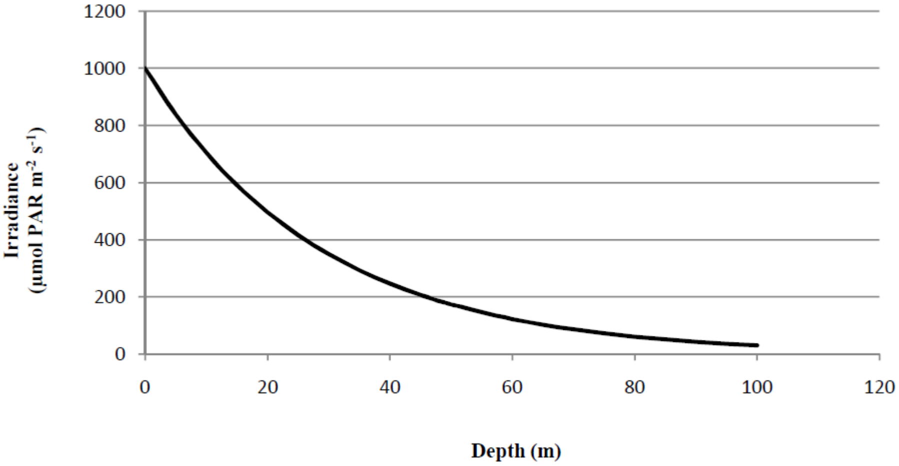


Figure 6.4: Irradiance extinction down the water column due to attenuation by particles ((from [206]).

Eq. 6.3a:

$$r_0(t;z) = \frac{v \cdot l(t;z)}{\kappa_{el} + l(t;z)} \tag{6.3a}$$

$$l(t;z) = l_0(t) \cdot e^{-\kappa z} \tag{6.3b}$$

here v and κ_{el} are suitable constants, while $l_0(t)$ is the season-dependent amount of light arriving at the sea surface. The resulting available light, responsible for regulating the bathymetric distribution and productivity of *Posidonia oceanica*, is formalized by the empirical relationship given by Beer-Lambert's law Eq. **??**:

$$I_z = I_0 \cdot e^{-\kappa_z \cdot z} \tag{6.4}$$

where:

- κ_z is the attenuation coefficient and is a typical constant of the medium crossed for a given depth: it is a function of water clearness and expressed as inverse relationship of the Secchi disk's depth;
- I_0 is the season-dependent amount of light arriving at the sea surface;

- I_z is the irradiance at the depth zeta into the water column.

As expressed prevoiusly, the plant's response to the light intensity is as Monod functions Eq. 6.5 according to experimental observations. ([22] [87] [72] [174]

$$RL = V \cdot \left(\frac{L_z}{\kappa_{el} + L_z} \right) \tag{6.5}$$

where:

- V is the theoretical maximum absorption rate
- κ_{el} is a semisaturation constant.

Finally the light available is a function of the light measured at the sea surface (the L_0 depending on the season) decreased by a factor due to the water itself and to the depth at which the meadow is located.

6.2.2 Shadowing

The effect of the light, however, not only depends on photosynthetic capacities but also on the seagrass bed morphology (self-shading effect) and on the shading due to epiphytes. To simulate the shadowing, in the model the amount of light is reduced by a fading factor Eq. 6.6 due to the presence and extension of the nearby plants depending on the position (i, j) in the grid:

$$e^{-\alpha \cdot O(\{i,j\},t))} \tag{6.6}$$

The quantity $O(\{i, j\})$ is taken simply as the biomass of the bundle surrounding the $\{i, j\}$-th bundle (as one expects the more massive leaves causing more shadowing): then a suitable α is assigned in order to turn this biomass into the shadowing factor. In a subroutine of the main model, the shadowing on each single tuft is calculated, considering the biomass present in all the cells surrounding the [*i*,*j*] tuft. Calculation is done at each time step (i.e., once per week) because, during the simulation, leaves can grow and die and therefore increase or decrease the shadowing on the surrounding beams.

6.2.3 Temperature

The surface water warms up in contact with the atmosphere and under the rays of the sun, but deeply accumulate the cold waters which, being thicker, are heavier. The surface temperature varies essentially with latitude and at medium latitudes even with seasons. At poles the temperature can drop to almost -2°C corresponding to the freezing point of salt water. At medium latitudes, as in the Mediterranean, the surface water temperature is linked to the seasons even though the high thermal water capacity causes the temperature to change very slowly: at sea there are no thermal excitations as in the atmosphere. In spring, especially along the coasts, the water temperature begins to rise from the surface thanks to the sun's rays. A layer of hot and thicker surface layer is then formed, while in the deep the temperature remains almost constant. There are thus two masses of water separated by a summer thermocline that prevents the exchange of nutrients and the passage of smaller organisms from one area to another. In the autumn, the first strokes mix the two layers and the temperature quickly uniforms over the entire water column. At this point, the surface water cools and the course is reversed. The surface temperature in the Mediterranean varies depending on the areas from a summer peak of 20-23°C to a minimum winter of 10-13°C; but in the northern Adriatic, where water does not exceed 50 m deep, surface temperatures can reach extreme values between 30°C and 6°C ([**?**]). At the present state of the model the temperature affects the growth rate by modulating the seasonal variability of the amount of nutrients in the water column Eq. 6.7:

$$N(t) = N \cdot e^{-\beta \cdot T(t)} \tag{6.7}$$

Where N is the initial input of nutrients, T the temperature in the t-week (derived from web information on Tuscany region, Italy) and β a constant: this relationship should simulate the trend that in winter the concentration of dissolved nutrients around is greater than in summer, as the water volume shrinks.

6.2.4 Nutrients

Nutrients availability may also play an important role in limiting production: Duarte (1995) describes the "cascade of direct and indirect effects interacting in a self-accelerating manner" that leads towards seagrass decline under increased nutrient loading. *Posidonia oceanica* leaves and epiphytes are able to utilize only water-column nutrients, while roots and rhizome can also take up nutrients in the sediment pore water. In this system we choose not to evaluate the nitrogen concentrations in the sediments because these amounts of nitrogen are assimilated by roots; we just want to follow leave growth and how leaves take up dissolved inorganic nutrients from the water column. The increase of he leaf's biomass is affected by a non-monotonic factor depending on the nutrients. The $F(N_t)$ Eq. 6.8c factor intends to simulate the condition for which the nutrients are the basic food for the growth of the leaves up to a maximum value above which they turn into poison making the environment a strongly anoxic one. We assume:

$$N(t) = N_0 \cdot e^{-\tau \cdot T(t)} \tag{6.8a}$$

$$F(N) = -AN^2 + BN, if N \in \left[0, \frac{A}{B}\right] \tag{6.8b}$$

$$F(N) = 0, if N \notin \left[0, \frac{A}{B}\right] \tag{6.8c}$$

This mean that the factor F is a convex parabola between $N = 0$ and $N = A/B$ nutrients, while it is zero outside this interval. Moreover, F is a growing function of N between zero and $N = A/2B$, while it is decreasing in the second half of the $[0; A/B]$ interval Eq. 6.8c. In turn, the amount of nutrients is a season-dependent quantity $N(t)$, which decreases with seasonal temperature $T(t)$ Eq. 6.8a: the factor N_0 is an overall amount of nutrients, while τ is a suitable parameter defined in order to dilute nutrients from N_0 to $N(t)$ as $T(t)$ increases.

6.2.5 Epiphytes

Another factor to take in account is that the leaves of *P. oceanica* support many plant and animal species, which can reach up 20-30% of the biomass of the leaves ([104]. The epiphytic community plays an important role in the productivity and growth patterns of the host plant in terms of competition for available light, energy and nutrients [157], [136], [192], [5]). It is assumed that organisms in the system living on leaves are the same species and they are considered in the only stock called epiphytes. Although this is not the same in the real system, the implications of such assumptions do not modify the interactions of our interest. The purpose of this model is replicate and simulate these interactions so the level of aggregation within it is enough. Epiphytes decrease the reinforcing contribution of light to growth dynamics such as illustrated in the figure Fig. (6.5):

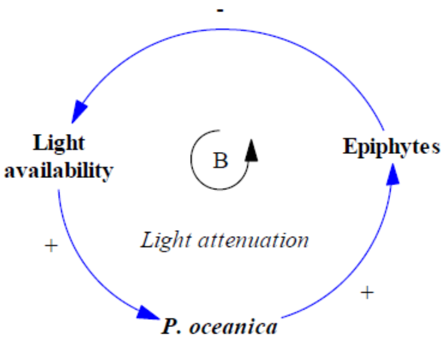


Figure 6.5: Figure Light attenuation by epiphytes brings about balancing feedback in *P. oceanica* habitat (from [206].

As *P. oceanica* grows, the associated epiphytes increase, thanks to the more availability of nutrients and substrate. Then when epiphytes become abundant, the attenuation of light due to their presence, increases. The presence of epiphytes is calculated as the percent coverage of *Posidonia oceanica*'s leaves, depending on their age and length. The quantity $(i - \Psi)$, which is smaller than 1 for Ψ between 0 and 1, reduces the factor $r(\{i, j, f\}, t)$ encoding the effect of epiphytes on the leave, shading it and reducing its growth capacity. The amount of epiphytes must be in the interval $(\Psi_{min}, \Psi_{max}) \subset [0, 1]$. Ruiz et al. (2011) noted that the increased nutrient concentration stimulates the proliferation of epiphytes, which in turn diminish the available sunlight. So the amount of epiphytes depends on the age and length of the leaf $AL(\{i, j, f\})$ (establishing the surface available for epiphytic growth) and on the availability of nutrients through the appropriate parameter g. All in all, we adopt the function Eq. 6.9:

$$\Psi(\{i, j, f\}) = \Psi_{min} \cdot \Psi_{max} \frac{e^{gAL(\{i,j,f\})}}{\Psi_{max} - \Psi_{min} + \Psi_{min} e^{gAL(\{i,j,f\})}} \tag{6.9}$$

Epiphytes are lost when the leaf on which they are attached falls from the beam due to leaf senescence.

6.2.6 Senescence

At this state of the model, the main factor reducing the biomass is the normal process of tissues senescence; removal of biomass by tidal currents, hydrodynamic transport and by grazing are not taken into account. The leaves are discerned in adult, intermediate and young according to their length and the presence of a lignified base ([101]); at the top of senescence (depending of the group the leaf belongs in) leaves break off mainly in autumn: so we have defined a standard age of A_{max}=46 weeks for a leaf's death, derived from the average value of the death of the three main classes of leaf age, based on the values provided by field ecologists. The rate at which matter from the *P. oceanica* biomass stock is lost with leaf shedding was assumed to be constant in the model and is set at an average of the age of adult leaves as identified from published studies. A function of the model updates and stores the age of each leaf, from the time of its emergence. When the $\{i, j, f\}$-th leaf reaches the age established, we simulate its death by setting its biomass to zero. At successive times, a new leaf may rise with a certain probability, with initial age equal to zero. Last but not least, a mechanism is introduced Eq. 6.10 giving rise to some "big death toll" of leaves in some interval of weeks (t_1, t_2), corresponding to the maximum of leaf extinction documented in literature over the year: in our case, this interval coincides with the month of August. Each leave is "processed" at each step $t \in (t_1, t_2)$: a random number between 0 and 1 is sorted, and compared to the threshold

$$\theta(\{i, j, f\}) = e^{\kappa \cdot [AL(\{i,j,f\}) - A_{max}]} \tag{6.10}$$

if the sorted number is smaller than $\theta(\{i, j, f\})$, then the age of the leaf is set equal to a maximum age A_{max} after which the leaf dies. Due to the dependence of $\theta(\{i, j, f\})$ on A, the older is the leaf the closer to 1 is $\theta(\{i, j, f\})$, the higher is its probability to decease due to this mechanism.

Chapter 7

Results and model scenarios

A model is considered as valid when it is fit to execute the purpose for which it has been designed. Model testing is often used to build confidence in a model's ability to perform its desired function. The intention behind this research work was to develop a working simulation model that would be able to simulate important dynamics in P. oceanica's growth pattern and their interactions with forcing factors such as light, nutrients and epiphytes. In order to validate the model, we must test the extent to which it is able to account for these relationships. In this chapter the results of the model are analysed, and an assessment on how far it may be considered satisfactory is done. The model validation occurs through tests whose results must be compared with data obtained from literature or field experiments. Then we observe how much the outputs of the model differ from the data used for comparison: this provides us with confidence level of our model. We have developed a set of training tests allowing the user to simulate specific environment scenarios (which may be a strong water pollution due to excessive inputs of nutrients, mechanical damage to the meadow or other different stressors): the simulations are executed by varying the values of some parameters(which makes the model very flexible). The outputs of the model are analysed to understand what information the model can provide about meadow responses at large time scale and in different environmental conditions. Finally a comparison with data from the literature is *carried out in order to check how our model can be considered close to reality, although it is a simplified reality.*

7.1 The landscape

The first step to contextualize our model was to define a spatial size of the simulated meadow. We chose to determine the extension of the whole meadow, considering the Pergent classification (1995) to connect the size of the meadow to its density, namely the number of beams per unit of surface. First, we performed simulations with different values of an initialization threshold a between 0 and 1 that, compared with a number produced by a random generator, determines the number of cells active within the matrix. At the beginning of the simulation the dice is "thrown" for each cell: a random number is generated between 0 and 1, and if this number is smaller than the value of a, the cell will be defined as inactive and remain an empty cell. Consequently, by placing the initialization threshold value very low, the probability that the random number is smaller decreases, and therefore more active stolons are expected to appear and the meadow is expected to be denser. Only in the active cells *P. oceanica*'s bundles can arise, and later produce leaves up to a maximum number of seven. All the other inactive cells will not participate to biomass production. In the present version of the model, the number of active cells is defined only once and forever at the beginning of the simulation; there are not functions simulating the possibilities that:

- some cells gets activated in order to produce new stolons;
- bundles into the active cells could colonize nearby cells.

The simulations carried out by changing the above-mentioned threshold value a, give as output the number of active cells and therefore the number of stolons present in our meadow Fig. (7.1).

For small value of the treshold, the number of active cells and, hence, stolons is big. In particular, the maximum value of active cells (897) was obtained in a test for a very low threshold value a=0.001. Such simulations are carried out at a depth of 5 m (putting z=5 m): the Pergent classification shows that, at 5 m, a widespread meadow has more than 749 bundles per square meter. So we can consider our 30×30 matrix as a simulated patch of a *Posidonia oceanica* meadow about 1 m^2 extended. Moreover Pergent [190]

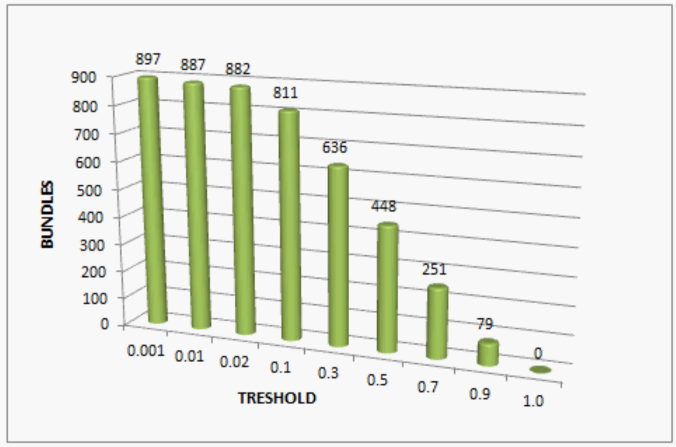
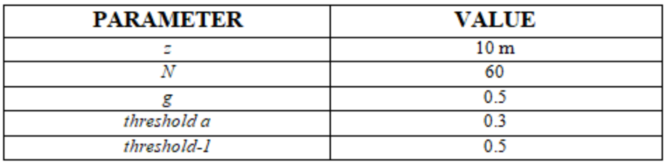


Figure 7.1: Number of bundles per square metre, for different initializing threshold a values.

asserts that a meadow with such density can be considered a meadow in excellent health condition, with high value of vitality; also Giraud [101], with his classification, confirms that a meadow with more than 700 tufts per m^2 constitutes well-developed matte and has an efficient rhizomatic growth. Pergent and Giraud classifications link decreasing numbers of tuft/m^2 to meadows with decreasing level of extension and development. This allows us, in the different runs, to define the health condition of the meadow we are simulating, simply by setting a convenient value of the initialization treshold a at the beginning.

7.2 Basic scenario

The model allows to simulate the evolution of the amount of the total leaf biomass over time and returns a numerical output: for each week of every year, the total leaf biomass value of the meadow is reported. It is possible to obtain other information like growth rates, number of born or dead leaves and other aggregated indexes. The predictive capabilities of the model are tested through a series of simulations performed under different conditions. By considering a variety of possible futures that include important uncertainties in a system, scenario projection may serve to improve the level of understanding of a complex system and reveal how the system reacts to stresses and influencing factors. Ultimately, scenarios may be used to better inform decisions and provide greater resilience to unexpected and untended consequences [195]. *Posidonia oceanica* habitat is one such complex system and this section is an effort to demonstrate the use of scenario analysis in revealing unexpected system characteristics and responses. Therefore, different simulation scenarios have been defined by modifying some of the initial configuration parameters. The first test was run in order to simulate the conditions considered in Elkalay model [87], used as reference, and to assign a realistic value to our arbitrary biomass unit. For this reason we initially set the depth to 10 m and consequently the value of K_z, the attenuation constant, was set at 0.17, which is its value, according to the Secchi disk at 10 m [22]. At the threshold a was assigned the value of 0.3 (A.U.) to have a number of beams between 550 and 650 per square meter and to simulate, according to Pergent, a meadow in good health conditions. Finally, the initial contribution of the nutrients was equal to 60 (A.U.) to simulate an amount of non-limiting nutrients (approximate conditions in Calvi Bay, where the Elkalay model was performed) Fig. (7.2). All other drivers considered have been modified to achieve the same result, obtaining data from the bibliography, when possible, or by using a suitable calibration of the model.



PARAMETER	VALUE
z	10 m
N	60
g	0.5
threshold a	0.3
threshold-1	0.5

Figure 7.2: Setting of comparison simulation

In the table:

- z, the depth, is set to 10 m;
- N, the initial amount of nutrients in the water column, has the arbitrary unit of 60 (in the model this value can range from 0 to 100);
- a, as described in the previous section, provides the number of active cells into the matrix.

The parameters g, and*threshold-1* are set to the average value of 0.5(in the model they can range from 0 to 1):

- g is a proxy of how fast epiphytes grow with respect to the leaf age;
- *threshold-1* defines the appearance probability of new leaves, for each bundle, and for each time step.

In the second test the conditions of a meadow at 20 m depth was simulated, with K_z estimated 0.089 m^{-1}, according to [22], and the treschold a is set equal to 0.5 to have a number of tufts more than 400 m^{-2} but less than 550 m^{-2} (according to [190]). Then the results of our simulations (obtained from 5 years “at regime”, i.e. after achieving a stable condition) were compared to results obtained by Elkalay under similar conditions to connect our unit (A.U.) to the units gDWm^{-2}. We show the results acquired from the comparison Fig. (7.3). From these and other simulations, performed between the two models, we observe that our arbitrary unit may correspond to a value between 0.15 and 0.18 gDWm^{-2} (e.g. $\frac{770}{3873} = 0.18$ and $\frac{550}{3739} = 0.147$) and, choosing an average value, we can assume that:

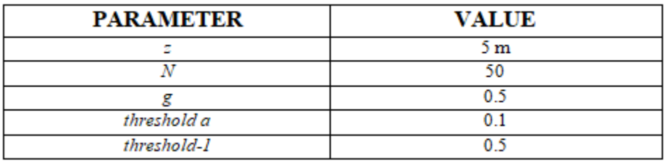
	10 m	**20 m**	
B^{max} Elkalay	700	550	g DW m^{-2}
B^{max} Model	3873	3739	A.U.

Figure 7.3: comparison between Elkalay model and our model in order torecognize the value of A.U.

$$A.U. = 0.16gDWm^{-2} \tag{7.1}$$

Now we have valid elements in order to run a check of the model potential and its ability to describe the growth dynamics of a *Posidonia oceanica* meadow. In one test the model is run under conditions descriptive of a Mediterranean environment, without stressors occurring: baseline conditions were set to reproduce conditions of an healthy meadow. In this first step we simulate the meadow's development at the bathymetric rate of 5 m, related to the corrisponding K_z=0.34m^{-1} (according to [22]) and with average values of the other coefficients; the treshold a is set equal to 0.1 A.U. to simulate a well extended meadow at 5 m according to [190]. The following table Fig. (7.4) describes the conditions of the basic scenario:

In the following Fig. (7.5) plot we report ten years of the total leaf biomass as a function of time, i.e. the basic model output.



PARAMETER	VALUE
z	5 m
N	50
g	0.5
threshold a	0.1
threshold-1	0.5

Figure 7.4: Setting of first simulation(basic scenario).

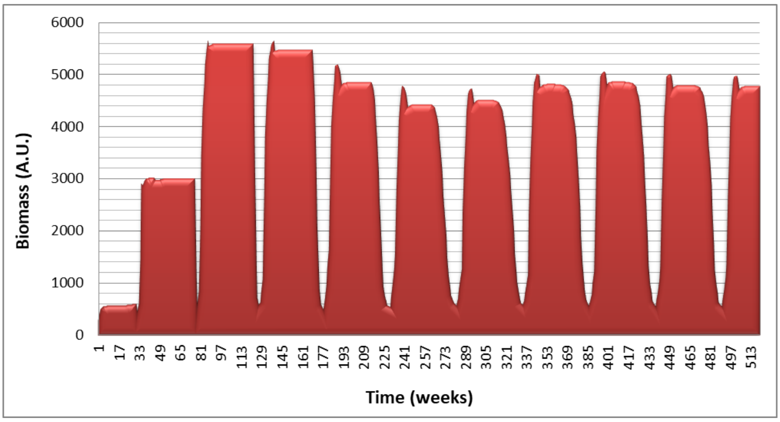
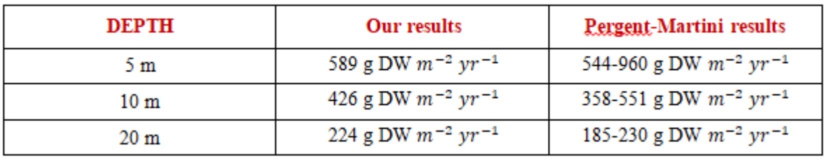


Figure 7.5: Biomass production: basic scenario (first ten years). 1 A.U.=0.16 gDWm^{-2}

For a very preliminary model validation we have considered estimates published by Pergent-Martini in 1994 [194] on the primary production of *Posidonia oceanica* in the Mediterranean basin. In this work leaf production alone varies, at 5 m, between 544 and 960 gDWm^{-2}. We calculated the average and the maximum of the 52 biomass values (1 for each week) produced during the 51st year of the simulation (assuming that meadow was then in stable state): the average is 3682.499 A.U., i.e. approximately 590 gDWm^{-2}, while the mawimum is equal to 4938.916 A.U., which is approximately 790 gDWm^{-2}, in agreement with the range estimated by Pergent-Martini. Later the same calculations and comparisons were performed at 10 m and 20 m, after calibrating parameters to simulate scenarios at different depths; we summarize the results (only for average biomass of the year 51) in a table Fig. (7.6).

In the plot showed previously Fig. (7.5) it is possible see that the leaf biomass increases realistically via the process of photosynthesis, from a set



DEPTH	Our results	Pergent-Martini results
5 m	589 g DW m^{-2} yr^{-1}	544-960 g DW m^{-2} yr^{-1}
10 m	426 g DW m^{-2} yr^{-1}	358-551 g DW m^{-2} yr^{-1}
20 m	224 g DW m^{-2} yr^{-1}	185-230 g DW m^{-2} yr^{-1}

Figure 7.6: Comparison between the results in Pergent-Martini [194] and the results of our model

initial value, until the equilibrium state (the system carrying capacity). There is a clear increase in biomass during the first two years in a run, showing a rapid early growth of the meadow. A period of stronger stability follows this transitory stage. The oscillations of the biomass,with grossly one year period, are due only to the effects of seasonality and to the mechanism simulating the intensification of mortality during summer. In nature, the bundle is renewing from inside to outside with greater development in the spring. The growth rate decreases during the summer when the leaves are longer, covered by epiphytes and begin to manifest a more advanced rate of senescence, characterized by the presence of brown tissue, photosynthetically inactive [48]. This fluctuation is even more evident if we focus only on a one-year pattern Fig. (7.7).

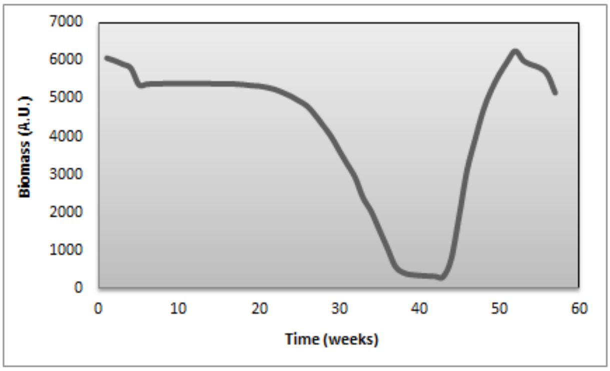


Figure 7.7: The within-the-year-variation of the leaf biomass according to the model. The year represented is the 50th one, well in the equilibrium phase of biomass evolution.

The plot Fig. (7.7) shows also the effect of the model function accelerating leaf senescence in the August month. It was chosen to show only the first

10 years because the single years' pattern, when it is achieved the stable state, is almost identical for all 100 years of simulation, due to the drivers determining the growth rate do not change and, at the present state model, there are no external forcing functions could modify production dynamics during the time. It was chosen to show only the first 10 years because the single years' pattern, when it is achieved the stable state, is almost identical for all 100 years of simulation, due to the drivers determining the growth rate do not change and, at the present state model, there are no external forcing functions could modify production dynamics during the time.

7.3 Several development scenarios

A way of testing and validating a dynamic model is to see if it is able to generate the various system responses that are observed in nature system. We have tested the model's behaviour under different conditions: if the model is sound, then it should continue to behave realistically. This section describes three conditions tests (i.e. parameter assortments) to test the model. These are:

1. Several depths
2. Several epiphytes developments
3. Several nutrient enrichments

7.3.1 Nutrient enrichment

The nutrient load is considered the most interesting proxy for directions in environmental management. Therefore different simulations are carried out by changing the availability of nutrients to investigate the meadow behaviour in function of nutrients and the effect of industrial or urban pollution, fish farms and other activities discharging nutrients into the water column. The initial amount of nutrients N is set from a minimum (0) to a maximum value (100): then these values are modulated by temperature during the year, to simulate seasonality (e.g. the nutrient load in the water column is higher in summer). Each simulation had a 52-week timeline and develops for 100 years, with a total time series of 5200 biomass values: for each simulation, an average of these 5200 biomass values is calculated.

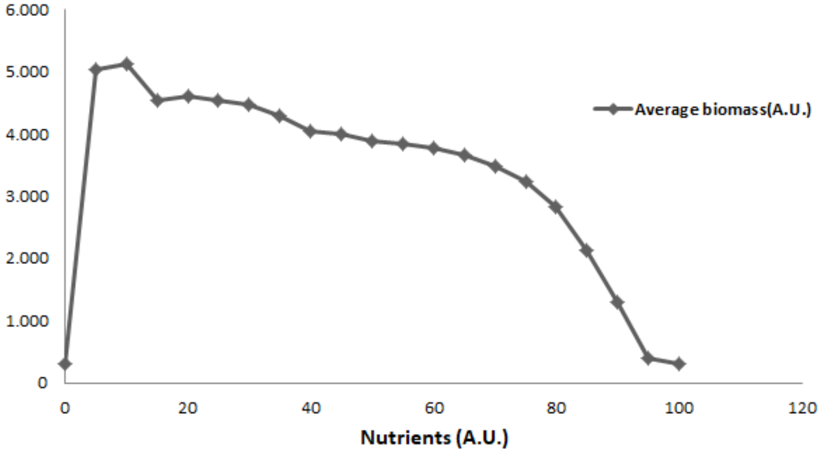


Figure 7.8: Average biomass (of 100 years) as function of nutrient availability.

The graph Fig. (7.8) shows the average biomass values as function of nutrient load in the water column. It is clear that nutrients are crucial to the growth of the meadow because they represent a source of the energy invested by the plant to grow. If a certain threshold is exceeded, however, nutrients turn into a poison by first slowing down, then by completely inhibiting the growth of new leaves and the accumulation of biomass. This allows us to estimate approximately the loss in terms of biomass: under conditions of low nutrient availability (N=30) one has an average biomass of 4483 A.U., i.e. about 720 gDWm^{-2}; in simulated conditions of high pollution (N=80) an average biomass of 2836 A.U., i.e. about 450 gDWm^{-2} is obtained which is about half of the low nutrient value. Finally, these estimates could be associated with the Carbon stock, by assumning that approximately 16% of the biomass produced by a *P. oceanica* meadowis converted to fixed C [152] [207] [78]. In the low nutrient (N=30) simulation, the 16% of 720 gDWm^{-2} is about 115 g which would be the C stored amount, in agreement with the estimates obtained from bibliografy, which are about 47-138 gCm^{-2} or 6-175 gCm^{-2} (average 90.5 gCm^{-2}). Indeed in the scenario with turbid and polluted water (N=80), the estimated C stock decrease drastically to about 72 gCm^{-2} (16% of 450 gDWm^{-2}). Taking into account the average C value of € 15 m^{-2} (from the range € 6-23 m^{-2} according to [213] [130]) we suppose a profit of € 1725 for the scenario with N=30 (115 gC$m^{-2} \times e15m^{-2}$), and a profit of € 1080 in the N=80 (72 g$Cm^{-2} \times e15m^{-2}$) with a resultant loss of € 640 m^{-2}

7.3.2 Depth and irradiation

At 0 m light has not yet passed through any medium and light availability in the water column is therefore expected to be equal to the irradiance present at the surface. At greater depths, light is attenuated as it passes through the water medium. Suspended particles and turbidity in the water column, additionally contribute to the effect of depth in decreasing the amount of light available for photosynthesis, by scattering or absorbing irradiance. The second test of the model simulate the condition in which the meadow is located at different depths and therefore it is in different conditions of available light. As expected the model Fig. (7.9) shows a decrease of the leaf biomass as function of the depth, according to [194]. If we link this decrease with an increasing water turbidity, we can suppose that it could produce a C loss estimated as about € 800 m^{-2}

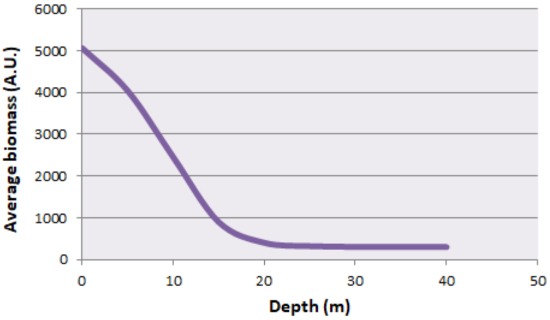


Figure 7.9: Average biomass (of 100 years) as function of depth.

7.3.3 Epiphytes presence

As a third test, the model performance is assessed in the absence or high presence of epiphytes. The term epiphytes is a generic term to indicate all those organisms that grow by adhering to the surface of *P. oceanica* leaves. They are, as discussed in a previous section, both vegetable (epiphytes) and animal (epibionta) organisms. In both cases, it is assumed that their presence on the leaves reduces the light reaching the meadow by shadowing. In total absence of epiphytes, the light available is all the light reaching the surface. Then, at an early stage, the absorption of light and the consequent photosynthesis carried out by the epiphytes increase the total amount of biomass produced by the whole meadow. The light absorption by epiphytes has a rapid initial increase until to a saturation point after which the epiphytes cannot further attenuate the light; this pattern is consistent with the general parabolic law that governs light capture by photosynthetic organisms ([43] [60]). Finally the biomass decreasse drastically due to the total light shadowing by epiphytes. In our model the absence of epiphytes is simulated by setting g (the growth rate of epiphyte stock) to 0 $week^{-1}$. In the absence of epiphytes the expectation is that *P. oceanica* photosynthesises and grows at higher rates due to the increased availability of irradiance Fig. (7.10). Indeed the biomass present in the *P. oceanica* stock and the growth rate are higher when epiphytes are absent from the system Fig. (7.10).

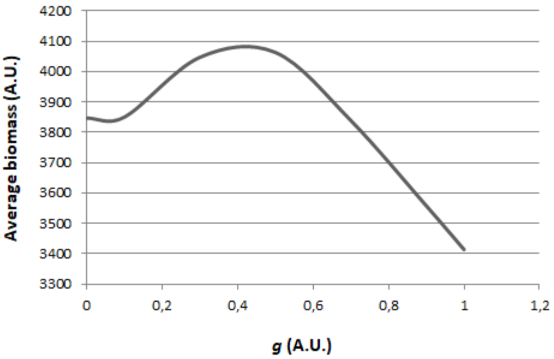


Figure 7.10: Average biomass (of 100 years) as function of epiphytes growth rate.

At the present state of the model, we can consider the increasing epiphytes coverage as corresponding to an eutrophication and, performing the calculations described previously, when the epiphytic coverage rate is high, we obtain a loss associated with the decreased C storage, equal to about € 260 m^{-2}. The lowest value obtain in this case maybe depends on the fact that the rate g is not a powerful driver like that nutrients and the depth, so we can propose, for the future, to modify the model in order to make the effect of this forcing function stronger.

Chapter 8

Conclusion

8.1 Ecological model

The present work represents a first attempt to model the seasonal dynamics of a *P. oceanica* meadow linking it with an economic value in order to stimulate the interest of the various stakeholders. Every equation within our model has been derived from published literature thus ensuring consistence between model structure and the descriptive knowledge of the system. For all scenarios analyzed, the model has shown to simulate effectively growth variations of a *P. oceanica*'s leaf over time. The "performances" achieved for the various simulations reveal how the model is a capable tool adequately reproducing the shape of the natural bands of *Posidonia oceanica* in different season. Therefore it is possible confirm that the model has the ability to generate responses that characterise the natural *Posidonia oceanica* system, it is stable over several years and it is structurally sound for its purpose. The functioning model described here restricts its boundaries to the ecological functioning of a hypothetical patch of *P. oceanica* habitat and does not address dynamics that span broad spatial scales beyond that meadow. This could be a model strength because the model structure could easily be adapted to a specific meadow by adjusting the starting values of several model parameters. It must be said that a comparison based only on data from the literature (although these derive from field experiments), may not be enough. For a more concrete validation of the model it would be advisable to apply it in a specific context and to insert in the model real data to obtain the model answer in real units of measure. This would allow a more direct comparison between the data obtained from the model and the actual data and therefore a more in-depth proofreading about parameters and variables into the model, and finally a validation of the model. On the other hand, it is recommended that future adaptations to present model should incorporate other limiting factors present in the real system, such as:

- salinity;
- burial and consumption of produced material;
- grazing (by mainly *Salpa Salpa* and *Paracentrotus lividus*);
- epiphyte growth dynamics;
- hydrodynamics of the water.

Converting model to a whole plant system, in which both above ground and below ground compartments are modelled, is central to capturing the way in which resources are translocated for improved survival during periods of stress as well as the value of *P. oceanica* habitat as a carbon and nutrient sink [79] [88]. Below-ground material is supported by photosynthetically produced carbon that is stored in rhizomes and used to maintain the plant during periods of low photosynthetic production [50]. Situations in which light is limited tends to result in increased biomass allocation to leaves while nutrient limitation tends to shift biomass allocation to roots [111]. This adaptation to our model is central to capturing the resilience of *P. oceanica* habitat to stressful changes in light and nutrient levels. The dynamics of roots and rhizome are decisive in determining the long-term storage potential of a *P. oceanica* meadow and the amount of carbon that can be extracted from the atmosphere and imprisoned in the matte. Furthermore a future model may also want to account for socio-economic factors or behavioural patterns at the coast given that humans are an integral component of coastal ecosystems. Future research work should adapt this model to encompass broad-scale, human-related dynamics in order to confirm its use in coastal management and decision making. An interesting development would be to consider the impact (including economic) of various stressors on other ecosystem services provided by the *Posidonia oceanica* ecosystem such as coastal erosion, nursery for commercial fisheries, conservation of biodiversity.

8.2 Assessment of carbon storage

The most effective approach for coastal management policy to promote C sequestration is to aim to maintain water quality conditions that encourage seagrass health [130]. Furthermore, it should be noted that there is equal or greater value in retaining the biodiversity, a range of ecosystem services, and healthy coastal wetland as a GHG sink rather than a source. The first priority is to develop global seagrass C budgets, which must include:

- quantification of C stock;
- verification of C stock over time;
- determination of how long does the C remain within the financial unit;
- estimates of the risk of losing C stock.

Our model provides a carbon storage value associated with the biomass production of a *P. oceanica* meadow. Moreover this research has shown that the accelerated decline of seagrass meadows represents a loss of carbon sink capacity. However, seagrass meadows also protect, by dissipating wave energy and reducing resuspension the massive sedimentary stocks of organic carbon accumulated over time. Current understanding of the functioning of seagrass meadows suggest that the loss of seagrass cover may, therefore, render the associated sedimentary carbon deposits vulnerable to be lost through erosive and resuspension processes. If seagrass decline rendered sedimentary carbon stocks vulnerable conservation strategies would be even more needed, since the consequences for carbon cycling will not be limited to the loss of carbon sink capacity but may include the remobilisation and eventual emission as CO_2 of carbon stocks accumulated over millennia. For this reason further work is probably needed in the future to calculate more accurately the amount of stored carbon, taking into account other carbon storage and dispersion factors that have not yet been considered. However, the fate of sedimentary carbon stocks following seagrass loss is as yet unknown, and resolving this unknown is, therefore, a matter of urgency. The task of identifying and understanding the many factors that can affect seagrass C capture and storage is colossal, which is why efforts towards achieving this task must be strategically prioritised. In terms of environmental factors affecting C capture and storage by seagrasses, we recommend the following as research priorities:

- impacts of common, large-scale environmental (floods, hurricanes, cyclones) and direct human disturbances (anchoring, trawling, dredging) on seagrass C stocks, particularly to test whether such disturbances can cause extreme CO_2 efflux from seagrass meadows;
- effects of altered physical-chemical sediment states (temperature [183]) on C remineralisation rates;
- effects of nutrient addition on C sequestration;
- role of fauna in facilitating mechanical flux of buried C out of sediment, as well as their indirect role in C mineralisation through mediating microbial communities;
- responses of seagrasses to CO_2 enrichment.

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