# Autochthonous Seagrasses

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**Abstract**

Seagrasses are flowering plants that undergo their whole life cycle within shallow coastal habitats. All species share analogous architectural and growth patterns. They are modular plants composed of units arranged by a set of modules: a piece of rhizome, a bundle of leaves (shoot) attached to the rhizome and roots. Four species occur in the Mediterranean bioregion: the endemic *Posidonia oceanica*, the tropical *Cymodocea nodosa* and the temperates *Zostera marina* and *Z. noltii*. *Posidonia oceanica* is the largest one, with very slow growth rates and being considered the climax stage of Mediterranean subtidal bottoms. Meadows extend on 2.5–4.5 millions ha that is close to 25 % of the Mediterranean basin shallower than 50 m. *Cymodocea nodosa*, *Zostera marina* and, particularly, *Z. noltii* are smaller in size but fast growing as typical of the pioneering species. Seagrass meadows are among the most productive ecosystems on earth, providing important ecological services: nursery grounds, biofilters, water cleaners, coastline protectors and carbon sinks. However, despite its paramount importance there is widespread regression of such habitats. Although the four Mediterranean species have been assigned to the "Least Concern" category of the IUCN Red List, *P. oceanica* populations are experiencing the highest rate of decrease. Given the extremely slow growth rate of this species such losses are virtually irreversible. Direct and indirect (i.e., climate change) human activities affecting mostly to physical integrity of habitats, sediment and water quality, coastal sedimentary balance or species composition are argued to be the main drivers of seagrass decline in the Mediterranean Sea. European (and Mediterranean) countries, aware of the key important role that seagrasses play, have established management and conservation plans for these habitats. Thereafter, the aim of the present contribution is to present basic information about the biology and ecology of the Mediterranean seagrasses, the main threats facing these habitats, as well as to provide some information on the main conservation and management strategies.

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## Introduction

Seagrasses are flowering plants that endure their whole life cycle within shallow coastal habitats, extending from tropical to temperate latitudes. Even though they can thrive together with seaweeds, there are considerable differences between them from an evolutionary perspective. Therefore, since algae evolved in the sea around a billion of years ago, seagrasses evolved from terrestrial plants over the past 100 millions of years. Such "unequal" evolutionary trip resulted in a seagrass taxonomic diversity (60 species) much more lower than that of seaweeds (c.a., 9,000 species). For seagrasses, the life in water required an array of important adaptations such as (1) complex pollination mechanisms (involving spawning); (2) internal gas lacunae to transport oxygen to the roots and rhizomes and to maintain shoots in upright position when submersed; (3) chloroplasts located at the outermost layer of the leaves to improve gas exchanges and light capture; (4) strap-like, fibre-filled leaves with basal meristems, to withstand high hydrodynamics, and (5) extensive network of rhizomes and roots to assure an optimum anchorage in soft bottoms (Hemminga and Duarte 2000).

Besides to the low species richness, all seagrass species share analogous architectural patterns and growth dynamics. They are modular plants composed of units (ramets) arranged by a set of modules: a piece of rhizome, a bundle of leaves attached to it (shoot), and a root system. Additionally, ramets can bear flowers depending on the season. Due to their clonal nature, seagrass growth and spreading take place throughout the regular addition of the basic set of modules (Hemminga and Duarte 2000; Brun et al. 2006). The resulting meadow (either patchy or continuous) is usually composed by a reduced number of genetically diverse individuals, genets or clones. However, although clonal growth is the main way of meadow spreading and persistence, it does not create new, genetically distinct individuals, and thus, does not provide greater evolutionary potential or increased resilience to environmental change. In this sense, sexual reproduction is essential for initiating the formation of new clones and so it is also necessary for the development and maintenance of seagrass beds (Short et al. 2011).

Seagrass meadows occupy less than 0.15 % of the seabed (Charpy-Roubaud and Sournia 1990) but they are among the most productive ecosystems on earth (0.49 PgC year⁻¹, or c.a., 1.1 % of the total marine primary production) (Duarte and Chiscano 1999) providing important ecological functions or ecosystems services estimated at 25,400 € ha⁻¹ year⁻¹,

higher than, for example, coral reefs (8,200 € ha⁻¹ year⁻¹), forests (1,300 € ha⁻¹ year⁻¹) or croplands (108 € ha⁻¹ year⁻¹) (Costanza et al. 1997, here recalculated to 2010 euros). Being aware of the caveats and limitations of such estimations, they highlight the importance of seagrasses. Among the principal ecosystems services are: (1) "promoters of biodiversity", since many organisms uses seagrasses (or its epiphytes) either as food, refuges or nursery ground (e.g., *Posidonia oceanica* meadows harbour 25 % of known Mediterranean species); (2) "biofilters" by stripping of nutrients and other contaminants from the water throughout foliar uptake; (3) "water clearers", since canopy enhances the settling probability of fine sediment particles increasing the water transparency; (4) "coastline protectors" since the belowground network of roots and rhizomes stabilizes sediment, besides the reduction of the erosive force of waves and tides by leaf baffling and leaf litter stacked on shore; (5) "carbon sinks", specially the long-lived-matt forming seagrasses such as the Mediterranean *P. oceanica*. In fact, seagrass meadows account up to 18 % (or 27.4–44 Tg C year⁻¹, with a maximum of 82) of all carbon storage ("blue carbon") in ocean sediments (Duarte and Cebrián 1996). Such carbon dioxide mitigation is especially valuable in the present (and future) situation of greenhouse gas increase causing climate change.

In addition to the goods and services provided by seagrasses, there is also ethnographic interest. Thus, since ancient times people from Mediterranean countries used these plants for different purposes. For example, dried leaves of *Posidonia oceanica* served as wrapping up material to carrying fragile pieces of glassware and ceramic (this is the origin of the name *Alga vitriariorum* as *P. oceanica* was known in ancient times); in the transportation of fresh fish from shoreline towns to inland cities; as building materials (roof insulation and adobes). Due to parasite-deterrent properties of seagrass leaves they were also used as material for stuffing pillows and mattresses (Pope Julius III popularized this use in the sixteenth century); mixed with lime and phosphates as a meal for feeding poultry; also in medicine *P. oceanica* was used to prevent respiratory diseases, alleviation of skin infections (e.g., acne) and leg pain by varicose veins; in some small villages of southern Spain the dried rhizomes of *P. oceanica* are still utilized as fuel to prepare traditional fish barbecues at the seashore (called *moragas*) (Pérez-Lloréns et al. 2012). Today, because of their sensitivity to water quality (transparency and nutrient concentrations), seagrasses are used as biological sentinels or "shore canaries" (Orth et al. 2006), for example as biological indicators in the

European Water Framework Directive (2000/60/CE) and Marine Strategy Framework Directive (2008/56/CE).

However, despite its paramount importance there is a worldwide regression of seagrass habitats (Orth et al. 2006; Short et al. 2011). Although there are somewhat contrasting estimates, a recent assessment indicates that about one-third of the global seagrass area has been already lost, and that losses are accelerating from less than 0.9 % year$^{-1}$ in the 1970s to more than 7 % year$^{-1}$ since 2000 (Waycott et al. 2009). In the Mediterranean, it is estimated that 46 % of the *Posidonia oceanica* meadows have undergone some reduction in range, density and/or extent, and 20 % have suffered acute regressions since 1970s (Díaz-Almela and Duarte 2008). Among the main causes, mostly anthropogenic (either direct or indirect), are: deterioration of light environment, physical disturbance, mechanical damage, eutrophication, introduction of invasive species and climate change (Duarte 2002). Many Mediterranean countries, aware of the key important role seagrasses plays, have established comprehensive and advanced monitoring programmes for seagrasses as well as management and conservations plans (Borum et al. 2004; Díaz-Almela and Duarte 2008).

Therefore, the aim of the present contribution is to provide basic information about the biology and ecology of the Mediterranean seagrasses, the main threats facing these habitats, and the principal conservation and management strategies.



**Fig. 9.1** The seagrass *Posidonia oceanica* is a Mediterranean endemism. Meadows can growth as deep as 40–50 m in clear waters (Photograph: Juanma Ruiz)

## Mediterranean Seagrass Species: Distribution, Biology and Ecology

Four seagrass species occur in the Mediterranean bioregion: the endemic *Posidonia oceanica*, the tropical *Cymodocea nodosa* and the temperates *Zostera marina* and *Z. noltii*.

### *Posidonia oceanica* (Linnaeus) Delile

*Posidonia oceanica* (common name: Neptune grass) is a Mediterranean endemism and constitute one of the main mature (or climax) stages of Mediterranean subtidal bottoms. Available information for *P. oceanica* is higher than that for the other Mediterranean seagrass species. Meadows extend on 2.5–4.5 millions ha that is close to 25 % of the Mediterranean basin shallower than 50 m (Pasqualini et al. 1998). The western boundary is at the Alborán Sea where its growth is limited due to the influence of Atlantic water that is colder and less salty than the Mediterranean. The most westerly remnants are recorded 20 km east from the Gibraltar Strait on the Spanish coast (Estepona Bay), and 280 km towards Morocco coasts, near Sebkha-bou-Areg, and Chaffarine islands (Meinesz et al. 2009). Its presence in the north-western Mediterranean is widely recorded, whereas in the south-western and eastern Mediterranean is scarcer (Green and Short 2003). Nowadays, there is no *P. oceanica* in the eastern Levant Sea (Gobert et al. 2006) where the most north-eastern boundary would be close to the Kizilliman Marine Protected Area (Turkish coast, Celebi et al. 2007) and Alexandria (Egypt) on the south shore. Nevertheless, there are old records on the Syrian coast, but in 1976 the species was reported to be highly threatened (Mayhoub 1976).

*Posidonia oceanica* forms extensive underwater meadows on sandy (sometimes rocky) substrates, in clear open waters, from less than 1 m down to 25 m depth (Alborán Sea) or to 40 m (Ligurian or Aegean Seas) (Fig. 9.1). Light availability (i.e., water transparency) often limits the depth at which meadows occur (Duarte 1991a). Its mean compensation irradiance for photosynthesis (i.e., the light intensity at which oxygen production by photosynthesis compensates for its respiratory consumption) (c.a., 8 µmol photons m$^{-2}$ s$^{-1}$) is lower than those reported for other Mediterranean species (Table 9.1). This characteristic and the large capacity to store and mobilize carbohydrates, allows *P. oceanica* to occur at deep locations. It is considered a stenohaline species

**Table 9.1** Mean values of photosynthetic parameters, plant architectural traits, dynamic characteristics and meadow properties of the four Mediterranean seagrass species

| | P. oceanica | C. nodosa | Z. marina | Z. noltii |
|---|---|---|---|---|
| *Photosynthetic parameters* | | | | |
| Light-saturated photosynthetic rate ($\mu mol\ O_2\ g\ DW^{-1}\ h^{-1}$) | 199.3 | 174.1 | 119.9 | 549.4 |
| Compensation irradiance for photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$) | 7.8 | 35.1 | 21.7 | 20.0 |
| Saturation irradiance for photosynthesis ($\mu mol\ m^{-2}\ s^{-1}$) | 73.3 | 149.2 | 116.0 | 250.0 |
| *Architectural traits* | | | | |
| Leaf abundance (nº leaves shoot$^{-1}$) | 6.1 | 3.3 | 4.2 | 3.2 |
| Leaf length (cm) | 75.2 | 34.6 | 39.7 | 10.8 |
| Shoot weight (mg DW shoot$^{-1}$) | 731.0 | 315.0 | 272.5 | 14.3 |
| Horizontal rhizome internodal length (cm) | 0.4 | 2.1 | 1.8 | 1.3 |
| Vertical rhizome internodal length (mm) | 1 | 1.4 | – | – |
| Rhizome diameter (mm) | 10 | 3.0 | 3.5 | 1.3 |
| Fruit size (mm$^3$) | 523.6 | 48.0 | 18.0 | 2.8 |
| *Dynamic features* | | | | |
| Shoot elongation rate (cm shoot$^{-1}$ day$^{-1}$) | 0.8 | 1.7 | 3.2 | 2.5 |
| Horizontal rhizome elongation rate (cm year$^{-1}$) | 4.2 | 40.2 | 40.9 | 54.8 |
| Vertical rhizome elongation rate (cm year$^{-1}$) | 1 | 1.4 | – | – |
| Leaf plastochrone interval (day leaf$^{-1}$) | 50.3 | 32.9 | 13.1 | 8.3 |
| Leaf production rate (leaves shoot$^{-1}$ year$^{-1}$) | 7.7 | 11.1 | 27.9 | 146.0 |
| Horizontal rhizome production rate (rhizome internodes year$^{-1}$) | 16.4 | 28.5 | 22.9 | 91.3 |
| Leaf longevity (days) | 302.8 | 45.0 | 51.4 | 25.0 |
| Generation length (year) | 35 | 3 | 1 | 1 |
| Shoot recruitment rate (ln units year$^{-1}$) | 0.2 | 1.4 | 1.5 | 1.4 |
| Shoot mortality rate (ln units year$^{-1}$) | 0.3 | 2.3 | 1.1 | 0.4 |
| *Patch/meadow properties* | | | | |
| Density (shoots m$^{-2}$) | 359 | 540 | 379 | 4945 |
| Aboveground biomass (AB, g DW m$^{-2}$) | 675 | 485 | 272 | 135 |
| Belowground biomass (BG, g DW m$^{-2}$) | 3785 | 500 | 147 | 88 |
| AB/BG ratio | 0.2 | 0.9 | 3.4 | 1.5 |
| Leaf area index (LAI, m$^2$ m$^{-2}$) | 3.9 | 3.5 | 2.8 | 1.9 |
| Aboveground production (gC m$^{-2}$ year$^{-1}$) | 392 | 446 | 568 | 875 |
| Belowground production (gC m$^{-2}$ year$^{-1}$) | 43 | 78 | 199 | 643 |
| Patch formation rate (nº patches ha$^{-1}$ year$^{-1}$) | 3 | 45 | 50 | 20 |

Data compiled from Bay (1984), Duarte (1991b), Pergent et al. (1994), Laugier et al. (1999), Hemminga and Duarte (2000), Brun et al. (2003b, 2006), Peralta et al. (2005), Lee et al. (2007), and Short et al. (2011)

supporting salinity values between 36.5 (e.g., Alborán Sea) and 39.7 (e.g., Cilician Sea), although it also occurs at lower salinities (e.g., from 21.5 to 28 in the Dardanelles Strait and in the Marmara Sea) or in hypersaline coastal lagoons (e.g., 39–44 in Farwà Lagoon on Libyan coast). However, low levels of carbon dioxide, rather than salinity, could be the limiting factor responsible for its absence in some coastal lagoons (Romero 2004). Its presence next to the mouth of large rivers (e.g., Rhône, Po or Nile) is limited by sediment and freshwater inputs. *Posidonia oceanica* withstand a rather wide range of temperatures, as inferred from its widespread latitudinal distribution (Green and Short 2003). The optimum temperatures range between 10 and 28 °C. Thus, its absence on a relatively narrow strip of the eastern Levant Sea (Lebanon and Israel coasts) has been associated to temperatures above the maximum range (Celebi et al. 2007).

The nature of the substrate, as well as the hydrodynamics, can also limit the growth of *P. oceanica*. Meadows thrive on sandy or rocky bottoms, but are rare on muddy substrates because of the deterioration of light environment as well as the poor oxygenation of sediments that affects the plant physiology and the overall performance (e.g., presence of phytotoxins like sulfide). Hydrodynamics, either as accretion/erosion balance or as wave exposure, also influences the bed development. Thus, *P. oceanica* rarely occurs nearby river mouths or in confined waters. In sheltered bays, meadows can grow up to the water surface, developing fringing reefs (Fig. 9.2), but in more exposed waters canopy usually does not reach the water surface (Sánchez-Lizaso 2004).

*Posidonia oceanica* is a large, slow-growing rhizomatous plant possessing both horizontal (plagiotropic) and vertical (orthotropic) rhizomes. Rhizomes are arranged as a sequence
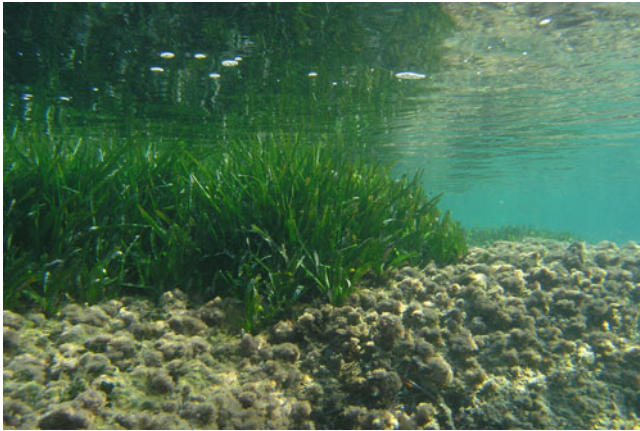
**Fig. 9.2** A typical *Posidonia oceanica* fringing reef in shallow waters (Photograph: Juanma Ruiz)



**Fig. 9.3** Detailed view of *Posidonia oceanica* shoots and orthotropic rhizomes fully covered by the fibrous rests of old leaf sheaths. The outermost leaves of the shoots (the oldest leaves) are covered by calcareous epiphytes (Photographs: Juanma Ruiz)

of segments (internodes) separated by nodes. Horizontal and vertical internodes are short (3.5–1 mm on average, respectively) and thick (up to 1 cm) revealing the slow growth of this species. Roots (up to 4 mm thick, and up to 40 cm long) are typically produced at the nodes of both kinds of rhizomes. Long (75 cm, on average) and wide (10 mm, on average) leaves (blade plus sheath) arranged in bundles on shoots (up to 8–10 leaves) arise from the nodes of the orthotropic rhizomes (Fig. 9.3). Leaf length undergoes seasonal variations being longer in summer (up to 1.4 m) and shorter in winter (20 cm, on average). Seasonal variations are also observed in biomass standing stocks and shoot density. On average, the aboveground biomass is 675 g DW m$^{-2}$, and the living belowground biomass is 3,785 g DW m$^{-2}$ (Sánchez-Lizaso 2004). These values, specially the belowground ones, are much higher than those reported for the other Mediterranean seagrasses (Table 9.1). Besides seasonality there is also a bathymetric (and site-to-site) variation in biomass standing stock and shoot density, with higher values usually at shallow waters (more than 1,000 shoots m$^{-2}$) and lower ones at deeper waters (70 shoots m$^{-2}$ or less). Meadows can be classified as a function of their densities into very sparse (50–150 shoots m$^{-2}$), dense (400–700 shoots m$^{-2}$) and very dense (700 shoots m$^{-2}$) (Giraud 1977).

Leaf longevity (303 days, on average), leaf plastochrone interval (i.e., elapsed time between the emergence of two successive leaves) (50 days leaf$^{-1}$) and generation time (35 years) are the highest among the Mediterranean seagrasses (Table 9.1). Senescent leaves are shed continuously throughout the year, but mainly in the autumn. Rhizomes are heavily lignified and easily recognizable by the compact fibrous rests of old, decaying leaf sheaths that remain attached to the rhizomes once the leaf blades have been lost (Fig. 9.3). The observed annual cyclic variation in the sheath thickness (and internodal length) has been used as a retrospective quantification method (known as
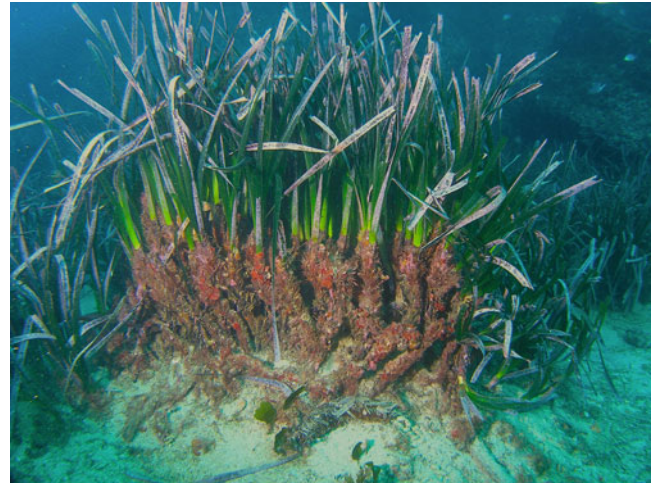
"lepidocronology") to study the dynamics of the *P. oceanica* meadows (Duarte 2004).

*Posidonia oceanica* is a monoecius species, with male and female flowers in the same inflorescence. Flowering fluctuates highly depending on populations, years and sites, but use to be a rather infrequent event (less than 20 % of shoots) that happens in autumn. Massive flowering events have been recorded associated to climatic extremes such as extreme warm summers (Díaz-Almela et al. 2007, 2009). Inflorescences are big and produce large fruits (known as "sea olives") that shed the following spring (Figs. 9.4a, b). The buoyancy of seeds could contribute to the dispersal of the populations, but no direct observations are available to corroborate it. There is not a seed bank of *P. oceanica* since seeds germinate after 10 days without a dormancy period. Seedlings are rarely found reflecting that spreading of populations would occur mainly by vegetative growth of rhizomes. It would explain the low genetic variability of the *P. oceanica* populations both at local and at broader spatial scales (although new data based on microsatellite markers show genetic distinction between east–west population, at scale of Mediterranean Sea, as a whole (Procaccini et al. 2002)). Thus, the little investment and low success of sexual reproduction, together with the extremely slow clonal spread (see below) would explain the extraordinarily slow colonisation rate of *P. oceanica*. In fact, the time required for the patches to develop meadows has been estimated in several centuries (Sánchez-Lizaso 2004).

Clones colonize a 3-D space throughout rhizome spreading and branching. Growth of plagiotropic (4.2 cm year$^{-1}$, on average) and orthotropic (1 cm year$^{-1}$, on average) rhizomes, as well as branching rate (every 30 year, on average) is the lowest among the Mediterranean seagrasses (Duarte 1991b)

**Fig. 9.4** (**a**) Detailed view of *Posidonia oceanica* inflorescence. (**b**) Fruit ("sea olive") (Photographs: Juanma Ruiz)
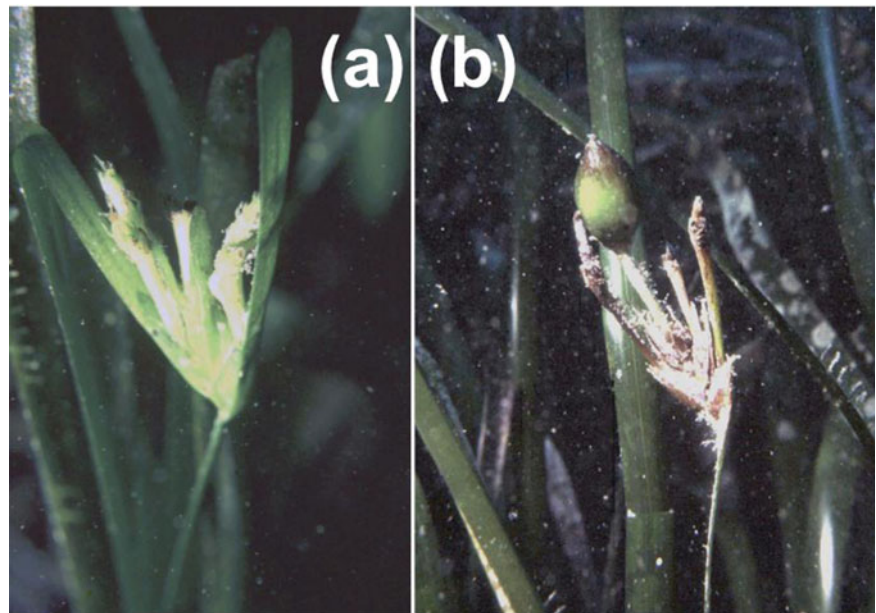
(Table 9.1). Besides the seasonal variation in growth rate (maximum in summer and minimum in winter, but smoother variations compared to the other Mediterranean seagrasses), the elongation rate of orthotropic rhizomes increases in response to burial resulting in a rise of the sea bottom. The network of interwoven fibrous live and dead rhizomes that decomposes slowly, mixed with sediment and organic debris can achieve several meters high and last for millennia. This bioconstruction is known as "matte" and the accumulation rate of such deposits has been estimated as 0.1–0.4 cm year$^{-1}$ (Romero et al. 1994; Mateo et al. 1997). The study of the matte allows the reconstruction of the past environmental conditions (paleoreconstruction) of the Mediterranean Sea.

*Posidonia oceanica*-dominated ecosystems are very productive fixing c.a., 400 gC m$^{-2}$ year$^{-1}$. Regardless of a large proportion (80 %) of the assimilated carbon is respired by the community itself, the net production of these ecosystems is about 72 gC m$^{-2}$ year$^{-1}$, which is a net carbon fixation 60 times higher than that of the coastal bare sediments (Barrón et al. 2006). A significant proportion (42–62 %) of this fixed carbon is retained and buried in the matte for millennia (Larkum et al. 2006). Considering that *P. oceanica* meadows cover up to 4.5 millions ha in the Mediterranean (Pasqualini et al. 1998), such beds would sequester about 2 Tg C year$^{-1}$. Since there are no estimations on the amount of carbon withdrawn in other Mediterranean littoral and open-water habitats, it is not an easy task to attain accurate estimations on the importance of the seagrass beds on a whole Mediterranean basin. However, it must be considerable since nearly 50 % of the carbon sequestered in the whole ocean is buried in coastal vegetated habitats, and that all seagrass species account for 15 % of the total carbon buried in the ocean (Duarte et al.

2005). Then, *P. oceanica* beds fix and sequester a portion of atmospheric $CO_2$, providing an important ecosystem service, as is the regulation of the Earth´s climate.

Besides the carbon burial, the fixed carbon can be also exported to adjacent systems. After heavy autumn storms, coinciding with the main period of foliar renewal, a variable proportion of production (10–90 %, depending on local hydrodynamics) is exported as detached leaves and rhizome fragments and stacked on shore forming structures known as "banquettes" (and "*Posidonia* balls" or aegagropiles when constant rolling action of the sea shapes this material into balls) (Romero et al. 1994) (Figs. 9.5a, b). The stranded biomass supplies important amounts of sediments and nutrients to beaches especially in those locations where sediments are of biogenic origin. Additionally, this litter covers the sand of the beaches keeping it from erosion during heavy storms. As well, some of the detritus piled up on the shoreline remain in the water, increasing its viscosity, and thus, lessening the energy of the swell and the risk of coastline erosion (Marbà 2009).

## *Cymodocea nodosa* (Ucria) Ascherson

*Cymodocea nodosa* (common name: Slender seagrass) is a warm water species widely distributed throughout the Mediterranean Sea, the eastern Atlantic, from south Portugal to Senegal and around the Canary Islands. It is a pioneering species that usually thrives in open sea (from shallow waters down to 30–40 m, depending on the water transparency), bays, small harbours and littoral lagoons (Fig. 9.6). This species prefers sandy or sand-muddy substrates tolerating a

**Fig. 9.5** (**a**) Debris of *Posidonia oceanica* (detached shoots, rhizomes and roots) deposited on shore forming accumulations known as "banquettes". (**b**) Detail of the accumulations showing the distinctive "*Posidonia* balls", and fragments of rhizomes and shoots (Photographs: Juanma Ruiz)

**Fig. 9.7** Mixed meadows of *Cymodocea nodosa* and the green seaweed *Caulerpa prolifera* are commonly found in shallow-sheltered bays (Photograph: Ángel Pérez-Ruzafa)

accumulate in crevices or small depressions on rocky flats. *Cymodocea nodosa* grows in warm environments with temperatures ranging from approximately 10 °C up to about 30 °C. Its sensitivity to temperature has been attributed to the tropical origin of this seagrass genus. It is also highly tolerant to salinity, withstanding fluctuations from 26 to 44. *Cymodocea nodosa* can occur either as monospecific stands (e.g., Urbinu lagoon, France) or as mixed meadows with *Zostera noltii* (e.g., Baia delle Saline, Italy)*, Z. marina* (e.g., Venice Lagoon, Italy) or with the green alga *Caulerpa prolifera* (e.g., Mar Menor, Spain) (Fig. 9.7)*.* In some locations it forms bands embracing the upper and lower limits of the *Posidonia oceanica* meadows (e.g., Natural Park of Cabo the Gata, Spain), colonizing also dead mattes of *P. oceanica* and enabling a further recolonization by this climax species (Marbà and Terrados 2004).

*Cymodocea nodosa* is a fast-growing rhizomatous plant that possesses vertical and horizontal rhizomes. Rhizomes are much more thinner (3.0 mm diameter, on average) than those of *Posidonia oceanica* (10 mm diameter, on average) and the orthotropic rhizomes lack the compact fibrous leaf sheath envelope (Fig. 9.8a). This species is easily distinguishable from *Zostera marina* by the long (2.1 cm on average) white to pink plagiotropic rhizome internodes and, mainly, by the presence of orthotropic rhizomes with slightly compressed and short internodes (1.4 mm, on average). Single, strongly branched roots (up to 3 mm thick and up to 40 cm long) appear at the nodes of both kinds of rhizomes. Leaves (34 cm long and 3 mm wide, on average) are arranged in bundles in shoots (3.3 leaves, on average) arising from nodes of horizontal and vertical rhizomes. The distinct lines identifying the nodes after leaf abscission are known as "leaf scars". Leaf length varies on season, depth and location. Leaf longevity and leaf plastochrone intervals depend on the time of leaf appearance but, on average, are 45–33 days leaf$^{-1}$,



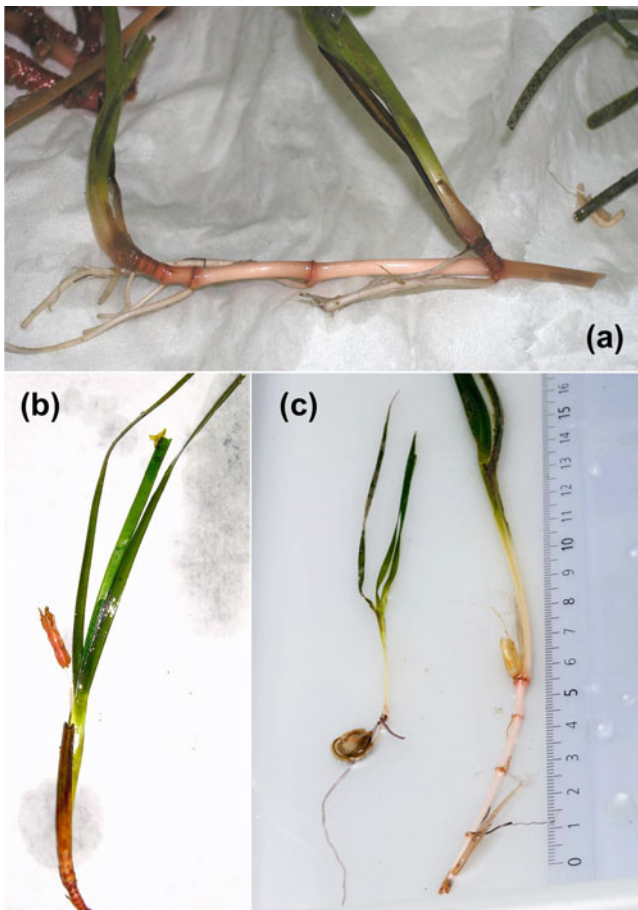**Fig. 9.6** General view of a shallow *Cymodocea nodosa* meadow (Photograph: Ángel Pérez-Ruzafa)

wide range of nutrient concentrations, reducing conditions of the sediments and moderate levels of physical disturbance. Patches are also found in small sandy or gravel pockets that

**Fig. 9.8** (**a**) *Cymodocea nodosa* showing the characteristic horizontal (plagiotropic) pinkish and vertical (orthotropic) rhizomes and the single white roots arising from nodes. (**b**) Male plant showing flowers. (**c**) Seedling and female plant with a seed at the base of the shoot (Photographs: EDEA)

respectively (Table 9.1). Thus, leaf replacement dynamics (turn-over) is faster than in *P. oceanica* (Terrados and Marbà 2004).

*Cymodocea nodosa* is a dioecius species. Reproductive effort and success is subjected to temporal and spatial heterogeneity. Flowering (spring-summer) is quite rare occurring only in shoots older than 1 year, but is enhanced in response to burial. Besides, the spatial distribution and abundance of male and female clones could limit seed production, and in turn, the reproductive success in those sites where only clones of one sex occur. Female flowers produce two lenticular seeds that are considerably bigger (48 mm³, on average) than those of *Zostera* spp. Seeds are formed at the base of the mother shoots and once detached they are rapidly buried into the sediment nearby the generative shoot because its negative-buoyancy building a rather ephemeral seed bank (7–9 months of dormancy period) (Figs. 9.8b, c). Although seed dispersal is rather limited, episodes of severe sediment dynamics can favour a long-distance dispersal.

Seeds germinate from April to June of the next year (Terrados 1993). Patch formation rate in areas undergoing intense sexual reproduction has been estimated c.a., 90 clones ha⁻¹ year⁻¹. However, clone mortality rate is about 50–70 % during the first year of life, hence, decreasing considerably the success of sexual reproduction (Duarte and Sand-Jensen 1990). Patches spread relatively fast since the growth rate of the horizontal rhizomes is among the highest of the Mediterranean seagrasses (40.2 cm year⁻¹, on average, but up to 200 cm year⁻¹ has been recorded) (Duarte 1991b) (Table 9.1). The rapid space occupation resulting from fast clonal growth and the relatively high patch formation rate (45 patches ha⁻¹ year⁻¹, on average) supports the colonizer role that *C. nodosa* plays during the succession process in the Mediterranean. The time span required for patches to develop meadows is estimated to be less than a decade. The vertical rhizomes of *C. nodosa* also extend, but at slower rates (1.4 cm year⁻¹, on average) than the horizontal ones. Thus, rhizome growth is plastic enough to allow this species to survive moderate environmental disturbances such as accretion/erosion episodes by increasing or decreasing the elongation rate of the vertical rhizomes, respectively (Duarte and Sand-Jensen 1990).

Growth, production, biomass standing stock and shoot density of *Cymodocea nodosa* beds undergo a marked seasonal pattern superposed to bathymetric and site-to-site variations. Growth rates vary highly throughout the seasonal cycle depending on temperature what it has been attributed to the tropical origin of this genus. Maximum values for growth (up to 6 cm shoot⁻¹ day⁻¹ for aboveground parts, and up to 0.6 cm day⁻¹ for horizontal rhizomes), production (up to 844 gC m⁻² year⁻¹ for aboveground, and up to 144 gC m⁻² year⁻¹ for belowground), shoot standing stock biomass (up to 945 g DW m⁻²) and shoot density (up to 2,000 shoots m⁻²) are achieved during the spring-summer period. A considerable proportion of the net primary production (48–67 %) is exported to adjacent systems, a small amount (9 %) serves as food for herbivores and the remaining enters into the detritus food web.

### *Zostera marina* Linnaeus

*Zostera marina* (common name: Eelgrass) presents a widespread and circumglobal distribution in northern latitudes: from artic waters to the Mediterranean Sea. It is abundant in the Baltic Sea, the North Sea and along the Atlantic coasts down to northern Spain. Further south it becomes less abundant and in the Mediterranean Sea it is considered a relict species. It forms small perennial isolated stands in shallow protected bays and coves of the northwestern Mediterranean (Spain, France, Italy) and Adriatic Sea extending from the intertidal to few meters depth (Fig. 9.9). However, denser

**Fig. 9.9** Patch of *Zostera marina* at low tide. The light green shoots are flowering shoots (Photograph: EDEA)



**Fig. 9.10** *Zostera noltii* meadow at low tide (Photograph: EDEA)

meadows occur regularly in coastal lagoons of the western Mediterranean such as the Thau lagoon (France) where it is often found with *Z. noltii* (Laugier et al. 1999) or in Venice Lagoon (Italy) where it forms mixed populations with *Cymodocea nodosa*. There are records of its presence in Tunisia and previously in the northern Aegean Sea (Boudouresque et al. 2009). Others old sightings as in Egypt or Syria (Mayhoub 1976) are doubtful due taxonomic confusion in the past. It has also been recorded in the Black Sea (Green and Short 2003). *Zostera marina* is mostly subtidal occurring down to 10–15 m depth (depending on water transparency) in sandy and muddy coastal bottoms of low to moderate wave exposure. It is a eurythermic (−1–25 °C) and euryhaline (5–35) species.

*Zostera marina* has only horizontal rhizomes (3.5 mm diameter, on average) with internodes (1.8 cm, long on average) that are white-green in recently produced ones to dark brown in the oldest. Two bundles of roots arise from the nodes. The roots are thin and long (up to 1 mm and 20 cm, respectively) covered by fine root hairs. Leaves (40 cm long and 6 mm wide, on average) are arranged in bundles in shoots (4.3 leaves, on average) arising from the nodes. Leaf length, biomass standing stock and shoot density are highly variable depending on season, depth and location. Thus, leaves up to 1.5 m long are observed in beds on soft sediments at intermediate depths. Leaf longevity and leaf plastochrone intervals are, on average 51.4–13.1 days leaf$^{-1}$ respectively (Table 9.1) (Pérez-Lloréns 2004a).

*Zostera marina* is a monoecius species. Inflorescences are produced in shoots (known as flowering shoots) arising from long and thin stems (Fig. 9.9). Flowering (spring-early autumn) is frequent and produces thousands of seeds per square meter. Once the seeds (18 mm$^3$, on average) are mature the flowering shoots die and shed. Detached shoots float away from the bed contributing to a wider dispersal of seeds, although the majority of seeds drop within the mother meadow because of its negative buoyancy. The majority of

patches (90–95 %) resulting from seed germination (50 patches ha$^{-1}$ year$^{-1}$, on average) die within the first year and only few spread and persist, even several centuries or millennia (up to 3,000 years) in locations (Baltic Sea) where sexual reproduction is rare (Reusch et al. 1999). In general, the spread of patches in the Mediterranean is throughout clonal growth and the time required for the patches to develop meadows has been estimated to be less than a decade (Hemminga and Duarte 2000).

*Zostera marina* meadows follow a seasonal pattern in growth, production, biomass standing stock and shoot density that can be tuned by depth and location. Seasonality in growth is highly dependent on irradiance and less on temperature. Maximum values for growth (up to 5.7 cm shoot$^{-1}$ day$^{-1}$ for aboveground parts, with a mean leaf production rate of 28 leaves shoot$^{-1}$ year$^{-1}$, and up to 0.25 cm day$^{-1}$ for rhizomes), production (up to 1,985 gC m$^{-2}$ year$^{-1}$ for aboveground, and up to 657 gC m$^{-2}$ year$^{-1}$ for belowground), shoot standing stock biomass (up to 960 g DW m$^{-2}$) and shoot density (up to 2,100 shoots m$^{-2}$) are achieved during the spring-summer period (Pérez-Lloréns 2004a).

### *Zostera noltii* Hornemann

*Zostera noltii* (common name: Dwarf eelgrass) is widespread in intertidal and shallow subtidal areas of the Atlantic coast of North America and Europe from the southern coast of Norway to the Mauritanian coast (Fig. 9.10). In the Mediterranean Sea it occurs in sheltered coasts such as bays, lagoons, small harbours or estuaries on sandy and muddy bottoms where can form monospecific or mixed meadows with *Cymodocea nodosa*, *Z. marina* or with the green seaweed *Caulerpa prolifera*. It is a eurythermic and euryhaline species with a wide range of salinity tolerance (25–51). Low
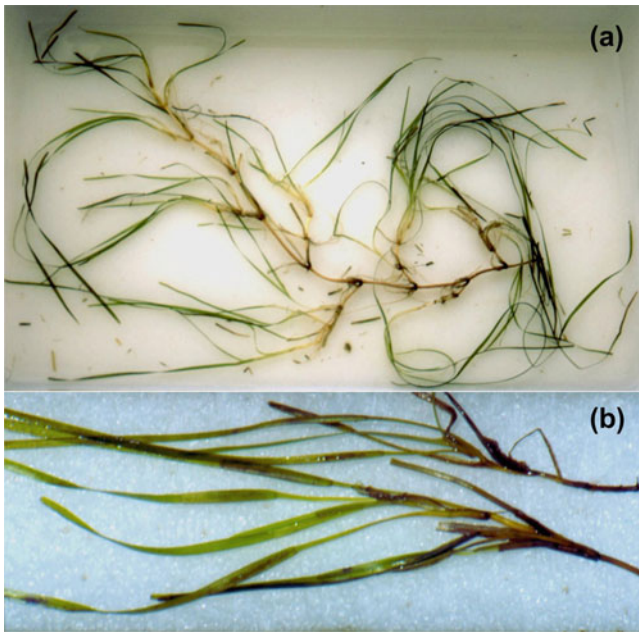
**Fig. 9.11** (**a**) Plant of *Zostera noltii* showing the rhizome network, branching pattern and shoots. (**b**) Flowering shoot (Photographs: EDEA)



**Fig. 9.12** *Zostera noltii* (*right*) is a pioneering species that use to colonize gaps after disturbance episodes in *Posidonia oceanica* meadows (*left*) (Photograph: José Antonio Rodríguez)

salinity improves germination and seedling development. Since it occurs at the intertidal or shallow subtidal (above 10 m depth) it is adapted to high irradiances (as the high saturating irradiance for photosynthesis denotes, Table 9.1), but can withstand relatively high turbidity episodes in estuarine water, as suggest its low minimum light requirement for growth (2 % of surface irradiance, Peralta et al. 2002). It is tolerant to the relatively anoxic conditions typical of the rich organic sediments where meadows thrive. The critical level of accretion or erosion tolerated by this species is extremely low due its small size and the presence of short vertical rhizomes (Pérez-Lloréns 2004b; Brun et al. 2005).

Architecture of *Zostera noltii* resembles that of *Z. marina* but reduced in the size of the modules. Rhizome internodes (3.5 mm diameter and 1.3 cm long, on average) are light green in the youngest parts and yellow or brown in the oldest ones. It has been reported recently the presence of short and thin vertical rhizomes in this species (Brun et al. 2005). Two bundles of thin roots (<1 mm) arise from rhizome nodes. Ribbon-shaped leaves (10.8 cm long and 1 mm wide, on average) are arranged in bundles in shoots (3.2 leaves, on average) arising from nodes. Each rhizome holds many shoots on short branches separated by rhizome internodes (Fig. 9.11a). As in the other seagrass species, leaf length, standing stock biomass and shoot density are highly variable depending on season, depth and location. Thus, leaves up to 65 cm long are observed in beds growing in deep areas. Leaf longevity and leaf plastochrone intervals vary depending on the recruitment season but on average, are 25.0–8.3 days

leaf$^{-1}$ respectively (Brun et al. 2003b; Peralta et al. 2005) (Table 9.1).

*Zostera noltii* is a monoecius species. Inflorescences are produced in flowering shoots arising from the rhizomes as the vegetative ones (Fig. 9.11b). Flowering represents less than 10 % of the shoots and can extend from March to November but usually varies among locations, since factors such as photoperiod, temperature, tidal amplitude and fluctuating salinity regimes control the flowering event. Seeds are very small (2.8 mm$^3$, on average) and are not likely to disperse far away because of its negative buoyancy. However, water currents may transport detached flowering shoots containing seeds over long distances. Seedling is also very infrequent (less than 5 % of patches are originated from seeds, on average, 20 patches ha$^{-1}$ year$^{-1}$) (Table 9.1) suggesting that clonal growth instead sexual reproduction is the main way of meadows spreading (Brun et al. 2003a, b).

The high internode production (91.3 rhizome internodes year$^{-1}$, on average), elongation (54.8 cm year$^{-1}$, on average) and branching rates (at every rhizome node) lead to a rapid spread of patches. In fact, the time required for patches to develop meadows ranges from several months to a year. In addition, *Zostera noltii* also have the highest turnover rates among the Mediterranean seagrasses (e.g., leaf production rate is, on average, 146.0 leaves shoot$^{-1}$ year$^{-1}$, and the leaf longevity 25.0 days), which is typical of colonising species allowing *Z. noltii* to cope with (or to recover after) considerable levels of disturbance. It is rather common that *Z. noltii* (or *Cymodocea nodosa*) colonizes gaps after disturbance episodes in *Posidonia oceanica* meadows (Fig. 9.12). As the other seagrass species, *Z. noltii* beds undergo clear seasonal cycles in growth, production, biomass standing stock and shoot density that can be altered by depth and location. Maximum values for growth (up to 3.5 cm shoot$^{-1}$ day$^{-1}$ for aboveground parts, and up to 0. 5 cm day$^{-1}$ for rhizomes),

production (up to 1,250 gC m$^{-2}$ year$^{-1}$ for aboveground, and up to 1,280 gC m$^{-2}$ year$^{-1}$for belowground), shoot biomass standing stock (up to 260 g DW m$^{-2}$) and shoot density (up to 10,000 shoots m$^{-2}$) are achieved during the spring-summer period. The annual foliar losses have been estimated in 420 gC m$^{-2}$ year$^{-1}$ that accounts for near 75 % of the aboveground production (Marbà et al. 1996; Brun et al. 2003b; Peralta et al. 2005).

## Disturbances in Seagrass Meadows

Despite the general agreement that seagrasses provide important ecosystem services and goods, being listed as priority habitats for conservation (e.g., Rio Biodiversity Convention, European Habitats Directive, European Water Framework Directive, National and Regional frameworks, etc.), there are growing evidences of a remarkable global regression (Orth et al. 2006; Short et al. 2011). Besides the natural disturbances affecting seagrass meadows, sometimes severely like the "wasting disease", a pathogen (slime mold) that caused the lost of many *Zostera marina* populations in the 1930s, direct or indirect human interventions are the principal drivers of the observed seagrass declines (Hemminga and Duarte 2000).

## Anthropogenic Non-climatic Causes

Seagrass losses of 2,900 km$^2$ were reported from mid-1980s to mid-1990s as consequence of direct or indirect human pressures. An extrapolation of these numbers to unreported parts of the coasts would render c.a., 12,000 Km$^2$ of meadows probably lost (Short and Wyllie-Echeverria 1996). Recent estimations, based on a longer time observations (20 years), give values of about 33,000 km$^2$ (Spalding et al. 2003). Assuming a conservative value of global seagrass cover of 177,000 km$^2$ (Spalding et al. 2003), losses would range between 7 and 19 % of the documented seagrass areas (with values up to 65 % within inhabited areas, Lotze et al. 2006). However, reported losses probably represent a small fraction because global estimations of seagrass cover are very rough and many losses may remain unreported (Duarte et al. 2004).

Yearly, an estimated 100 million tourists visit the Mediterranean coasts, making it the European centre for international tourism, receiving around a third of all international tourists. About 60 % of the coastline is currently urbanized and up to more than 75 % in the regions with the most developed tourism industry, with harbours and ports occupying 1,250 km of the European Mediterranean coastline (French 1997). Such demographic pressure results in important disturbances of seagrass meadows. For example, it has been estimated that, on average, 46 % of the *Posidonia*

*oceanica* meadows underwent some decline in range, density and/or coverage, and 20 % were severely deteriorated since the 1970s, and most dramatic large-scale losses happen in the northern Adriatic Sea where *P. oceanica* beds present at the beginning of the twentieth century have almost disappeared. However, it must be taken into account that some declines can be the consequence of long-term climate tendencies (e.g., the post-Last Glacial Maximum rise in sea-level, the Little Ice Age (LIA) cooling and the post-LIA warming) resulting in potential misinterpretation of the human influence in matte forming species as *P. oceanica* (Boudouresque et al. 2009).

Human activities affecting mostly to meadow physical integrity, sediment and water quality (including water transparency), coastal sedimentary balance or species composition are argued to be the main drivers of seagrass decline in the Mediterranean Sea (Boudouresque et al. 2009). Frequently, a single activity (e.g., coastal development) can involve both direct (e.g., mechanical damage) and indirect impacts (e.g., sediment unbalances, eutrophication, pollution, siltation, etc.) with synergistic effects on seagrass decline. In addition synergy can also emerge when several activities converge in a single location (Orth et al. 2006).

## Mechanical Habitat Destruction

Direct habitat damage by land reclamation and port or infrastructure construction is a major cause of disturbance for seagrass meadows. For instance, the construction of Pointe-Rouge harbour (Marseille, southern France) directly destroyed 11 ha of a *Posidonia oceanica* meadow (Boudouresque et al. 2006).

Trawling is probably the most important and concerning activity causing large-scale destruction of *Posidonia oceanica* beds, especially that at deepest locations and with exposed rhizomes (González-Correa et al. 2005), since a standard trawler uproots 99,000–363,000 shoots h$^{-1}$ (Martín et al. 1997). As an example, this fishing technique has been responsible for loss of the 12 % of the meadow extension in Corsica, almost 50 % in Alicante (Spain) or above 80 % in the Gulf of Gabe´s (Tunisia) (Boudouresque et al. 2006). Recovery of damaged beds might occur if trawling is forbidden, but the time span needed to recuperate the previous state may take almost 100 years given the very slow growth rate of *P. oceanica* (González-Correa et al. 2005).

Digging for clams can also harm seagrass meadows. It has been reported that fast-growing pioneering species like *Zostera noltii* are able to support certain threshold of disturbance. However, intensive clam harvesting practices (i.e., high frequency and intensity of disturbance, particularly during summer) may not allow the full recovery of *Z. noltii* meadows (Cabaço et al. 2005) (Fig. 9.13a).

Mooring can also affect meadows by uprooting shoots in those locations supporting high densities of small pleasure ships. It has been estimated that, on average, a single anchor
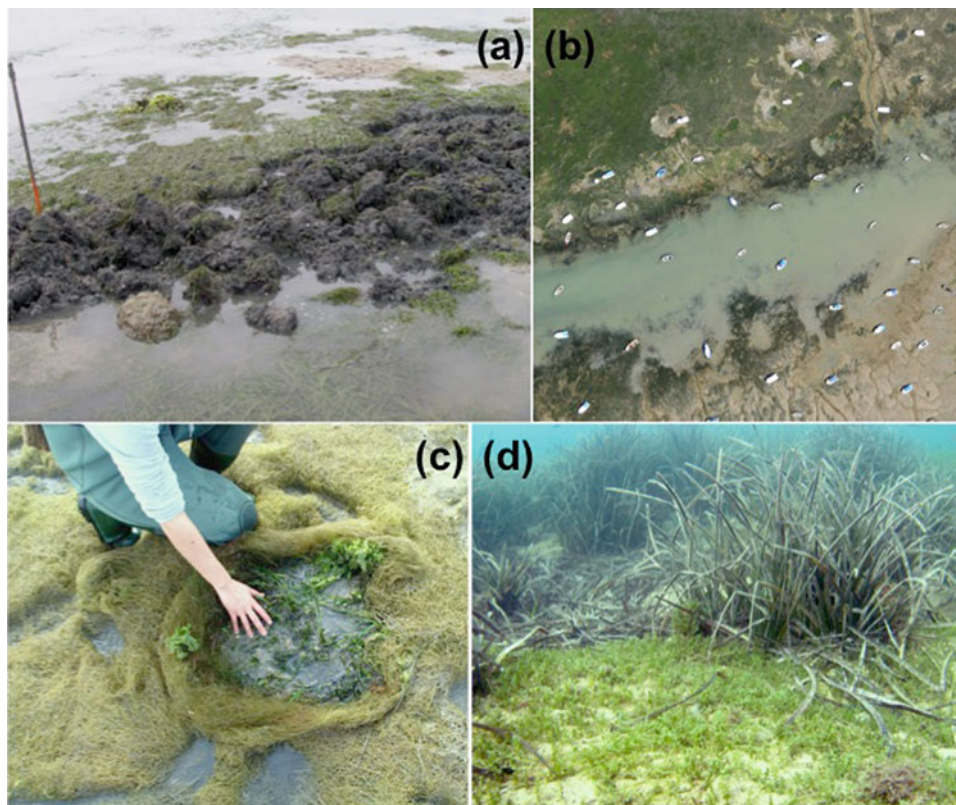
**Fig. 9.13** Some direct and indirect human impacts on seagrass meadows. (**a**) Digging for clams. (**b**) Boat anchoring: the circular marks on intertidal seagrass meadows are produced by the drag of anchored boats due to their movement with flowing and ebbing tides. (**c**) Dense mat of the green algae *Chaetomorpha linum* growing on *Cymodocea nodosa-Zostera noltii* mixed meadow. The black colour of sediment denotes the anoxic conditions due to the loading of sediments with organic matter from algal die-off (Photographs: EDEA). (**d**) Habitat perturbations make *Posidonia oceanica* meadows more vulnerable to be invaded by alien species such as the green algae *Caulerpa racemosa* (Photograph: Juanma Ruiz)

uproots 34 shoots (Francour et al. 1999) or 68,000 shoots ha⁻¹ (Corsica) (Boudouresque et al. 2006). If anchoring is in an intertidal domain, the movement of boats by ebbing and flowing tides and currents cause scars in intertidal populations of *Zostera noltii* or *Cymodocea nodosa* (Fig. 9.13b).

Dredging and sand withdrawal (e.g., for beach nourishment) are major causes of seagrass loss. Although the existence of a compact matte of *Posidonia oceanica* often keeps these areas from sand extraction it is not always the case, as for example, in Ischia (Italy) where 4 ha of meadow were directly destroyed by sediment pumping or, indirectly, by turbidity and burial by sand re-deposition (Flagella et al. 2006).

As just mentioned, meadow removal can led to a set of secondary effects like, increased turbidity (due to sediment resuspension), alteration of sediment dynamics (burial/erosion balance), and modification of physical processes (e.g., water currents) as a consequence of the sediment redistribution (Ruiz and Romero 2003). For example, nearby Toulon (south eastern France) the construction of artificial beaches buried 22 ha of *Posidonia oceanica* meadows, but sediments relocated during and after works buried 10 additional ha (Astier 1984). As consequence of sediment erosion/accretion episodes survival of shoots decreases. However, species with orthotropic rhizomes (*P. oceanica* and *Cymodocea nodosa*) can tolerate moderate burial since shoot recruitment is favoured because of the growth and branching of the orthotropic rhizomes are enhanced under such conditions. For example, *P. oceanica* beds can cope with burial rates of up to 4–5 cm year⁻¹. If sediment accretion exceeds such level bed decay accelerates, and accumulation of 14 cm result in 100 % shoot mortality (Manzanera et al. 1998). Analogously, orthotropic rhizome and leaf growth rates are kept at minimum when sediment is eroded. The seagrass response to sediment dynamics remains imprinted on rhizomes. It has been used for retrospective identification of burial/erosional events (Marbà and Duarte 1994). Fast-growing species lacking vertical rhizomes (*Zostera marina*) or with short and thin vertical rhizomes (*Z. noltii*) are most sensitive to burial. However, the high elongation rate and branching of the horizontal rhizomes allow a fast recovery after moderate burial events (Brun et al. 2007).

## Eutrophication

Eutrophication (i.e., nutrient over-enrichment, especially nitrogen and phosphorus) observed in many coastal waters has been considered as a major cause of seagrass decline, especially in heavily developed parts of the world (Hemminga and Duarte 2000). Although currently eutrophication and pollution are not a generalized problem in the Mediterranean Sea (Jackson et al. 2006), some seagrass meadows are heavily affected because of localized human activities (e.g., domestic and industrial sewage outlets, agricultural runoff, aquaculture activities, etc.).

Eutrophication can harm seagrasses in two ways: directly because of the toxicity of some nutrients (e.g., ammonium) (Brun et al. 2002) or indirectly, by stimulating the growth of phytoplankton, epiphytes (micro- and/or macro-) or pleustophytic opportunistic macroalgae (Fig. 9.13c). Although the type of blooming algae will depend mostly on the water turnover rate (i.e., sheltered *vs* open locations), the overall consequence will be shading seagrasses beneath. Due to the high proportion of non- photosynthetic tissues (mostly roots and rhizomes), seagrasses require for survival and growth underwater irradiance values generally above 11 % of that incident on the water surface (Duarte 1991a) making them very vulnerable to deterioration of the light environment. However, despite the respiratory burden that belowground biomass represents, rhizomes are the main reservoir of soluble carbohydrates that are mobilized to meet whole-plant carbon demands for growth and survival under low light conditions (Hemminga and Duarte 2000). Accordingly, tolerance to prolonged shading is expected to be higher in *Posidonia oceanica* than in the other small-size Mediterranean species because of the largest capacity of *P. oceanica* to store carbohydrates (i.e., low AG/BG ratios, Table 9.1).

Besides the negative effects of light reduction on seagrass meadows, unfavourable biogeochemical alterations of the habitat arise: the loading of sediments with organic matter from algal die-off enhances the respiration of the benthic microbial community leading to anoxia. Such conditions are harmful to seagrasses not only because anoxia restricts starch (sucrose) translocation from rhizomes to shoots to meet the carbon demands under low light periods (Brun et al. 2003a) or impedes root respiration and nutrient uptake, but also because sulfide compounds in the surroundings of the rhizosphere may be toxic. Such reduced sediment conditions are long lasting even after the organic inputs stop, outspreading meadow deterioration (Hemminga and Duarte 2000).

Fish farms and other aquaculture developments are good examples of activities that are becoming increasingly in the shallow, sheltered coastal Mediterranean waters where seagrasses thrive, and are causing localized but significant impacts on meadows. Shading and high inputs of organic matter from fish cages lead to seagrass decline below and around fish cages, through processes comparable to those of the eutrophication outlined above (Ruiz et al. 2001). A comparative study addressing the effects of fish farming on *Posidonia oceanica* meadows across the Mediterranean Sea reported a negative impact on beds extending up to 200 m away from fish farms (Holmer et al. 2003), and, in Sicily, a negative impact on the orthotropic rhizome growth rate was detected as far as 1 km from a large fish farm installation. Since the resilience of this species to fish farm impact is overall very low (Marbà et al. 2006), the decline meadows due to the growing fish farming activities is currently rising (Jackson et al. 2006).

## Introduced Species

The term 'introduced species' refers as any species introduced, intentionally or not, beyond its native range through human activities. In the last decades about 100 exotic macrophyte species have been introduced in the Mediterranean Sea mostly through shipping and aquaculture activities. At least five of them have an invasive behaviour to affect Mediterranean seagrass habitats: two Australian chlorophytes (*Caulerpa taxifolia* and *C. racemosa* var. *cylindracea*) and three Indo-Pacific rhodophytes (*Lophocladia lallemandii*, *Acrothamnion preissii* and *Womersleyella setacea*; Boudouresque et al. 2009).

The most well-known and studied case was the effect of *Caulerpa taxifolia* and *C. racemosa* var. *cylindracea* on *Posidonia oceanica* (e.g., Villèle and Verlaque 1995; Jaubert et al. 1999) and, to lesser extent, on *Zostera noltii* and *Cymodocea nodosa* meadows. Beyond the contrasting observations that literature brings on their influence on *P. oceanica* stands decline, it seems that habitat perturbations (e.g., trawling, eutrophication) makes seagrass beds more vulnerable to be invaded (Williams 2007) (Fig. 9.13d). It would explain that invasions have been mostly recorded in previously impacted and/or sparse meadows and not in dense and vigorous ones (Klein and Verlaque 2008).

The invasive rhodophyte *Lophocladia lallemandii* has been detected growing as dense mats of filaments on rhizomes and old leaves of *Posidonia oceanica* specimens occurring in small patches or at the periphery of denser meadows. Such mats can be so thick that produce mortality of the shoots (Ballesteros et al. 2007). *Acrothamnion preissii*, a new exotic rhodophyte that invades *P. oceanica* rhizomes has no evident effects on plants itself but it shifts most of the autochthonous rhizome epiphytes reducing the meadow's taxonomic diversity and habitat complexity. The rhodophyte *Womersleyella setacea* forms thick and long lasting turfs in several Mediterranean habitats, including *P. oceanica* beds. Mixed turfs of *A. preissii* and *W. setacea* may promote drastic declines in species richness of the understory assemblage in the invaded meadows (Piazzi et al. 2001).

Besides the cited observations, more surveys and experimental studies in invaded seagrass meadows would be necessary to quantify damages due to exotic species (Williams 2007). As abovementioned, dense *Posidonia oceanica* meadows seemed to cope with invasive species well, and no widespread losses have been reported. Nonetheless, competition can be a long-term ecological process and that short-term observations may be unsuccessful in detecting slow tendencies (Boudouresque et al. 2009).

## Climate Change Potential Causes

Since the first Intergovernmental Panel on Climate Change report (IPCC 1990), numerous reports and scientific articles have addressed both the observed and the potential impacts of climatic change on species and their habitats. Although these studies documented changes that are clearly related to climate trends, they also revealed many challenges in predicting the outcome on species and ecosystems (Burkett et al. 2005). For example, climate change is thought to influence seagrass meadows by the rise in sea level (and associated coastal erosion and turbidity), the increased partial pressure of $CO_2$ and acidification of seawater, the elevated seawater temperature and the increasing frequency and strength of climatic extremes. However, it is important to remind that the ability to forecast the effects of the climate change depends largely on the uncertainties about (1) future emissions and concentration of greenhouse gases, (2) constructing scenarios of climate change, (3) sensitiveness of the climate change to perturbations and (4) influence of nonclimatic drivers. In addition, there is an established, but incomplete evidence of critical ecosystem thresholds and the increasing likelihood of triggering non-linear responses (i.e., the output is not directly proportional to the input) once thresholds have been exceeded, resulting in abrupt changes and novel states (e.g., dystrophic crisis). Moreover, projecting the impacts of climate change on seagrass ecosystems is further complicated by a patchy knowledge of the interlinked temporal and spatial scales of ecosystem responses and the multiple (climatic *versus* non-climatic) drivers involved. Accordingly, predictions about the extent and direction of climate change on seagrass habitats will be associated with varying degrees of confidence. Thus, there is an acceptable level of confidence in predictions of global warming effects on dissolved inorganic carbon concentrations, sea level and on seagrass physiology; even in forecasting the effects of sea level rise on shoreline erosion and enhanced storm surges. However, there is a greater uncertainty to predict the effects of climate change on biotic interactions, wind patterns, and the frequency of extreme climatic events (IPCC 2007). It makes that forecasting the outcome of climate change on seagrass habitats becomes rather speculative.

## CO₂ Increase and Acidification

It has been demonstrated that the anthropogenic $CO_2$ concentrations in the Mediterranean Sea are much higher than those of the Atlantic Ocean (Schneider et al. 2007). Accordingly, the expected pH drop in the Mediterranean would be relatively larger than that predicted globally (i.e., 0.5 pH units for the year 2100), resulting in $CO_2$ and $HCO_3^-$ levels 50–6 % above those forecasted for the global ocean (IPCC 2007).

Ribulose-biphosphate carboxylase oxygenase (Rubisco) is the key enzyme involved in carbon fixation, using only $CO_2$ as substrate for carboxylation. In angiosperms, semi-saturation constants for $CO_2$ (30–250 μM) are higher than the $CO_2$ concentration in air-equilibrated seawater (10–15 μM, at pH 8.1). Furthermore, the $CO_2$ supply is often severely limited in dense seagrass canopies experiencing high biological activity (i.e., high C demand) under calm conditions (i.e., low hydrodynamics) (Enríquez and Rodríguez-Román 2006). To cope with the physical limitation of C mass transport, different carbon concentration mechanisms (CCMs) have evolved such as direct or indirect use of $HCO_3^-$ (James and Larkum 1996) and/or the catalytic dehydration of $HCO_3^-$ to $CO_2$ by the enzyme carbonic anhydrase (CA) (Invers et al. 1999). Despite such CCMs, and in contrast to many seaweed species, seagrasses are not fully saturated (i.e., 100 %) at the present $CO_2$ concentration in seawater (at pH 8.1), ranging from c.a., 91 % in *Cymodocea nodosa* to c.a., 60 % in *Zostera marina* with intermediate values for *Z. noltii* (c.a., 86 %) and *Posidonia oceanica* (c.a., 82 %) (Invers et al. 1999; Hellblom et al. 2001; Mercado et al. 2003). Thus, increased $CO_2$ and acidification would favour the competitive advantage of dense Mediterranean seagrass stands over seaweeds by rising photosynthesis and productivity and, probably, the depth limit of seagrass occurrence (Hemminga and Duarte 2000; Mercado 2011). However, it would be probably counterbalanced by the forecasted sea level rise and increased water turbidity (see below). The likely responses of seagrasses to climate change are forecasted mostly from physiological responses obtained in laboratory experiments (e.g., Zimmerman et al. 1997; Invers et al. 1999). However, present evidences that such physiological responses have led to observable changes in seagrass ecosystems are scarce, and other variables such as for example, the expected increase in water turbidity, temperature or nutrients (eutrophication) could hamper the effects of increased $CO_2$ and acidification on seagrass meadows dynamics.

## Temperature

According to IPCC (2007) the global atmospheric temperature will raise by 1.1–6.4 °C by 2100, with a parallel increase of 0.053 °C year$^{-1}$ observed in the Mediterranean since 1970s, but not homogenous throughout the annual cycle (Brunet et al. 2007). Many biological processes are

tightly controlled by temperature. Therefore, a change in the thermal regime (e.g., extreme temperatures, their extent, and seasonal rates of change) can directly affect several processes involved in seagrass growth and reproduction (e.g., respiration, photosynthesis, nutrient uptake, flowering and seed germination) as well as shifts in species composition, depending on the species-specific thermal tolerance ranges. At larger temporal and spatial scales changes in the biogeographic ranges are expected, with major effects suffered by those native populations of seagrasses existing nearby their boundaries of distribution.

It is well known that respiration increases more than photosynthesis as temperature rises. Thus, it is likely that global warming will result in higher respiration demands, that combined with reduced photosynthesis due to the forecasted light reduction (a combination of sea level rise and coastal erosion), will alter carbon balances compromising the maintenance of a positive carbon budget and, in turn, seagrass survival (Zimmerman and Alberte 1996). Mediterranean warming would benefit tropical species, such as *Cymodocea nodosa* or the newly established seagrass *Halophila stipulacea*, with higher photosynthetic and growth optimum temperatures than temperate species (*Zostera noltii, Z. marina, Posidonia oceanica*), which are likely to suffer a progressive regression. However, projecting the effects of increased temperature (and light availability) to the photosynthetic physiology of Mediterranean seagrasses, as well as to forecast the likely outcome driven by the climate change is highly speculative since effects appear to be rather species-specific (Enríquez et al. 2004) and because multiple (antagonistic, additive or synergistic) interactions with other human-related perturbations are expected.

A study carried out in several *Posidonia oceanica* meadows from the western Mediterranean revealed that elevated summer temperatures and persistent heat waves were associated with reductions in shoot growth and increases in shoot mortality and flowering intensity (Díaz-Almela et al. 2007, 2009). However, despite the observed massive flowering, the little success in seedling resulted in a sexual recruitment much more lower that the vegetative recruitment, and the total recruitment (sexual + vegetative) was, on average 4.5 times lower than mortality causing a progressive decline of those meadows. This study suggested that general regression of meadows could be enhanced by the Mediterranean warming trend, being such decline accelerated when seawater temperature rises above 28 °C. Moreover, enhanced temperature promotes microbial growth of sulphate-reducing bacteria and, consequently sulfide concentration in the sediment and anoxia. Under light-limited conditions with sulfide level rising toxicity in the sediment, seagrass carbon balance, growth and survival may be seriously harmed, as previously stated (Vaquer Sunyer and Duarte 2010).

## Sea Level Rise, Coastal Erosion and Climatic Extremes

It is estimated that sea level in the Mediterranean will raise about 50–60 cm during the twenty-first century (IPCC 2007; Marcos et al. 2009). Moreover, precipitation trends in the Mediterranean basin during the last 50 years show an increase in both frequency and intensity of severe drought events, although the spatial distribution is not homogenous (Vicente-Serrano 2007). In the western Mediterranean basin the increase of drought events alternates with episodes of heavy rainfall and flooding (Millan et al. 2005). Therefore, sea level rise combined with climatic extremes will result in enhanced erosion of shores, increased water turbidity, modified currents and tidal ranges, altered salinity, as well as changes in sediment inputs and nutrient loadings to the coasts (Scavia et al. 2002) each of which could have major impacts on seagrass habitats. For example, rising sea levels will create new shallow areas for expansion allowing intertidal or shallow-subtidal populations of fast-growing pioneering species like *Zostera noltii* or *Cymodocea nodosa* to expand into these new inundated areas landward. However, the colonization of newly inundated areas upslope is only possible in zones free of shoreline constructions, which is not a common feature along the majority of Mediterranean coasts (Duarte 2002). On the contrary, meadows that currently occur at profundities close to its compensation depths (i.e., the depth at which photosynthesis equals respiration) will be probably hampered. Those species with orthotropic rhizomes (*Posidonia oceanica* and *C. nodosa*) would be able to maintain stands at similar depths, provided they can also trap particles to raise the seabed surface. However, increased background turbidity, due to coastal erosion, sediment resuspension or siltation, would clearly reduce the colonization depth. In addition, the UV-B/PAR ratio would decrease with increasing water turbidity, counteracting the reported beneficial role of UV-B radiations against stress conditions, since UV-B seems to be involved in the impairment and recovery of photosynthesis in *P. oceanica* (Figueroa et al. 2002). Also massive sediment movements associated to heavy storm events will affect meadows by burial or shoot uprooting (see "Anthropogenic non-climatic causes" section). Overall, the net effect of increasing frequency and strength of storm episodes on seagrasses is not clear and, as for the other climatic change drivers, rather speculative (Hemminga and Duarte 2000).

## Interaction Between Non-climatic Anthropogenic and Climatic Drivers

As it has been previously stated, seagrass meadows decline can be the consequence of a combination of climatic and non-climatic causes. A good example was the regression and
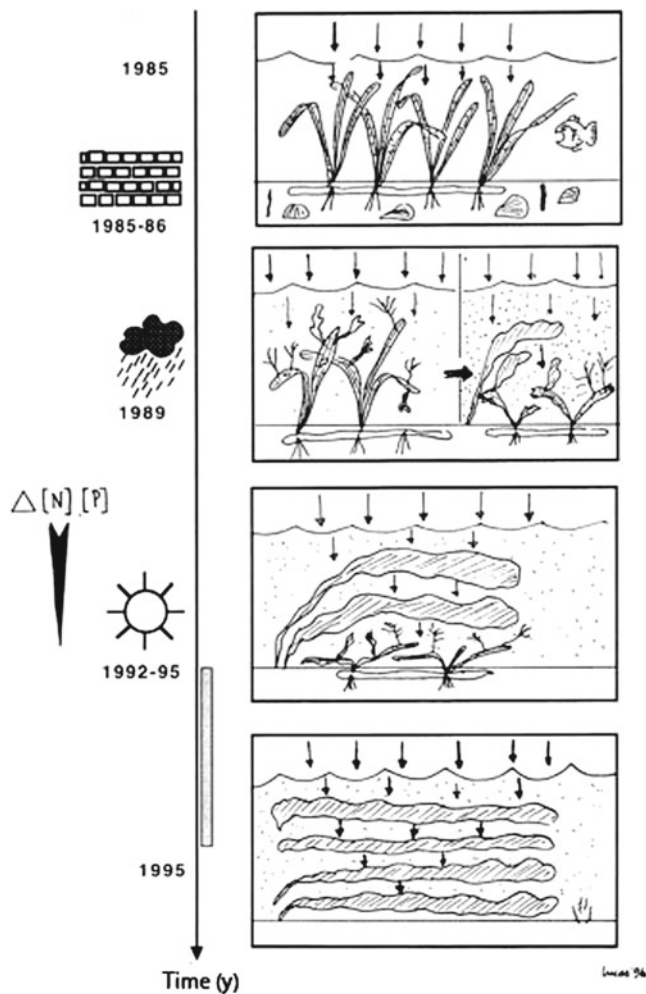
**Fig. 9.14** Schematic sequence of events occurred at Palmones river estuary (southern Spain) due to human disturbances (dam construction, eutrophication) and extreme climatic episodes (flooding, drought) that resulted in a shift of species (Drawing: José Lucas Pérez-Lloréns)

the final loss of the *Zostera noltii* beds in Palmones river estuary (Algeciras Bay, southern Spain) close to Gibraltar Strait (Pérez-Lloréns and Niell 1993; Carreira et al. 1995) (Fig. 9.14). Briefly: in early 1980s intertidal mudflats of the estuary were fully covered by *Zostera noltii* stands and water quality and biodiversity were high. The construction and operation of a dam (mid 1980s) in the headwaters of the river reduced both the water flow (the area covered by water decreased by four in a decade) and the current speed, affecting nutrient exchange processes and sediment input to the estuary. In autumn 1989, recurrent and heavy rainfalls with flooding affected severely this location, specially the estuary and the seagrass meadows. Plants were uprooted by the opening of the dam or buried by large sediment loads from upstream. The intertidal mudflats were fully inundated by turbid water for weeks. The few surviving seagrass patches started to be epiphyted mostly by microalgae. A long lasting

and extreme drought period (from 1992 to 1995) reduced drastically the freshwater inputs to the estuary. This reduction together with increasing nutrients loads (N, P) from agricultural and domestic runoff resulted in a widespread eutrophication that triggered massive proliferation of epiphytes and other opportunistic macroalgae (e.g., *Ulva*) that outcompeted seagrasses by shading and suffocation (Hernández et al. 1997). The system shifted from being seagrass-dominated to algal-dominated and underwent a dystrophic crisis, since dissolved oxygen dropped drastically due to the microbial remineralisation of the massive algal biomass die off, affecting not only to its structure and functioning, but also to the incomes of some local fishermen.

## Management and Conservation of Mediterranean Seagrasses

According to Short et al. (2011), the four seagrass species occurring in Mediterranean waters can be assigned to the "Least Concern" category of the IUCN Red List. However, there are some differences in population trends. Thus, whereas *Cymodocea nodosa* populations seem to remain stable (with an annual distribution change estimated in 0.6 % year$^{-1}$), the populations of the other three species are decreasing, mostly due to human perturbations, at estimated rates of −1.4 % year$^{-1}$ for *Zostera marina* and −5 % year$^{-1}$ (and −10 % over the last 100 years) for *Posidonia oceanica* (Marbà et al. 2005). No estimations are available for *Zostera noltii*. Although for *P. oceanica* this estimation is more than twice the value of global rate of decline in seagrass ecosystems (2 % year$^{-1}$) (Orth et al. 2006), it does not meet the threshold for the "Threatened" category of the IUCN Red List (Short et al. 2011). However, as it has been aforementioned, given the extremely slow growth rate of *P. oceanica*, such losses are virtually irreversible. Declines of *P. oceanica* meadows have been reported in many parts of the Mediterranean, including pristine areas where no apparent human impacts exist. Such widespread regression could be due to the existence of a background decline, possibly related to general changes in the climate of the Mediterranean Sea (Duarte et al. 1999), or to the cumulative effects of natural and anthropogenic local processes (González-Correa et al. 2007). Taking into account all the Mediterranean species the decrease in extension possibly ranges between 0 and 10 % (considering as a baseline the beginning of the twentieth century) with a manifestly growing trend associated to human impacts (see Boudouresque et al. 2009, for further details). In this context there is an urgent need to develop and implement different measures of protection, management and/or restoration to counterbalance the deterioration of Mediterranean seagrass habitats.

**Table 9.2** Metrics used to determine the ecological status of seagrass meadows and of water bodies on the basis of seagrass characteristics

| Species | Characteristics | Reference |
|---|---|---|
| *Posidonia oceanica* (Spain) | Physiological: phosphorus, nitrogen and sucrose content, and $^{15}$N and $^{34}$S isotopic ratios in rhizomes. Copper, lead and zinc concentration in rhizomes | Romero et al. (2007) |
| | Individual morphological status: % leaves with necrosis and shoot leaf surface | |
| | Population status: meadow cover, shoot density and % plagiotropic rhizomes | |
| | Community: nitrogen content in epiphytes | |
| | Shoot density, shoot foliar surface, dead-matte cover, meadow cover, herbivore pressure, rhizome baring/burial, foliar necrosis, percentage of plagiotropic rhizomes, and leaf-epiphyte biomass | Fernández-Torquemada et al. (2008) |
| | Lower limit depth, lower limit type | López y Royo et al. (2009) |
| | Shoot density, shoot length | |
| *Cymodocea nodosa* (Spain) | Physiological: phosphorus, nitrogen, $^{15}$N and $^{34}$S isotopic ratios in rhizomes. Cadmium, copper and zinc concentration in rhizomes | Oliva et al. (2011) |
| | Individual morphological status: shoot size | |
| | Population status: root weight ratio | |
| | Community: epiphytes load | |
| Multispecies (UK) | Change in taxonomic composition from reference conditions | Foden and Brazier (2007) |
| *Zostera marina* | Shoot density | |
| *Z. angustifolia* | Spatial extent | |
| *Z. noltii* | | |
| Multispecies (NL) | Taxonomic composition | de Jonge in Foden and Brazier (2007) |
| *Z. angustifolia* | Area (bed extent) | |
| *Z. noltii* | Coverage (bed density) | |

## Protection and Management Measures

Because of the growing concern about the progressive regression of Mediterranean seagrass habitats they have special protection in most of the laws and treaties like OSPAR or EU's Habitats Directive (Dir 92/43/CEE). *Posidonia oceanica* is explicitly considered by the EU Habitats Directive; however, in many cases (e.g., *Cymodocea nodosa* and *Zostera* spp.) such protection is still ambiguous and seagrass species are not protected by themselves, but either through indirect references as vegetated shallow stands, or by protecting their habitat as the case of "coastal lagoons" or "sandbanks which are slightly covered by seawater all the time". On the contrary, the European Water Framework Directive (WFD) considers seagrasses itself as an indicator of water quality (see below).

Setting management measures for conservation and recovering of seagrass meadows is a challenge and can be a daunting task. In Europe, the ecology, sensitivity, conservation and management requirements of *Zostera* spp. have been documented as part of the UK Marine SAC project and of the action plan process at a UK level (Davison and Hughes 1998). For the Mediterranean, there are also some international initiatives as the Action Plan for the Conservation of Marine Vegetation in the Mediterranean

Sea (Pergent-Martini and Le Ravallec 2007). The first step for managing seagrass habitats is to develop adequate monitoring programs to control the regression or, optimistically, the recovery of these communities following implementation of management plans. In Europe, the WFD has meant a boost in the development of indicators to establish the ecological status of water bodies and the reference conditions in transitional and coastal waters. Different indices and methodologies based on seagrasses as biological indicators (since they are considered as "shore canaries", Orth et al. 2006) have been proposed (e.g., Orfanidis et al. 2003; Krause-Jensen et al. 2005; Foden and de Jong 2007; Foden and Brazier 2007; López y Royo et al. 2009). Most of the conventional indices only consider the presence, coverage or density of seagrasses as an indicator of good ecological status; however, new indices have been recently proposed based on physiological, morphological, and structural characteristics of individuals and meadows, such as the POMI index for *Posidonia oceanica* (Romero et al. 2007; Montefalcone 2009), the CYMOX index for *Cymodocea nodosa* (Oliva et al. 2011) or the ZoNI index for *Zostera noltii* (García-Marín et al. 2013) (Table 9.2).

Mapping seagrass extent and structure (patchiness, corridors, etc.) is one of the actions recorded in all management plans. Bionomic cartographies were common in the 1980s

and early 1990s in the Mediterranean. However, such monitoring programs based on evaluation of cover and shoot density are not a reliable assessment of decline, as they have a high associated error and only detect changes when substantial damages on seagrass meadows occur (Duarte 2002). Remote sensing techniques, using aerial photography (Pasqualini et al. 1998), satellite images (Barillé et al. 2010) or acoustic methods (Freitas et al. 2008), can help to monitor long or medium term changes in extension, but do not provide information on shoot density or ecological status; it is also quite difficult to differentiate seagrasses from benthic macroalgae.

The most difficult, and costly issue for implementing management plans is to reduce nutrient and sediment discharges from both diffuse and point sources in surrounding watersheds (Orth et al. 2006). To keep nutrient and organic matter inputs in a minimum, urban and industrial sewages must be diverted to treatment plants to reduce nutrient loads. In addition, uncultivated soils along rivers and wetlands (that intercept agricultural nutrient runoffs and reduce siltation) must be also protected (Díaz-Almela and Duarte 2008). It is also imperative to prevent loading from fish farms, which must not be allowed in bays, and at a reasonable (at least 800 m) distance in open waters (Marbà et al. 2006). The undesirable effects of outlets from desalination (i.e., brine discharges) and power plants, which may increase salinity and seawater temperature in the vicinity of the meadows, must be also avoided (Sánchez-Lizaso et al. 2008). Dredging activities must be also prevented in the meadow or its vicinity.

Efficient management strategies may also include the protection of seagrass meadows with artificial reefs against trawling, the use of seagrass-friendly moorings, the wise management of seagrass litter stranded in the beach, and the control of invasive species such as *Caulerpa* spp. (Díaz-Almela and Duarte 2008). The establishment of "marine protected areas" is one of the main management measures. Most of these initiatives have been adopted as a fisheries management tool, but they are also very effective protecting biodiversity of fishes and invertebrates including genetic structure of the populations (Pérez-Ruzafa et al. 2006). However, little research has been done on the effects of these areas on seagrass populations. Marbà et al. (2002) reported that patch formation and patch growth rates of *Posidonia oceanica* in active colonizing areas increased after implementation of mooring regulations in the Cabrera National Park (Spain). Similarly, the leaf production tended to increase, and vertical rhizome growth to decrease, following the onset of regulation measures.

Preservation of genetic diversity can be a more complex task. The knowledge of the spatial patterns and scales of the genetic structure of most of the seagrass species is very scarce (Hemminga and Duarte 2000). The available information suggests that spatial heterogeneity can be very high, mainly in species inhabiting coastal lagoons and semi enclosed seas.

## Restoration Measures

Another important management measure is to restore damaged seagrass meadows. Habitat restoration can be used to compensate for losses, not only for seagrasses itself, but also for fish, invertebrates, and other aquatic fauna inhabiting meadows. Habitat restoration modelling approaches, based on food-chain transfers, showed that restoration of seagrass beds would be more productive even than that of the salt marshes (McCay and Rowe 2003). Numerous restoration projects have been attempted, mostly at small scales (<1 ha) with a variety of techniques using either adult plants or seeds (Orth et al. 2006). Worldwide, the success of seagrass transplantation and restoration is around 30 % (Fonseca et al. 1998). In the Mediterranean, the first experiences with *Posidonia oceanica* date back to the 1990s (Molenaar et al. 1993; Piazzi et al. 1998) with positive results at small scale (70–100 % survival after 1–3 years). However, transplantation of meadow blocks (1 m²) form donor sites showed little success (Sánchez-Lizaso et al. 2009). Genetic polymorphism favours the transplantation success in this species (Procaccini and Piazzi 2001), but the low growth rate of *P. oceanica* preclude that transplantation techniques can be implemented to recover large areas at short or medium term. In addition, seagrass transplantation is too costly to be implemented at large scale, which is specially a major drawback in developing countries (Duarte 2002).

In conclusion, seagrass ecosystems are among the most productive of the Biosphere, providing important ecosystems goods and services. Despite this paramount importance, they (including the seagrass meadows of the Mediterranean Sea) are in a vulnerable state showing worrying trends of decline. The main causes in the Mediterranean are the anthropogenic non-climatic drivers. It is expected that climate change will also affect these habitats. However, it is rather speculative to forecast the outcome of such effect because to the likely multiple interactions among different non-climatic and climatic drivers. A challenging issue to cope with the ongoing deterioration must be an effective management, including programs to promote public awareness, to increase the resilience, especially against the non-climatic causes, of these important Mediterranean habitats.

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