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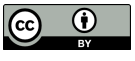
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Review

Restoration of Seagrass Meadows in the Mediterranean Sea: A Critical Review of Effectiveness and Ethical Issues

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Abstract: Some species of seagrasses (e.g., *Zostera marina* and *Posidonia oceanica*) have declined in the Mediterranean, at least locally. Others are progressing, helped by sea warming, such as *Cymodocea nodosa* and the non-native *Halophila stipulacea*. The decline of one seagrass can favor another seagrass. All in all, the decline of seagrasses could be less extensive and less general than claimed by some authors. Natural recolonization (cuttings and seedlings) has been more rapid and more widespread than was thought in the 20th century; however, it is sometimes insufficient, which justifies transplanting operations. Many techniques have been proposed to restore Mediterranean seagrass meadows. However, setting aside the short-term failure or half-success of experimental operations, long-term monitoring has usually been lacking, suggesting that possible failures were considered not worthy of a scientific paper. Many transplanting operations (e.g., *P. oceanica*) have been carried out at sites where the species had never previously been present. Replacing the natural ecosystem (e.g., sandy bottoms, sublittoral reefs) with *P. oceanica* is obviously inappropriate in most cases. This presupposes ignorance of the fact that the diversity of ecosystems is one of the bases of the biodiversity concept. In order to prevent the possibility of seagrass transplanting from being misused as a pretext for further destruction, a guide for the proper conduct of transplanting is proposed.

Keywords: *Cymodocea nodosa*; ecosystem diversity; Mediterranean; natural recolonization; *Posidonia oceanica*; seagrass decline; seagrass restoration; transplanting; *Zostera marina*

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1. Introduction

Seagrasses are part of the Magnoliophyta (flowering plants), which number more than 295,000 species [1]. The vast majority of these species are terrestrial, while freshwater taxa represent ≈2450 species [2] and seagrasses only represent 67 species, including *Ruppia maritima* [3,4].

Despite their small number, seagrasses play a role of paramount importance in coastal habitats worldwide. They provide ecological goods and ecosystem services that contribute to human welfare, e.g., habitat for a wide diversity of species, nursery, enhanced fisheries, nutrient cycling, carbon sequestration, production of sand (the "sand factory"), beach, and shoreline protection [5–10]. In the Mediterranean Sea, seven species of seagrasses occur [11,12]. *Posidonia oceanica* is the only one that is endemic to the Mediterranean [13]. *Cymodocea nodosa*, *Zostera marina* and *Z. noltei*, native to the Mediterranean, have a broader temperate distribution. *Ruppia maritima* (synonym *R. cirrhosa*) is almost entirely restricted to brackish lagoons and salt marshes [14]. Finally, *Halophila stipulacea* and *H. decipiens* are introduced species, via the Suez Canal and ballast water, respectively [15–17].

The severe worldwide decline of the seagrass meadows is a classic refrain in the literature (e.g., [18–25]). The most spectacular and best documented decline is that of *Z. marina*, known as the "wasting disease", which occurred in the 1930s; its cause remains

controversial: a stramenopile parasite or a climatic episode [26–30]. Since then, other decline events of *Z. marina*, conspicuous but more localized than the wasting disease, have been reported in Chesapeake Bay (USA), Portugal, Arcachon Bay (France), Netherlands, Japan, California (USA), etc.; they have been attributed to local disturbances, e.g., pollution, turbidity, and oyster dredges [28,31–37]. Some were also due to natural events, such as the passage of the tropical storm Agnes in 1972 in Chesapeake Bay [31].

There can be no doubt that seagrass meadows have declined worldwide, in particular *Z. marina* meadows. However, it is legitimate to wonder whether the overall decline of seagrasses has not been exaggerated by certain authors, as evidenced in the case of the Mediterranean Sea [11,24,38–40]. As Boero [41] and Duarte et al. [42] suggested, it is easier to publish in high IF (Impact Factor) journals if you announce the apocalypse than if you describe moderate changes. Very few articles describe the recent (2000s) reversal of decline for European seagrass meadows [24].

Thousands of cases of the decline of seagrass meadows have been reported in the global ocean, and they are completely credible. It should just be noted that cases of subsequent recolonization, as well as cases where a seagrass is expanding at the expense of a declining species [11], are more rarely published. Therefore, adding together the episodes of decline without taking into account the cases of recolonization or substitution can constitute a bias. Extrapolation of the cases of decline to the entire seagrass distribution area constitutes another bias: the "undocumented" areas may correspond to areas where nothing is happening, and regarding which it is therefore difficult to publish in high IF journals. Such extrapolations would result in an overestimation of global seagrass decline. Finally, although the authors indicate clearly, in general, whether they are referring to the percentage of surface area lost (or gained) by a species, or of the percentage of sites where the species is in decline, without change or in progression (trajectories), the authors who quote them sometimes confuse the two; however, a 33% decrease in surface area is not synonymous with 33% of the sites where a decline has been observed.

Waycott et al. [19] stressed the acceleration of seagrass declined from 1% per year before 1940, 1–7% per year between 1940 and 1990, to 7% per year since 1990. Although the authors clearly warned that these estimates were based on data available at the time, from a limited number of regions of the world ocean, and reported the geographical and historical bias in their dataset, some later authors cited this article without reference to these caveats. Yet a very simple mathematical model indicates that these estimates cannot be extended to the world ocean: there would be hardly any seagrass meadows left in the world today, which is clearly not the case [11,43].

Therefore, the debate on the reality or the extent of the decline of seagrasses is important, insofar as this decline is at the basis of attempts to restore seagrass meadows.

Here, we have considered the case of the Mediterranean, which is of particular interest because a considerable corpus of data is available on the decline, the non-decline, or the recolonization of seagrasses, and we have examined the justification for and effectiveness of seagrass restoration operations. Furthermore, the Mediterranean is often regarded as representative of the world ocean in miniature [44].

2. Are Seagrasses on the Decline in the Mediterranean Sea?

First of all, it is important to clarify that the general perspective (a combination taking all seagrasses together) may be different from the specific perspective (a particular species). One species can be in decline while another is progressing at its expense. Adding together all the episodes of decline, without considering subsequent recolonization as well as the progression of other species, can therefore lead to a biased view of the general situation [11].

Mapping a seagrass meadow, and comparison with previous maps, can provide a reliable basis for inferring changes over time [11,39]. However, differences between maps might be due to errors in the ancient maps and/or the improvement of mapping methods rather than to changes over time, as emphasized by Leriche et al. [45], Astruch et al. [46], Pergent-Martini et al. [47], and Valette-Sansevin et al. [48]. For example, in Corsica, the

surface area of *Posidonia oceanica* beds was estimated at 624 km^2 [49], then at 537 km^2 [47,48], which obviously is not due to a decline, but to an improvement in the accuracy of the mapping. In the same way, in Provence and the French Riviera, the surface area of *P. oceanica* was estimated at 255 km^2 [50] and subsequently at 265 km^2 [51]; in the Port-Cros Archipelago (Provence), estimates of the surface area of *P. oceanica* increased from 345 ha in the 1980s [52] to 418 ha in the 2000s [53] and to 439 ha in the 2010s [46]; again, it is prudent to attribute these increases to improved mapping methods.

2.1. Posidonia Oceanica

A variety of natural processes can generate dead *matte* of *P. oceanica*, i.e., areas where the *P. oceanica* shoots have died, but where the dead rhizomes may persist for millennia since their decay is very slow [6,54,55].

(**i**) The increase in the thickness of the *matte*, in shallow areas, can bring the meadow too close to the sea surface; there, the shoots encounter conditions that are no longer compatible with their survival, giving way to a dead *matte* of natural origin; this is the case in the Bay of Giens (Provence, France) [50].

(**ii**) A *P. oceanica* ramet (i.e., a set of shoots interconnected by live rhizomes) allows photosynthates and nutrients from a shoot to be exported toward rhizomes and then allocated to the other shoots of the ramet [56]. For a given shoot, this constitutes a kind of insurance: should its budget go into deficit (e.g., due to the covering of leaves with epibiota, overgrazing, self-shading, etc.), its needs will be supplied by neighboring shoots. However, when an orthotropic (i.e., vertical) rhizome exceeds a certain length, this process becomes inefficient, making the survival of the shoot precarious [57]. Hence, small patches of dead *matte* in a healthy *P. oceanica* meadow may result simply from the death of such vulnerable shoots rather than from a disturbance; these structures, of natural origin, have been termed "autogenic dead *matte* patches" (Figure 1) [11].

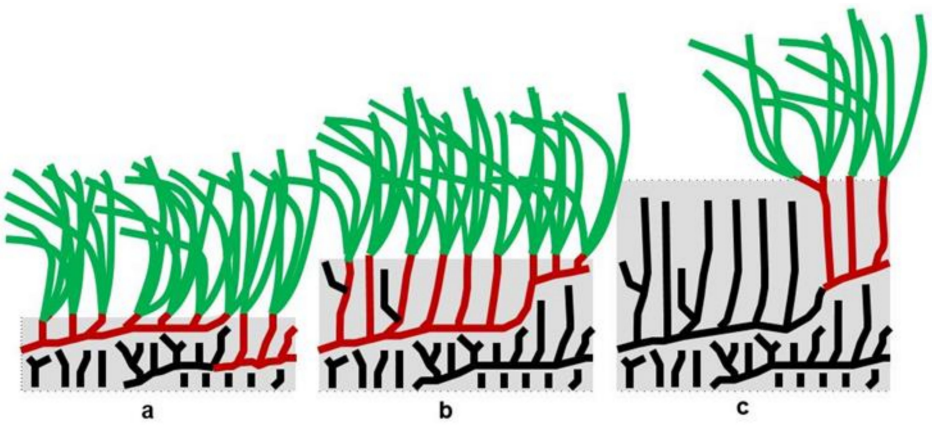


Figure 1. Formation of an autogenic dead *matte* patch within a *Posidonia oceanica* meadow. Orthotropic (vertical) rhizomes react to the trapping of sediment and their burial by vertical growth so that the sea bottom rises (**a**–**c**). Leaf shoots located at the tips of orthotropic rhizomes, that are too long, will die, which results in the formation of a patch of dead *matte* of natural origin. On the right side of (**c**), a new plagiotropic (horizontal) rhizome is starting to recolonize the dead *matte* patch. Green: leaves; red: live rhizomes; black: dead rhizomes. From Boudouresque et al. [11], adapted.

(**iii**) In plain type meadows (see [55,58]), areas of dead *matte* and sand *intermattes* (breaks within the meadow, filled with sand) can be of natural origin. In addition, shifting *intermattes* are furrows several dozen metres long and several metres wide, lying parallel to the shore; the side of the shifting *intermatte* that is closest to the shore is made up of an erosion scarp, which is actively eroded; the central part of the shifting *intermatte* is made up of dead *matte*; the side that is furthest away from the shore is made up of a meadow front with plagiotropic (horizontal) rhizomes that tends to recolonize the *intermatte*. Over time, the shifting *intermatte* moves along in a parallel direction toward the shoreline

(Figures 2 and 3). Typical shifting *intermattes* have been observed in Calvi Bay and off Aleria (Corsica), in the bays of Giens and Hyères (Provence, France), and in southern Latium (Italy) [50,55,59–63].

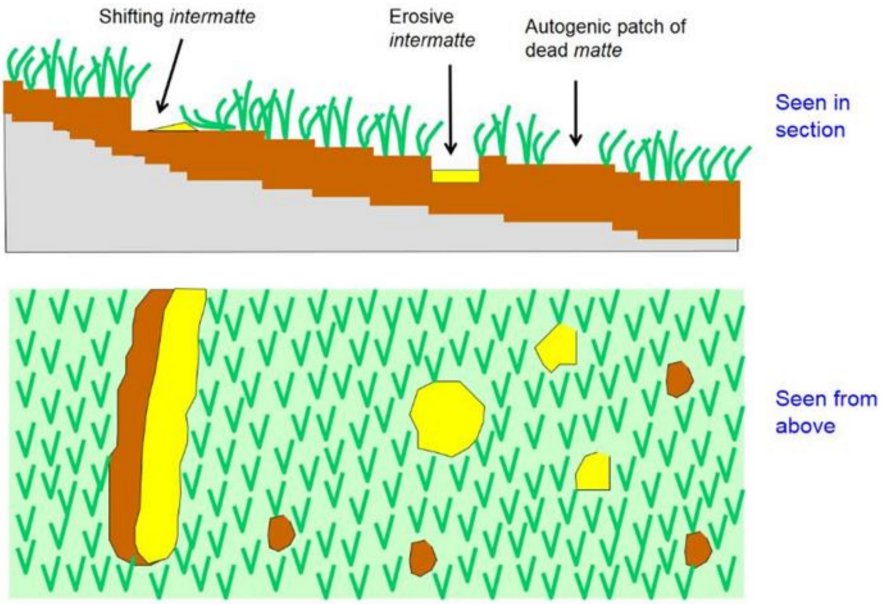


Figure 2. Areas of dead *matte* of natural origin in a plain type meadow of *Posidonia oceanica*. The shoreline is to the left. From Boudouresque et al. [55], adapted.

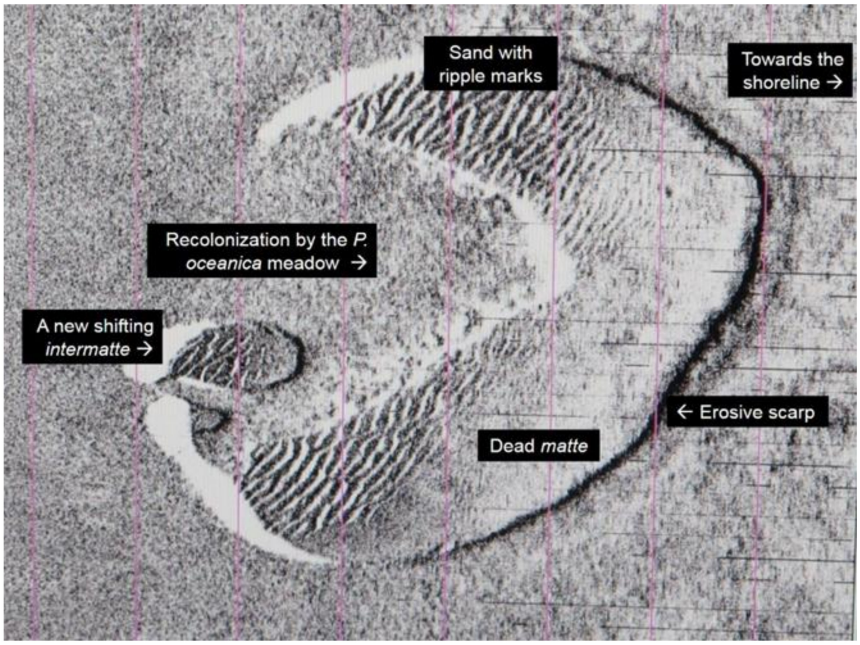


Figure 3. Shifting *intermattes*. 30 m depth. U Caterraghju (Aleria, eastern coast of Corsica). Side-scan sonar image. Mission Coralcorse (Gérard Pergent and Ifremer). Photo © Charles-François Boudouresque.

(**iv**) Dead *matte* of natural origin also occurs in the hill type meadow [55,58]. In the striped meadows, which occur in shallow areas in Corsica (Portivechju), Sardinia and are widespread in Tunisia and Libya, 1–2 m-wide and several dozen metres long strips of *P. oceanica* are separated by extensive areas of dead *matte* occupied by a *Cymodocea nodosa* and/or *Caulerpa prolifera* meadow; each *P. oceanica* strip shifts, parallel to itself, against the dominant current, at an average speed of 10 cm per year (Figure 4). A cross-section of a

strip shows on one side a front of plagiotropic (horizontal) rhizomes that progress onto the dead *matte*, a gentle slope behind the front, and a small erosive scarp where the strip disintegrates (Figure 5) [55,64,65].



Figure 4. A striped meadow of *Posidonia oceanica*. Kerkennah Islands, Tunisia. From Blanpied in [55].

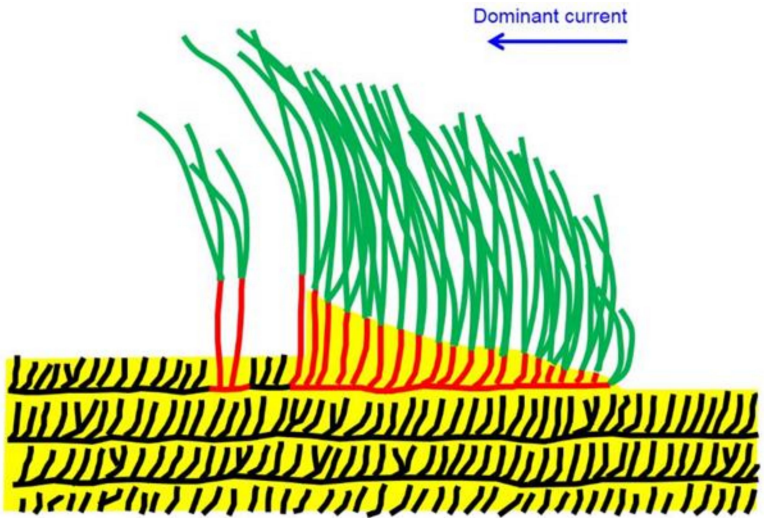


Figure 5. A cross-section within a strip of striped meadow. The progression is made toward the right by a plagiotropic (horizontal) rhizome, whereas the strip is eroded on the left by the hydrodynamism (generated by the dominant current). Black: dead rhizomes; red: live rhizomes; green: leaves; yellow: sediment.

(**v**) In many areas, an extensive belt of dead *matte* occurs beyond the lower limit of the *P. oceanica* meadow. This has been considered as a consequence of modern pollution and water turbidity. In the Gulf of Marseille (Provence, France), this belt occurs between 22 and 30 m depth; however, ^{14}C dates these dead *mattes* from 573–885 CE [66]. The same phenomenon occurs in the Bay of Hyères [67]. If we consider a longer time scale, at the time of the Last Glacial Maximum (LGM), about 18,000–20,000 years ago, the sea level was 120–140 m below that of today [68–70]. From that time to the present, the sea level has risen continually [71,72] Any rise in sea level resulted in a withdrawal of the lower limit of the *P. oceanica* meadow. Where sediment deposition is weak, the resulting belt of dead *matte* may give rise to misinterpretation, for instance as a case of decline due to human impact (Figure 6) [11,67].

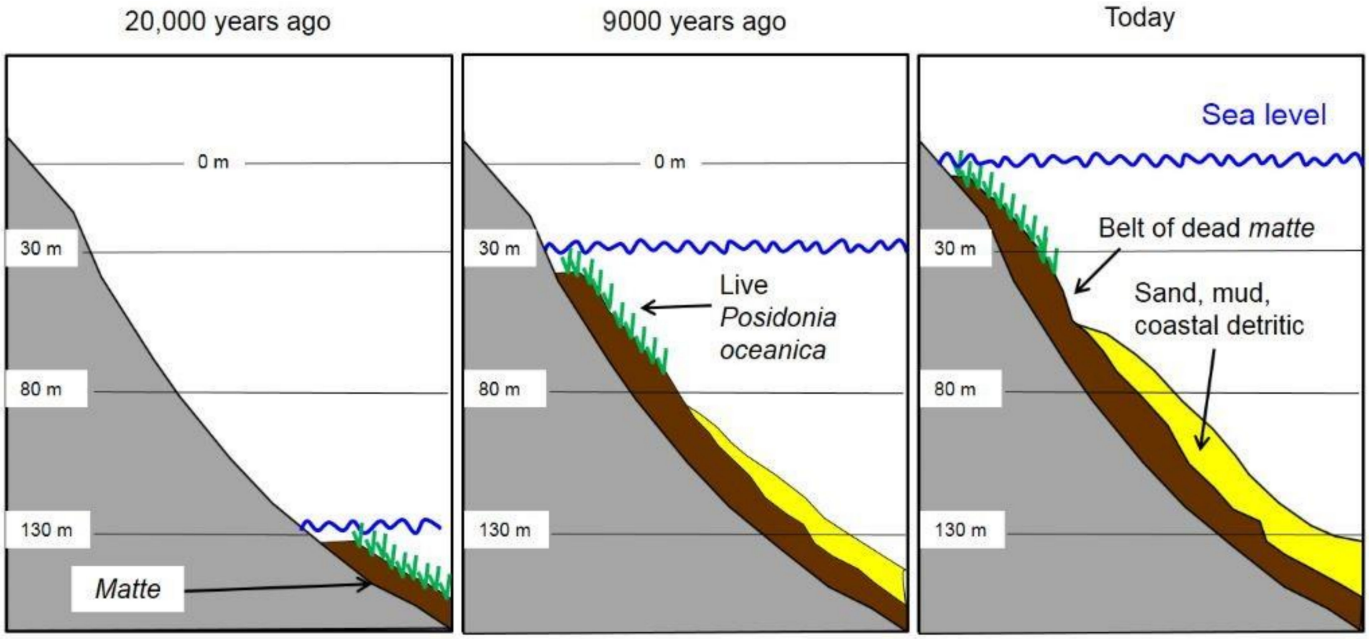


Figure 6. The post-LGM (Last Glacial Maximum) rise in sea level. *Posidonia oceanica* meadows have spread upwards, following the rise in sea level, leaving behind a belt of dead *matte* of natural origin. This belt could be confused with modern withdrawal.

The fact that dead *matte* of *P. oceanica* may be of natural origin is often underestimated by authors, which may lead to an overestimation of the withdrawal. The paradigm example is that of the Bay of Giens (Provence); Blanc and Jeudy de Grissac [73] reported in the 1970s a 40-m per year withdrawal of the meadow, on the basis of snorkelling near the shore, above a natural dead *matte*, without any means of geographical positioning; subsequently, accurate mapping of the Bay of Giens (side-scan sonar, with ground truths) revealed that this meadow was in an excellent state of health, perhaps the best along the whole of the French mainland coast [11,50]. However, certain authors of scientific articles still refer to Blanc and Jeudy de Grissac [73]. Another example is that of the whole Provence and French Riviera region (one of the most human-impacted regions in the Mediterranean); according to Deter et al. [74], Andromede oceanologie [51], and Holon et al. [75], over one century (since 1922 CE), between the sea surface and 15 m depth, 86% of the *P. oceanica* meadow remained unchanged, 13% regressed, and 1% progressed. These figures are relatively moderate and do not validate the claims of certain authors.

In any case, there is no doubt that *P. oceanica* has strongly declined around the major Mediterranean ports (Barcelona, Marseille, Genoa, Naples, etc.), and on a large scale in Liguria (Italy), where the loss could be over 30% [76–79]. However, the estimates of Marbà et al. [80] indicating that between 13% and 50% of the overall area of *P. oceanica* was lost during the last 50 years, and that the loss was about 6.9% per year, obviously concern local areas, not the whole Mediterranean, as stressed by the authors.

2.2. *Zostera Marina*

In the northern part of the Mediterranean Sea (western Mediterranean, Adriatic and Aegean seas), the decline of *Zostera marina* meadows has been related to human activities: pollution, turbidity, freshwater inputs, anoxy.

Until the 20th century, Berre Lagoon (southern France) harboured a 60-km^2 meadow of *Z. marina*, which is perhaps the largest in the Mediterranean [81]; during the 20th century, *Z. noltei* progressively replaced *Z. marina* [81,82]. Since 1966, the diversion of the Durance River toward the lagoon resulted in the extinction of both *Zostera* species and their replacement by the freshwater species *Stuckenia pectinata* (synonym *Potamogeton pectinatus*).

The reasons for the failure of *Zostera* spp. to recover, despite a drastic reduction in pollution and freshwater and silt inputs, remain unclear [81].

Similar declines of *Z. marina* have been documented elsewhere in the Mediterranean. In Venice (Italy) and Thau (Occitania) lagoons, episodes of decline have been followed by more or less rapid natural recolonization [83,84], with the exception of the northernmost part of Venice Lagoon [85]. At Toulon (Provence), a small stand, in a sheltered bay subject to several human disturbances (coastal development, mooring, aquaculture and urban waste), has totally disappeared since the 1970s [11]. In Ghar el Melh Lagoon (northern Tunisia), the extirpation of *Z. marina* can be related to the restriction of water exchange with the open sea, salinity increase, pollution and silting [86]. In the Alboran Sea, from Málaga to Almeria (Spain), *Z. marina* has undergone a strong decline from 2005, to the point of becoming extinct in most coastal areas where it used to form extensive meadows [33].

In spite of local losses (e.g., Berre Lagoon, Toulon; see [87]), and in contrast with the Atlantic and Pacific coasts [29], no general regression of *Z. marina* has occurred in the Mediterranean. On the contrary, extensive meadows are still thriving, despite conspicuous human impact, in many localities, e.g., Venice Lagoon, Thau Lagoon, the Gulf of Fos (west to Marseille, France), Bizerte Lagoon (Tunisia), Els Alfacs Bay (Ebro delta, Spanish Catalonia), Alboran Sea, Marmara Sea, etc. [83,88–90]. This is surprising, insofar as the warming of the waters should make this species of cold affinities decline throughout the Mediterranean, which, at least for the moment, is not the case, whereas in the Atlantic, for instance, *Z. marina* is classified as the most endangered seagrass in Portugal [36,91].

2.3. Zostera Noltei

At sites with fluctuating salinity and turbidity, e.g., in Camargue (SE France), the extension of *Z. noltei* presents consistent patterns of change over the years [92,93]. In Berre Lagoon (Provence), the disappearance of extensive *Z. noltei* meadows and their replacement by the freshwater species *S. pectinata* can be related to the diversion of the Durance River toward the lagoon, the decrease in salinity, and the increase in turbidity [81].

As in the example of Berre Lagoon, *Z. noltei* meadows in Canet Lagoon (Occitania) were replaced in the early 1950s, after an exceptional spate of the tributary river, by *S. pectinata* [94,95]. In Ghar El Melh Lagoon (N Tunisia), *Z. noltei* and *Z. marina* were replaced by an extensive *Ruppia maritima* meadow after the reduction of seawater exchanges with the open sea [86]. In Venice Lagoon, the dramatic loss of *Z. noltei* (1990–2002) can be ascribed to the spectacular recovery of *Z. marina* [84,96]. In the Port-Cros Archipelago MPA, in the lagoon located behind a *Posidonia oceanica* barrier reef, *Z. noltei* disappeared in the 1990s [97].

However, the decline of *Z. noltei* does not constitute a universal feature. *Zostera noltei* frequently derives benefit from the decline of other seagrasses and the introduction of restoration plans. In the heavily populated and industrialized Gulf of Thermaikos (Greece), *P. oceanica* and *C. nodosa* losses were followed by the conspicuous expansion of *Z. noltei* [98]. In the Tunis northern Lagoon (Tunisia), after the virtual collapse of *Z. noltei* due to a dramatic increase in pollution (1920s through 1980s), an ambitious plan for sewage treatment, improvement of water exchange with the open sea, and establishment of a counter-clockwise water circulation system led to the recovery of mixed meadows of *Z. noltei*, *R. maritima*, and *C. nodosa* [99].

2.4. Cymodocea Nodosa

Cymodocea nodosa meadows are subject to wide natural fluctuations. Meadows rapidly spread during warm episodes and shrink during cold years. They also rapidly respond to human-induced environmental changes. In Mar Menor Lagoon (Spain), increased water exchanges with the open sea have led to a decrease in salinity and the expansion of the green alga *C. prolifera* at the expense of *C. nodosa* [100,101]. In Ghar El Melh Lagoon (Tunisia), a reduction in the number of channels between the lagoon and the open sea induced the replacement of *C. nodosa* by *Z. noltei* and *Z. marina* in the early 1980s, before they were

replaced by an extensive *R. maritima* meadow [11,86]. The 44-ha Le Brusc Lagoon (eastern Provence) was almost entirely colonized by *C. nodosa* in the mid-20th century [54,102]; this meadow (≈30 ha) was still present five decades later [103,104]. Subsequently, it declined to 17 ha in 2008 [105] and almost collapsed in 2011 [106,107], possibly as a result of overgrazing by the teleost *Sarpa salpa*.

Overall, *C. nodosa* meadows are expanding, firstly because the species is favored by the sea water warming, and secondly, because it benefits from the decline of the *P. oceanica* meadows [11,90]. This is particularly the case in Liguria (Italy), with an ecosystem regime shift, the dead *matte* of *P. oceanica* being colonized by *C. nodosa* and the non-indigenous green macroalga *Caulerpa cylindracea*, which is an alternative state that seems unlikely to be reversible [108–110].

2.5. Ruppia Maritima

Ruppia maritima (including *R. cirrhosa*, now considered as a heterotypic synonym; but see [111]) is usually restricted to brackish lagoons. There, a highly variable environment induces wide fluctuations in the surface area of the *R. maritima* meadows. Salse-Leucate Lagoon (Occitania, France), Ichkeul Lagoon and Ghar El Melh Lagoon (northern Tunisia) illustrate the abrupt fluctuations of this species.

Some populations of *R. maritima* have been totally lost, such as an 8-km^2 mixed *R. maritima* and *S. pectinata* meadow in Bolmon Lagoon (Provence), due to hypereutrophication and restriction of seawater exchanges [112,113]. In contrast, following the 1988 restoration plan for the Tunis northern Lagoon, the recovery of *R. maritima* has been spectacular: locally extinct in the 1970s, it is now the dominant species of this lagoon, with a 17–20 km^2 surface area [99].

2.6. Halophila Stipulacea

Halophila stipulacea is native to the Red Sea. It probably entered the Mediterranean Sea via the Suez Canal a few years after its inauguration (1869 CE), since it was observed at Rhodes in 1894 [15]. Since then, it has slowly but steadily spread northwards and westwards, reaching Sicily, southern mainland Italy, Tunisia, Albania, and the northern Aegean Sea; its spread is obviously enhanced by sea water warming and by pleasure boat anchoring [17,90,114–117]. From the Mediterranean, functioning as a hub, it reached the Caribbean Sea, where its expansion has been extraordinarily rapid [17].

Once installed at a new station, *H. stipulacea* stays there and often progresses. The only case of local extinction was in the harbor at Palinuro, 130 km south of Naples (mainland Italy): first sighted in 2006, the species was no longer detectable after 2011 and was considered extinct in the area; in 2017, the species was recorded again in the area, possibly as the result of a new colonization event [115,118].

2.7. All Seagrasses

There is no doubt that some seagrass species have dramatically declined in the Mediterranean. In Berre Lagoon (Provence, France), large *Z. marina* meadows totally disappeared in the late 20th century [81,82]. In Liguria (Italy), the decline of *P. oceanica* is cause for concern [77,79,119]. In the region of Alicante (Spain), the decline of *P. oceanica* is also conspicuous [76].

The main causes of decline of *P. oceanica* are land reclamation for coastal development, such as in the French Riviera and Monaco, the construction of harbors such as at Marseille (Provence) and Piombino (Liguria), the anchoring of cruise ships such as at Villefranche-sur-Mer (French Riviera), and trawling, such as in Corsica and the Alicante region (Spain) [11,55,76,90,120–124].

The replacement of one seagrass by another, namely *P. oceanica* by *C. nodosa*, cannot be considered as a neutral balance, as the total surface area of the seagrasses remains unchanged; the former species is a "constructional" species, while the latter is a "non-

constructional" one, which results in a conspicuous alteration in ecosystem structure and functioning [11,110].

Interestingly, all the native Mediterranean seagrasses (*C. nodosa*, *P. oceanica*, *R. maritima*, *Z. marina*, and *Z. noltei*) are considered as LC (Least Concern) in the IUCN red list.

3. Concerning Natural Recolonization

Assessment of natural recolonization after a disturbance is essential when considering seagrass restoration operations, as stressed by Cunha et al. [125]. The slow growth of *Posidonia oceanica* is a well-known feature: 1–7 cm per year for orthotropic rhizomes and less than 14 cm per year for plagiotropic rhizomes [55,126–132]. The mean growth of plagiotropic rhizomes, over a period of several decades, was 2–4 cm per year [121,133,134]. The idea that natural recolonization by *P. oceanica* is very slow is mainly based on observations dating from the peak of pollution and coastal development; these human impacts hampered recolonization. Today, the perception would undoubtedly be different.

Natural recolonization can take place in three ways: (**i**) the progression of a meadow margin owing to plagiotropic rhizomes, (**ii**) the export of cuttings through to the currents, in particular during storms, and (**iii**) seed germination.

For a long time, cuttings were considered the main, if not almost the only, way of dispersal of *P. oceanica* (e.g., [54,55,127,135]). The relative scarcity of flowering sightings [136–142], perhaps due to the fact that flowering occurs in the fall, a season when divers are also scarce, may explain the underestimation of dispersal by seeds. The arrival of lepidochronological analysis, which allowed the exploration of past flowering within the *matte*, showed that flowering events were not so uncommon [139,141,143–145]. In addition, the fact that *P. oceanica* flowers and produces seeds only at intervals of several years has sometimes been interpreted as a mismatch with regard to the environmental conditions of the Mediterranean or a weakness explaining its modern decline. (**i**) To refer to a mismatch with the Mediterranean environment (e.g., [54,146,147]), for a species that has been present there for millions of years, which has gone through the Messinian salinity crisis and around thirty glacial and interglacial episodes, and which is today the most widespread macrophyte in the Mediterranean, is barely credible. (**ii**) For a long-lived species, K strategist, fruiting every year is not an optimal strategy; fruit predators adapt their number to a predictable resource, so that all seeds are consumed. The flowers and fruits of *P. oceanica* are much appreciated by herbivores, such as the fish *Sarpa salpa* and the sea urchin *Paracentrotus lividus* [148–151]. The predator saturation strategy consists in synchronized heavy seed production at unpredictable time intervals so that herbivores are unable to consume all the seeds, allowing a large amount of seeds to escape consumption and germ [152–154]. Therefore, the irregularity of flowering and fruiting is not a weakness but rather a strength for *P. oceanica*. All in all, there is growing evidence that seedling recruitment plays a major role in the process of recolonization after disturbance [43].

Meinesz and Lefèvre [133] provided a good example of the slowness of recovery. In 1943, during World War II, in the Bay of Villefranche-sur-Mer (French Riviera), a bomb missed a ship at anchor and destroyed the *P. oceanica* meadow over a circular area with a radius of 85 m, between 6 and 15 m depth. Forty years later, only one-third of the destroyed meadow has been recolonized. Patches of *P. oceanica* progressed at an average speed of 4 cm/year; new patches (from seeds or cuttings) appeared at a rate of 3/ha/year. A similar example is that of the Plateau des Chèvres bomb (Marseille, Provence), in 1942; the initial surface area of the crater was 1.13 ha; total recovery is expected to have occurred by 2030, i.e., after 90 years [155–157]. At Bergeggi (Liguria, Italy), following a dramatic decline of *P. oceanica*, there are signs of slow recovery of the upper limit of the meadow, which is progressing shoreward; *P. oceanica* also increases at the expense of sand patches [110]. At depth (14 to 28 m; region of Alicante, Spain), in an area severely affected by illegal trawling, the natural recovery was studied after the installation of anti-trawling artificial reefs; the extrapolated time of total recovery could be almost 100 years [130].

Unexpectedly, natural recolonization by marginal growth can be relatively rapid, when the causes of the decline have ceased to act, for example after the setting up of a sewage treatment plant, at Marseille (Figure 7) and in the Bay of Giens (Provence) [158]. In the Bay of Giens, in a permanent quadrat of 36 m^2, located 60 m from the outlet of the discharge from the sewage treatment plant, the *P. oceanica* cover increased from 19% in 1987 to 52% in 2000, which represents a remarkable rate of progression [159]. In the Marine Protected Area (MPA) of Egadi Islands (off Sicily, Italy), patches of *P. oceanica*, up to 1-m in diameter, have begun to colonize a metallic 40-m long wreck, at 15 m depth [160].

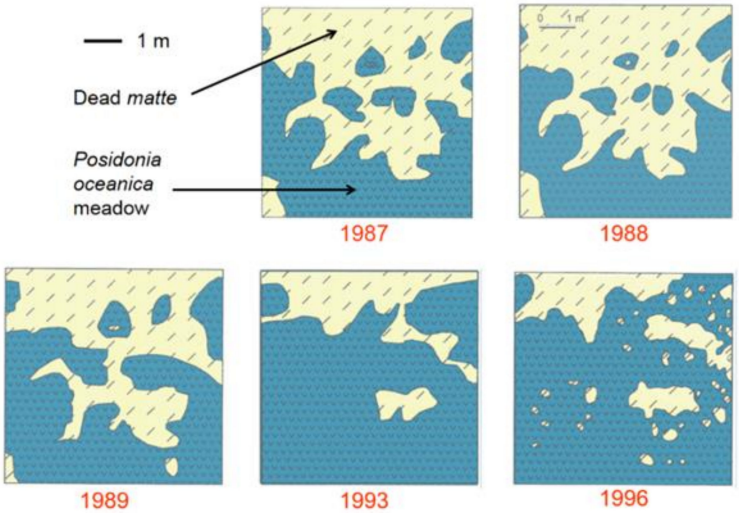


Figure 7. A permanent quadrat (5 m × 5 m) in Prado Bay, Marseille (France). The sewage water treatment plant was put in operation in 1987. From Gravez et al. [158], adapted.

Off the harbor at Ischia (Gulf of Naples), a 300-m trench was dredged in a *P. oceanica* meadow to set up a gas pipeline; then, it was filled with rubble after the deployment of the pipeline in 2009. Ten years later, 121 patches of *P. oceanica* had spontaneously colonized the rubble substrate, probably from cuttings coming from the surrounding meadow; these patches cover an area of 334 m^2, corresponding to 12% of the surface area of the trench (Figure 8) [161]. In a same way, in Sicily, a gas pipeline trench, crossing a *P. oceanica* meadow between the shore and 20 m depth, was in part backfilled using calcareous rubble; 8 to 10 years later, the rubble became naturally and partially recolonized by *P. oceanica* [135,162–164].

Sightings of seedlings and of young plants grown from seeds are more common than previously thought, either because of an increase in flowering events, perhaps linked to warming, or because of a greater interest of scientific divers in such observations. Seedlings, at least one year old, were observed on hard substrates at 0.5 to 2 m depth in the Egadi Archipelago (Sicily) [165]. Other sightings were reported from the central Adriatic Sea (Croatia), Tuscany, Ustica, Ischia Island (off Naples) and Calabria (Italy), from a few centimetres to 10 m depth, in a variety of habitats: rocky bottoms with a dense macroalgal cover, large cobbles, pebbles, dead *matte*, *Cymodocea nodosa* meadows, and sand [139,166–174]. Anchorage of the seedlings, through adhesion by sticky root hairs, is firmer on rocky than on sandy substrates [175]. In Croatia and Tuscany, densities of up to 50 and 60 seedlings per m^2, respectively, were recorded [169,171]. In Tuscany, dead *matte* was the best substrate for the survival of plants proceeding from natural seedling (dead matte > rock > gravel); the 2-year survival rate was better at 10 m than at 2 m depth, 70% vs. 46%, respectively [170]. Overall, mounting evidence, e.g., the high density of natural seedlings, at least in the northwestern Mediterranean and the Adriatic Sea, their survival and development, demonstrates that sexual reproduction and the natural recolonization by seedlings assume a much greater importance than was hitherto believed, at least in the late 20th and early 21st centuries [141,170,176].

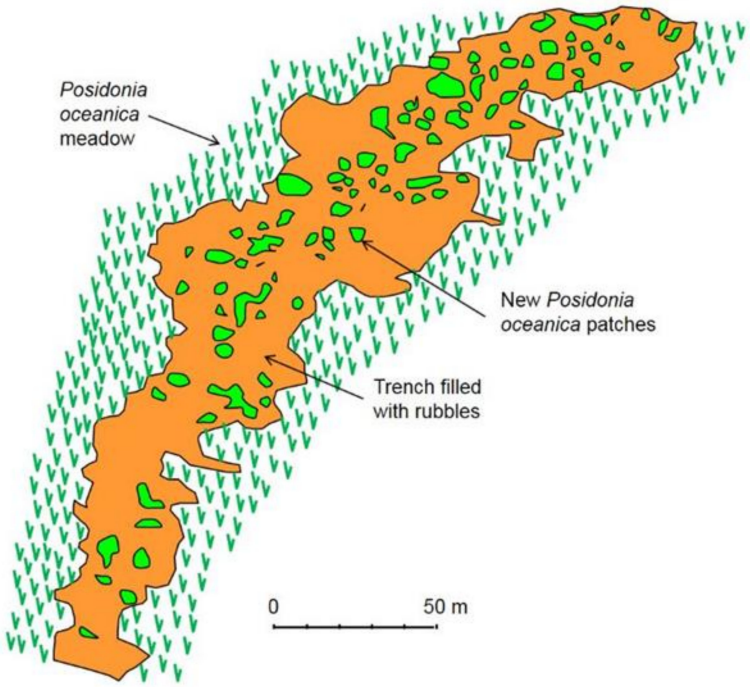


Figure 8. A trench dredged to set up a gas pipeline, then filled with rubbles in 2009, off the harbor at Ischia (Italy). Ten years later, 12% of the surface area of the trench had been spontaneously recolonized by *Posidonia oceanica*. From Cotugno et al. [161], redrawn and adapted.

In the 20th century, it was believed that the genetic variability of *P. oceanica* was low, in relation with the scarcity of its flowering [147,177,178]. Therefore, the decline of *P. oceanica* was attributed to this low genetic variability. More recent studies have shown that this was not the case: the genetic variability of *P. oceanica* is higher than previously thought, and it even demonstrated the efficiency of its sexual reproduction and the long-distance dispersal of its seeds [179–181].

In contrast with *P. oceanica*, natural recolonization can be relatively rapid in other seagrasses, such as *Zostera marina, Z. noltei, C. nodosa*, and *Ruppia maritima*, both in the Mediterranean and elsewhere.

4. The Techniques of Seagrass Restoration

Reintroduction is the re-establishment of a species in an area where it has definitely existed in the past, but where it has become locally extinct as a result of human-induced impacts or a reversible natural disaster. Re-stocking is the strengthening of the populations of a species, in a region where it has not disappeared, but where one wishes to restore its former abundance [182,183]. Habitat creation establishes new meadows in areas historically uninhabited by a seagrass species [25,184]. All the restoration operations that will be discussed here (chapter 5) are in the domain of re-stocking and habitat creation. It is the extent, real in certain regions, of the decline of seagrass meadows, and the slowness, supposed or real, of their natural recolonization, which led to the idea that it could be necessary to proceed to re-stocking or habitat creation, in the Mediterranean [185,186] and worldwide (e.g., [25,36,187–191]).

As stressed by Thoraug [188], the purpose of a restoration attempt for seagrass beds cannot be the laying of end-to-end sods of the seagrasses, but to speed up the process of nature in as rapid a way as possible by cost-efficient means. Seagrass restoration studies date back to 1939, which were largely focused on *Zostera marina* [25,187,192,193].

Techniques of seagrass re-stocking and habitat creation, usually known as "transplanting", roughly come within seven categories [55,183,194,195]: (**i**) cement slabs with holes; (**ii**) cement frames around a wire mesh retaining cuttings; (**iii**) metallic or plastic wire mesh, laid flat on the bottom, retaining cuttings; (**iv**) fixing the cuttings to the bottom

by means of stakes or staples; (**v**) the digging of holes in which blocks of *matte* are placed; (**vi**) the planting of seedlings, germinated in the laboratory; and (**vii**) finally planting seeds, collected at sea or on beaches.

We have classified these techniques from the most intrusive, those that involve durable artefacts (cement, metal, etc.), to the most ecologically friendly, those that do not use any artefacts. It is clear that our preference is for environmentally-friendly methods.

4.1. Cement Slabs with Holes

Cuttings of *Posidonia oceanica* were placed in the 36 holes of 1-m^2 cement slabs. We only know of one example of using this very intrusive method [196]: Saint-Mandrier, near Toulon (eastern Provence), at 8-m depth, in a sandy *intermatte*. The inappropriateness of trying to plant *P. oceanica* in natural sandy *intermattes* will be discussed later (Section 5). In addition, cuttings may die, but cement slabs will persist for centuries.

4.2. Cement Frames around a Wire Mesh Retaining Cuttings

Cement frames around a wire mesh retaining ortho- and plagiotropic cuttings of *P. oceanica* were first used in the Bay of Giens (eastern Provence) [197,198]. They were subsequently used in the French Riviera, western Provence, and Italy [194,199–201].

A similar technique was the setting up of small artificial reefs, made of reinforced concrete, with multiple communicating shelters, harboring *P. oceanica* cuttings; the modules (three types) were placed on hard substrates; the survival of *P. oceanica* cuttings was relatively good [202].

As for cement slabs with holes (Section 4.1), cuttings may die, but cement frames will persist for centuries [183].

4.3. Metallic, Plastic, or Biodegradable Wire Grid, Laid Flat on the Bottom, Retaining Cuttings

Wire or plastic grids, laid flat on the bottom and retaining *P. oceanica* cuttings, have been used in Provence, the French Riviera, Corsica, Tuscany, and Sicily [203–212]. Wire grids were fixed at the corners with 20–70 cm long steel bars [206]. This method has also been used in Australia, with *Posidonia australis* [213] and in the United States with *Z. marina* [214].

A similar technique is the laying down on the bottom of wire bags lined with a geotextile membrane, filled with sand, in which cuttings of *P. oceanica* are placed [215,216]. Gabions, i.e., metallic grids filled with rocks, on which cuttings were secured, were used in Sicily [217,218].

4.4. Fixing the Cuttings to the Bottom by Means of Stakes or Staples

Fixing the cuttings to the bottom by means of stakes or staples was first used at Beaufort (North Carolina) with *Z. marina* [189,190,219]. This technique has also been used successfully in the Great Bay Estuary (New Hampshire), in the framework of the largest eelgrass transplanting project ever attempted on the east coast of the USA [220], and in Australia with *P. australis* [191].

This transplanting technique has also been used in the Mediterranean, with *P. oceanica*) [211,221,222], *Cymodocea nodosa*, *Z. marina*, and *Zostera noltei* [223].

A similar technique was the use of a starch-based biodegradable anchor modular system for transplanting *P. oceanica* cuttings. Modules were positioned at a depth of 6 m on sand with *C. nodosa* and dead *matte* of *P. oceanica*; after 20 months, the rate of survival of *P. oceanica* shoots was good [224]. In the same way, cuttings were attached with natural links (sisal) on 1 m^2 woven bamboo grids, in Corsica [209]. Coconut biodegradable plant pots, placed upside down with an incision to allow the rhizome of the cutting to penetrate into the sediment below, were used in Greece [222].

In Le Brusc Lagoon (eastern Provence), transplants of *C. nodosa* were fixed to the bottom by means of staples; the 1-m^2 transplant areas (80 in total) were covered by a low

(20 cm in height) wire cage made of 5-cm mesh, in order to preserve the transplants from grazing by the teleost *Sarpa salpa* (Figure 9) ([106] Couvray, pers. Comm).



Figure 9. Transplantation of *Cymodocea nodosa* cuttings in Le Brusc Lagoon (eastern Provence). A wire cage preserves cuttings from *Sarpa salpa* grazing. For the purposes of photography and monitoring, the cage was raised vertically. From Couvray et al. [106]. © IOPR (Institut Océanographique Paul Ricard), courtesy of the authors.

4.5. The Digging of Holes in which Blocks of Matte are Placed, and Similar Techniques

Shoots of the eelgrass *Zostera marina* and the shoalgrass *Halodule wrightii* were woven into biodegradable paper meshes (20 cm × 20 cm); this transplanting was intended to mitigate damage to seagrass meadows by scallop dredging in North Carolina [219,225]. This technique bypassed logistical problems encountered when handling numerous bulky turfs or plugs of seagrass with attached sediment (see below).

Cylindrical plugs (20 cm in diameter, 30 cm deep, with seagrass intact in the native sediment) were used to transplant *Thalassia testudinum* and *H. wrightii* in Redfish Bay, Texas [226,227]. This method was also successfully used in the Canary Islands with *C. nodosa* [228] and in Portugal with *Z. marina* [36].

In the Mediterranean Sea, cylindrical plugs (plant, roots, and sediment) were used to transplant *Zostera noltei* in Provence [229–231]. Similar plugs, 20 cm in diameter, together with individual rhizomes, were used in Venice Lagoon (Italy) to transplant *C. nodosa*, *Z. marina*, and *Z. noltei* [85,223,232,233]. Near Ancona (Adriatic Sea, Italy), plugs of *Cymodocea nodosa* were placed within biodegradable bags and containers [234].

In 2005, before a planned enlargement of the marina at Campomanes (Valencia, Spain), the block of *matte* technique was used on a much larger scale. Clods of *P. oceanica* of 1 m^2 in surface area and 40 cm depth lifted with balloons were transported underwater to the transplantation sites, sand *intermattes* in a *P. oceanica* meadow, 600 to 1400 m from the marina; nearly 200 m^2 of seagrass were transplanted, with disappointing results: the rate of shoot survival decreased to 15% after three years [235].

To accommodate cruise ships, the depth of the harbor at Piombino (Liguria) had to be increased. The clods (2.0 m × 1.5 m × 1.2 m; i.e., about 3 m^2) were removed from the seabed by a boat crane, carried out using a spilt-barge motor ship and transplanted to a sandy bottom (*intermatte* channel of a *P. oceanica* meadow) in Piombino Bay. Overall, 1020 m^2 of *P. oceanica* were transplanted. In fact, the clods were simply placed on the sand, forming a kind of hill. The strong point of this technique is (**i**) that thousands of shoots were transplanted simultaneously and (**ii**) that the whole of the invertebrate fauna of the shoots and the *matte* were preserved and transferred with the clod [124].

A similar technique (called "Safebent") was used to transplant *P. oceanica* blocks (shoots and *matte*) with a surface area of 0.8 m^2, 0.6 m thick, with an average of 130 shoots. It was tested in Monaco in 2017 (Figure 10) [236,237] to relocate, at the government's request, nearly 500 m^2 of a *P. oceanica* meadows threatened with destruction by coastal developments (public land reclamation project). The blocks of *matte* were placed in metal baskets covered with a biodegradable structure (coconut fiber), transported within the water column (at 10 m depth) to the transplant sites, between 17 and 20 m deep, and placed in holes previously dug in a sandy bottom (Figure 11). A different technique was to place the blocks of *matte* in cement planters, which were built for this purpose on a hard bottom

(Figure 11). The latter operation is not environmentally-friendly (see Sections 4.1 and 4.2), since the cement structures persist in the event of failure; this was actually the case, since the transplantation ended in failure, and very few shoots survived after three years (in 2020). In contrast, transplants on a sandy substrate had more success after three years: most of the blocks of *matte* still contained living shoots, and the decrease in the density of the shoots had stabilized, while an increase of plagiotropic rhizomes that tend to colonize the adjacent substrate was observed ([236] Gérard Pergent, unpublished data).



Figure 10. (**Left**) The excavator, on a pontoon anchored to the bottom. From Descamp et al. [236]. Courtesy of the author. (**Right**) A view of the clod transplanter in operation. Photo © Andromède océanologie. Courtesy of the author.



Figure 11. (**Left**) Cement planters with transplanted clods of *matte* (*Posidonia oceanica*), on a hard bottom at Fonvieille (Monaco), 14 m depth. (**Right**) The transplant site of Larvotto (Monaco), on a sandy bottom, 17–20 m depth. Photos © Jérémie Godefroy, Sectec, courtesy of the author.

In Australia, underwater seagrass harvesting and planting machines ('ECOSUB1' and 'ECOSUB2') were designed to transplant clods (blocks of '*matte*'), 0.25 m^2 in area and 0.5 m deep, of *Posidonia sinuosa*, *P. coriacea* and *Amphibolis griffithii* [238].

4.6. Planting of Seedlings, Germinated in the Laboratory

The planting of seedlings, germinated in the laboratory, is an ecologically-friendly and low-cost technique that has been used successfully worldwide, with e.g., *Z. marina*, *T. testudinum*, and *C. nodosa* [188,192,239–241]. In the Mediterranean, it has been used with *P. oceanica* [22,170,205,207,242].

For example, seedlings of *P. oceanica*, grown under aquarium conditions for six months, were successfully transplanted at Port-Cros Island (Provence) at a depth of 11 m on a dead *matte*. They thrived for at least two years [243].

4.7. Planting Seeds

Planting seeds, collected at sea or on beaches, is probably the most ecologically friendly technique. It has been successfully used at Hornillo Bay (southern Spain) with *P. oceanica*

seeds, at a site where the *P. oceanica* meadow had been lost as a consequence of fish farming; after two years, the survival rate and leaf development of seedlings planted with mesh-pot anchoring was similar to that of seedlings planted without anchoring [244].

In Virginia (USA), an unparalleled large-scale restoration effort has been maintained annually for 20 years (1999 through 2018) via seed broadcasting of 75 million seeds of *Z. marina* [245]. In Chesapeake Bay, restored *Z. marina* meadows, through shoot transplanting and seed planting, exhibited a genetic diversity similar to that of the donor areas [31].

5. Seagrass Restoration: Where? When? Why?

5.1. The Diversity of Ecosystems Does Matter

Biodiversity means the variety of life, encompassing levels of complexity from within species to across ecosystems. Therefore, biodiversity includes several dimensions [246]. (**i**) **Evolutionary scale**, i.e., diversity within species (genetic diversity), diversity between species, diversity between taxa higher than species (genera, families, orders, classes, phyla, kingdoms), and phylogenetic diversity (mean phylogenetic distance between taxa [247]). (**ii**) **Functional scale**, i.e., diversity in the functional role of species, functional groups and guilds within ecosystems, e.g., photosynthetic or chemosynthetic primary producers, diazotrophic species, filter feeders, suspension feeders. (**iii**) **Organizational scale**, i.e., diversity between patches, communities, ecosystems, landscapes/seascapes, including beta diversity. (**iv**) **Spatial scale**, from local and regional to global [248,249]. As far as species diversity is concerned (evolutionary scale), it can be considered at the scale of a sample (point diversity) of an ecosystem within a region (alpha diversity), of all the ecosystems of a region (gamma diversity), and of all the ecosystems of a large biogeographic province (epsilon diversity). The spatial (geographic) scale matters a great deal for biodiversity estimates [246,250–252]. (**v**) In addition, biodiversity includes the proportional distribution of the individuals among the species, the so-called **heterogeneity diversity**, abundance diversity, or evenness [249].

Biodiversity metrics (more than a hundred) combine several of these scales [246]. It is important to note that the same human-induced impact can increase the value in one metric (for example, the number of species in an ecosystem at the scale of the sample) and reduce it in another metric (for example, the number of species in a region-wide ecosystem). For the general public, biodiversity comes down to the number of species, which is an indicator that is meaningless if it is not combined between several scales [246].

The diversity of ecosystems constitutes an often-neglected scale of biodiversity, while it is (along with functional diversity) one of the most important. This diversity of ecosystems determines the seascape. In addition, coastal ecosystems interact with each other in complex ways (Figure 12). Just as each species plays a role in the ecosystem, so too does each ecosystem play a role in the functioning of the coastal system. There is a complex network of interactions between ecosystems: flows of carbon, of nitrogen, via the litter (e.g., dead *Posidonia oceanica* leaves) or the migration of individuals. There is also a specialization between ecosystems, some of them being highly productive and exporters, or deficit and importers, and/or spawning sites, nurseries, etc. [6,55,253–255].

For example, sandy bottoms are not deserts that should be transformed into hard substrates (by installing artificial reefs) or meadows (by transplanting seagrasses). The sandy bottoms host an original flora (e.g., diatoms) and an original fauna (e.g., infauna), highly diversified, even if they are less spectacular for the diurnal diver than those of the coralligenous, the seaweed forests, and the *P. oceanica* meadows. In addition, the sandy bottom ecosystems constitute an important player in the overall balance of the coastal system: e.g., sites of feeding, spawning, and nursery (Figure 12).

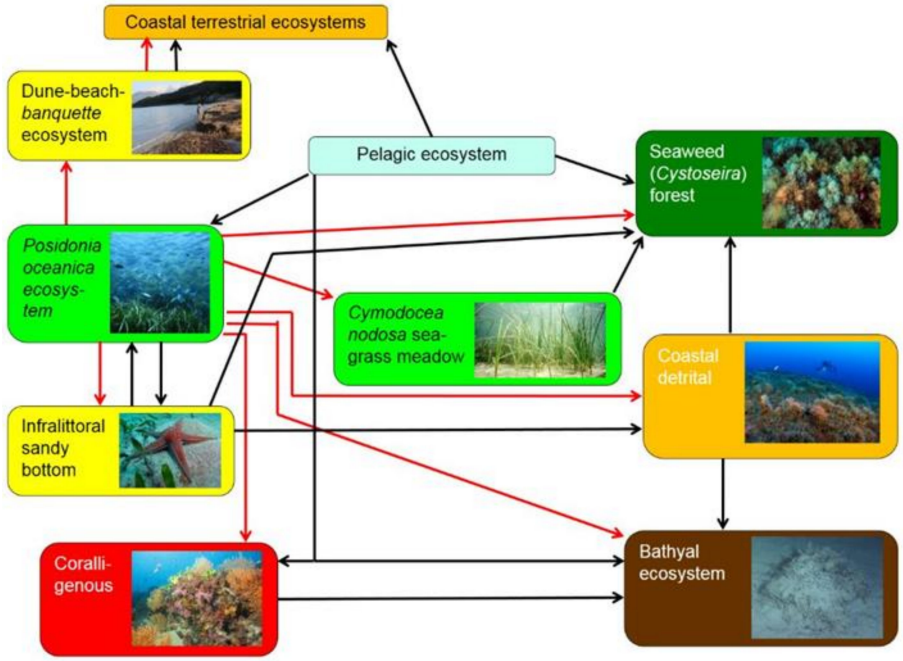


Figure 12. Some interactions between Mediterranean coastal ecosystems. Red arrows: export of litter. Black arrows: other carbon and nitrogen flows. Other interactions are not shown, e.g., nurseries and spawning sites.

5.2. Seagrass Restoration: Where?

Before restoring seagrass meadows, it is worth asking the question: is there decline in the region? In some areas, there has been a real decline, for example *Zostera marina* and *Zostera noltei* in Berre Lagoon, *Cymodocea nodosa* in Le Brusc Lagoon of and *P. oceanica* at Alicante, Marseille, Genoa, and in Liguria in general [76,81,106,108,109,256,257]. In other regions, Corsica and Sicily for example, the decline of *P. oceanica* is negligible [39,257,258].

Seagrass restoration should not be a business, exploiting literature that is sometimes misinterpretated, but it should be based on real needs at the local level. An emblematic example is that of the Bay of Giens (Provence (see Section 2.1), where dead *matte* of natural origin has been the target of transplanting attempts [197,198].

Seagrass restoration should follow the cessation of the causes of the regression. Transplanting to an area where the seagrass is still in decline is obviously an absurdity [32,193]. Yet this is what happened at Marseille (Provence) in 2004. The municipality's Environment department had commissioned a study to find out whether *P. oceanica* planting was possible, and where; the conclusion was that in the west of Prado Bay, the decline had ceased and that therefore, transplanting was possible; on the other hand, in the eastern part of this bay, near the Pointe Rouge marina, the decline continued [66]. However, the public relations department of the same municipality decided to proceed with a highly publicized transplanting operation in front of the marina, the worst possible place; for television purposes, it was considered the most suitable site. Last but not least, the technique used was the worst possible: the use of cement frames (see Section 4.2). All the cuttings died quickly, but there is no doubt that the cement frames will persist on the bottom for decades, perhaps for one century (Charles-François Boudouresque, unpublished data). In Le Brusc Lagoon (eastern Provence), where the collapse of *C. nodosa* is probably due to the overgrazing by the teleost *Sarpa salpa*, it was thought necessary to install protective wire cages above each of the 80 transplanted quadrats (Figure 9) [106], which constitutes an inappropriate artificialization of the lagoon. It would of course have been better to first try to understand the reasons for the proliferation of *S. salpa* and then, if it was determined that it was not natural to take action to reduce it.

Before planting seagrasses at a site, it is worth asking the question: has the species ever existed there? [32,183]. What justification can there be for trying to replace an infralittoral

sandy bed (certainly not a biological desert, but the public does not always know this) by e.g., a few clumps of *P. oceanica*? Such a replacement is in fact a matter of habitat creation, not re-stocking.

For 6000 years, the post-LGM natural rise in sea level has been relatively slow [71,259]. The natural processes of ecological succession have had several millennia in which to act. Therefore, the current mosaic of coastal ecosystems can be considered natural (in the absence of human impact): *Cystoseira* forest on reef habitats, *Posidonia oceanica* meadow with sandy *intermattes* (Figure 2), *C. nodosa* meadow, sandy habitats, coralligenous, etc. (Figure 12). Of course, this mosaic is not based on the short term (that of a research program, or of a doctoral thesis), nor the medium term (the memory of a researcher; see the concept of shifting baselines and historical amnesia) [260–262], but over the long term, taking into account centennial or millennial storms [263–268]. Unless there is precise and well-argued historical information, relocating a seagrass to a habitat that it did not naturally occupy is an ecological absurdity. However, anticipating the warming of the water can be a valid reason to plant a species in a region where it did not exist previously; this is the case with *C. nodosa* in Portugal, near its current northern limit [36]. In addition, rejecting transplantation to sites where a seagrass species never occurred may be viewed as somewhat hypocritical, given the extent to which humans have already transformed the planet through other, much more destructive activities. This question deserves consideration in the Mediterranean, although the marine realm has in general been much less transformed by humans than the terrestrial realm. Finally, in Europe, the problem of the public not understanding the values associated with seemingly "barren" ecosystems, that are devoid of more "valued" seagrasses, could partly stem from EU legislation and the 1992 Habitats Directive, which has raised (and in a way deified) the status of seagrasses.

Most of the seagrass transplant operations in the Mediterranean have been carried out in habitats where the transplanted species was not naturally present. The promoters of these transplants are far from following an ecosystem-based approach (see Boudouresque et al. [269]); they consider that there are "noble" ecosystems (such as *P. oceanica* meadows) and ecosystems of minor importance (for example, sandy bottom ecosystems). Transplanting was done (**i**) in natural *P. oceanica* sandy *intermattes*, such as *P. oceanica* in the Bay of Piombino (Italy) [124,242], in the Bay of Calvi (Corsica) [270], near Toulon (Provence) [196], and in the Valencia region (Spain) [235]; (**ii**) on sandy infralittoral bottoms, such as *P. oceanica* at Larvotto (Monaco) [236] and in Sicily [271], Tuya et al. [22] even proposed surrounding transplanted seedlings with artificial seagrass leaves (a non-natural feature) and showed that this reduced grazing (although obviously a natural feature) and improved the survival rate; (**iii**) in mud infralittoral habitats not previously colonized, such as *Z. noltei* at Martigues-Ponteau (western Provence); transplants initially proliferated before being extirpated after three months by a winter storm [229]; (**iv**) on infralittoral reefs, such as *P. oceanica* at Fonvieille (Monaco) [236] and in Sicily [202]; (**v**) in natural *C. nodosa* meadows, such as *P. oceanica* at Cannes (French Riviera) and in Sicily [271]; both *C. nodosa* and *P. oceanica* are protected species in France; replacing one protected species with another protected species is not a very coherent restoration strategy [183].

An emblematic example is that of the '*Graines de mer*' project of the company SM2. The objective was to collect *P. oceanica* seeds, to germinate them in an aquarium, and then to plant them in the sea between La Grande Motte and Frontignan (Occitania, France) in order to create 400 m^2 of meadow. This project received 490,000 € from a French state agency; it even received a prize awarded by the French Ministry of the Environment ("*Prix entreprise et environnement*") [272]. Unfortunately, *P. oceanica* is naturally very rare in Occitania and does not flower there, undoubtedly because of the too low water temperatures and the influence of the Rhone River discharges: it is at the limit of its range area [90]. Therefore, the seeds had to be collected elsewhere; unfortunately, flowering does not occur every year (see Section 3) and did not occur in those years. In any case, wanting to create a *P. oceanica* meadow in a region where the species is naturally rare is a really strange idea. Of course, the project was a total failure; it did not give rise to any publication, or even to any

document referable to as gray literature. Our reason for citing this tale is (**i**) to underline the lack of professionalism of state agencies in charge of the environment, and (**ii**) so that the record of this story will not be forgotten. Funding of nearly half a million euros could undoubtedly have been put to better use for the real protection of seagrasses.

As concerns the transplanting of *P. oceanica*, the only habitat where such an operation would be justified, from an ecologically ethical point of view (taking into consideration the above-mentioned caveats), is dead *matte* resulting from human impact, which is exemplified by attempts in Provence [211] and Sicily [43,212,271,273]. The case of trenches opened in a meadow to place a pipeline, then filled with rubble, should be considered; natural recolonization seems relatively rapid [135,161–163]; however, if this were not the case, transplanting would be justified [217]. The transplanting of *Z. marina* and *Z. noltei* in Berre Lagoon (Provence) and Venice Lagoon was also justified [85,231,256,274]: the sites chosen have definitely been occupied by *Zostera* species in the past [81,85], and despite a considerable improvement of the conditions (freshwater discharge, silt input, pollution), the natural spread of *Z. marina* and *Z. noltei* is extremely slow; in Berre Lagoon, a regime shift seems to have occurred [11,81].

Habitat creation (see Tan et al. [25]), i.e., transplanting a seagrass species in a habitat that never previously housed the species, and therefore destroying a natural community, must be rejected in most cases (see the above-mentioned caveats). The restoration should not entail the aggravation of the human impact. The only case in which habitat creation would be justified would be if the seagrass species was threatened with extinction in its natural habitats: to our knowledge, this is not the case for any seagrass species in the Mediterranean (LC—Lesat Concern—in the IUCN Red List).

5.3. Seagrass Restoration as a Pretext for Future Destruction?

The possibility of planting *P. oceanica* has often been used as a pretext for destruction, in the context of coastal development projects (new harbors, expansion of existing harbors and marinas, land reclamation)—"*No worries: we are destroying meadows, but we are doing compensatory replanting*." The destruction is definitive. On the other hand, planting in habitats where *P. oceanica* never existed may be a failure, in addition to destroying natural habitats (e.g., sandy bottoms), as stressed by several authors [55,183,235].

Therefore, mitigation (or compensatory measures, or even accompanying measures) should only be envisaged as an attempt at restoring approximately what was destroyed in the past, not as a justification for future destruction based on hypothetical compensation [55,183]. Furthermore, any compensation measures announced at the time when a development decision is made do not legally commit the developing company, which may not have legal authority or financial resources to put them into effect [183].

The expansion project for the marina at Sanary-sur-Mer (Provence) was accompanied by the planting of a few thousand cuttings of *P. oceanica*, in an area where there was no indication that the species had existed in the past [183]. Fortunately, in France, *P. oceanica* is a protected species and the law is strictly enforced, which now makes this type of project difficult [275,276]. However, the same is not true in other Mediterranean countries, e.g., Monaco and Italy (see for example, Descamp et al. [236] and Bedini et al. [124]).

In most cases, a proposal for planting *P. oceanica* as a compensatory measure for the destruction of a healthy meadow is a trap and should be rejected. The paving of the bottom with end-to-end cement frames (Figure 13), at Punta San Pietro, Ischia Island (Naples, Italy), as a compensatory measure for the digging of a trench for a gas pipeline [194], is probably the worst example of unethical and inappropriate transplanting operations.



Figure 13. A nightmarish *Posidonia oceanica* transplanting operation, in the framework of a so-called compensatory measure. Punta San Pietro, Ischia Island, Naples, Italy). From Carannante [194].

In some cases, when a political decision, for example the expansion of the port of Piombino (Liguria) or an offshore urbanization project (Monaco) involves the destruction of a seagrass meadow (*P. oceanica*), a backup transplant may seem legitimate [124,236]. The problem is to find a site for this transplant; generally, the targets of such operations are habitats considered of less importance by managers, such as sandy bottoms, sandy *intermattes* within a *P. oceanica* meadow, or seaweed forests on hard substrates (see e.g., [124,236]).

5.4. Why Restore Seagrass Meadows and When?

Obviously, seagrass restoration only makes sense if the cause of the decline has disappeared (see Section 5.2). In addition, destroying important ecosystems, such as sand bottoms or rocky reef forests, to replace them with seagrasses makes no sense. It is only on dead *P. oceanica matte*, when its origin is not natural but due to man, that replanting is justified [55,183]. Thus, the restoration of the *P. oceanica* meadows destroyed over large areas by the anchoring of cruise ships, in the French Riviera [123], which is now banned by French authorities on seagrass meadows or on sites previously occupied by seagrass meadows, is justified.

It is also necessary to consider the surfaces re-implanted vs. the capacity for natural recolonization [125]. The most extensive replanting operations in the Mediterranean are those at Monaco (500 m^2) and Piombino (1020 m^2) [124,236]. On the Plateau des Chèvres (Marseille), the natural recolonization of an area destroyed by a bomb during World War II extended over 1250 m^2 per year (calculation from data of [155–157]. In Prado Bay (Marseille), after the installation of the sewage treatment plant, natural recolonization has amounted to several tens of thousands of m^2 per year (Boudouresque, unpublished data). Unfortunately, comparison between the transplanted surface areas and the capacity for natural recolonization by local seagrasses is rarely considered by proponents of replanting operations.

Many authors see themselves as lobbyists for a technique and therefore publish only the most optimistic results. A critical analysis of the results, generally in the case of a failure, is less frequent, as stressed by Bedini et al. [242]. From this point of view, it is worth underlining the ethical aspect of the work concerning the relocation of *Z. marina* and *Z. noltei* in Berre Lagoon [231,274]. The authors recognized the poor success of the replanting and the fact that the progression of the transplants was less extensive than that of natural populations.

All in all, transplanting must be integrated within an overall meadow management strategy at the scale of a bay or a region [32,277–280]. This strategy must take into account the following elements [55,125,183]: (**i**) the total surface area of the existing meadows;

(**ii**) the area lost every year due to decline and the causes of this decline; (**iii**) the area reclaimed each year through natural regeneration (if this occurs); the area that one may hope to reclaim through transplanting, within a 10, 20, or 50 year timescale; (**v**) the cost of transplanting, and a comparison with the effects of an identical alternative investment in mastering the cause of the decline (sewage treatment, laying anti-trawl reefs, providing ecologically friendly moorings for leisure boats, creating Marine Protected Areas, etc.): seagrass transplanting is worldwide the most expensive restoration method, with a median of 106,782 US$/ha [25,281]; (**vi**) lastly, in any case, it is necessary that a trial be done on a small control plot and monitored over at least three years; only a favorable result can justify a large-scale operation.

A decision-making strategy for transplanting *P. oceanica* and other seagrasses (Figure 14) and a code of conduct (see Box) have been proposed [55,183] (see also [36]). It is regrettable to note that almost no replanting project has used this decision tree, which might be because the answer was obviously "no"? From this point of view, the strategy for selecting *P. oceanica* transplantation sites implemented in the Gulf of Palermo (Sicily) by Pirrotta et al. [212] is almost unique in the Mediterranean and therefore deserves to be highlighted and praised.

A code of conduct

To avoid techniques for transplanting *Posidonia oceanica* being used as a pretext for going ahead with the destruction of existing meadows, a code of good conduct has been proposed, at the request of the French Ministry of the Environment (Boudouresque et al., 1994; Boudouresque, 2001). The main principles are as follows:

1. The exact site and the biotope where the transplanting will be done must have been occupied previously by *P. oceanica*.
2. The causes of the disappearance of *P. oceanica* (pollution, trawling, anchorage, etc.) from the site where the transplanting will be done must have ceased to operate. Thus, before any transplanting is done, it must be demonstrated that the meadows or isolated clumps of *P. oceanica* that are nearest to the transplanting site have started a process of natural recolonization.
3. Transplanting must not be done near very extensive meadows. It is useless to add several dozen or hundreds of square metres (0.001 to 0.01 ha) to a meadow consisting of several hundreds or thousands of hectares.
4. Transplanting must not be done to compensate for the destruction of a meadow. To avoid such abuse, no transplanting must be done within a distance of 10 km from the site of deliberate destruction of a meadow (as part of coastal development) for a 10-year period.
5. However, transplanting on the exact site of the temporary destruction of a meadow may be possible, at least in the countries where the legal protection of *P. oceanica* is not opposed to this. This is the case when an open trench for an archaeological dig is covered over, or a pipe (or cable) crossing a meadow is buried.
6. With the exception of this special case above (point 5), any transplanting of *P. oceanica* must be undertaken after experimental transplanting of several hundred cuttings; scientific monitoring for at least 3 years must show that the experiment has been a success before a larger scale operation can be envisaged.
7. The removal of cuttings for transplanting must not endanger existing meadows. Therefore, it must be spread over a large area of meadow (less than 2 cuttings/m^2). The use of cuttings detached naturally, although giving less good results, or plantlets from seeds, can also be envisaged.
8. Lastly, transplanting must be done within an overall strategy of *P. oceanica* meadow management of the concerned region.

Similar procedural guides for decision-making, suited to local concerns and species, have been crafted in the US [282,283] and in Australia [277,284].

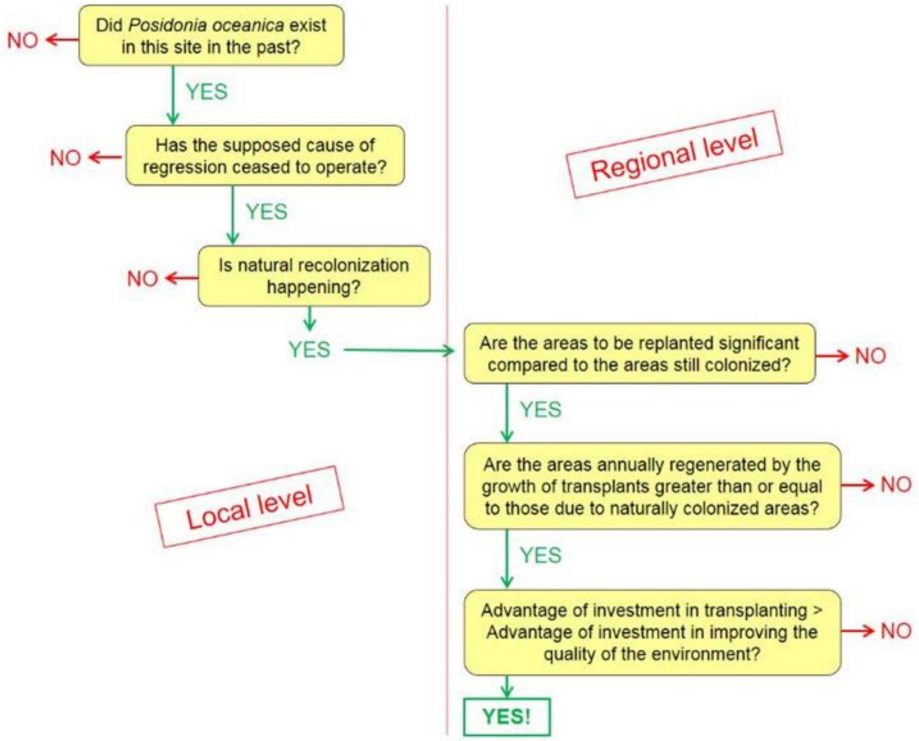


Figure 14. Decision-making strategy for transplanting *Posidonia oceanica* and other seagrasses. The question–answer sequence first looks at the local level (the site of the anticipated transplanting) and then the regional level (a homogenous area, such as a bay). "No" answer should lead to the project being abandoned. From Boudouresque [183], adapted and redrawn.

Taking into consideration certain genetic, physiological, and morphological parameters can improve the chances of success of the transplanting operation. In *P. oceanica*, cuttings transplanted from 20 m to 5 m depth displayed a better survival rate than those transplanted from 5 to 20 m, perhaps in relation with their carbohydrate content [185]. Plagiotropic (horizontal) rhizomes were more successful than orthotropic ones [206,285,286]. The size of the transplanted plots matters; only the largest plots (11 m^2) of *Z. marina* persisted over a long time in Portugal [36]. The reallocation of nitrogen from leaves and rhizomes to ensure the growth of the roots could constitute a major cause of failure for transplantations [270]. In Australia, the high genetic diversity of the source population of *Posidonia australis* cuttings has been shown to be a factor of success [287].

Seagrass restoration has been suggested as a Blue Carbon strategy for climate change mitigation. The effectiveness of this strategy remains to be demonstrated [288]. Considering the huge cost of transplants, it is also necessary to question the cost–benefit ratio compared to the strategy of reducing carbon emissions.

6. Discussion and Conclusions

A recurring issue with regard to the literature dealing with seagrass restoration in the Mediterranean Sea is that the bulk of the literature deals with techniques, describes experiences on a very local scale, and only concerns the short term [125]: one year [106,125,208,215,222,234,236,241,270], two years [22,209,217,223,224,231,232], three years [124,210,235,256], four years [55,183,242,274], or five years [194], rarely longer [211,212]. The longest monitoring survey (17 to 24 years) does not concern a restoration operation but rather a scientific study of the morphological characters of strains coming from 11 Mediterranean regions (mainland Spain, Balearic Islands, French Catalonia, French Riviera, Corsica, Italy, Malta, Greece, Turkey, and Algeria) and transplanted at the same site in the Port-Cros National Park (Provence) [211]. In contrast with seagrass restoration in North America, where *Zostera marina* and *Thalassia testudinum* meadows proceeding from transplanting

operations can be sighted (e.g., [219,289,290]), in Australia with *Posidonia australis* [191] and in New Zealand with *Zostera muelleri* [291], in the Mediterranean, restoration biology is sorely lacking in scientific articles showing a site before (e.g., a dead *matte*) and after 10 or 15 years (e.g., a lush meadow of *Posidonia oceanica*). The reason may be due to the functioning of scientific research: the short duration of doctoral thesis projects, short-term funding, the need to publish quickly, the lack of interest of scientific journals and reviewers in what seems routine, etc. However, it may also be surmised that authors, who quickly published results that were not too disappointing (acceptable mortality rate, presence of some plagiotropic rhizomes), were reluctant to publish a report of a definitive failure a few years later. On the basis of an analysis of the literature, Cunha et al. [125] showed that none of the seagrass restoration programs developped in Europe during the 2000s was successful.

In most Mediterranean seagrass restoration programs, a clear stipulation of aspects such as the goals targeted and a quantification of whether or not those goals are met is lacking.

Another problem is that of the preference of politicians, the media, and the general public for *grand spectacle*, high profile, possibly colossal scale, operations. Budgets are limited for the protection of non-iconic species and for the improvement of the conditions of their environment; they are unlimited when the aim is to enable man, *deus ex machina*, to take control of the environment. To say that it is best to allow nature to take its course, that nature generally does things better than humans (and for free!), as stressed by Leakey and Lewin [292], and Schnitzler et al. [293], is often unacceptable to politicians and managers of state agencies. The case of the obviously unrealistic project to create *P. oceanica* meadows in Occitania [272] is the perfect example of this. Fortunately, some operations perfectly meet the requirements of the code of conduct, such as the widespread transplantation of small sods and individual rizomes of seagrasses (mainly *Z. marina* and *Z. noltei*) in the northern part of the Venice Lagoon; in addition, this operation engaged the local population in the restoration of the environment, making the action not only environmentally friendly (methods) but also economically inexpensive [85].

In any case, the decline of some species of seagrasses, in certain regions of the Mediterranean, is a worrying reality. As part of a regional strategy, relocation may be justified, provided that the most environmentally friendly techniques are used. The regional strategy must take into account (**i**) natural recolonization vs. assisted recolonization; priority should be given to natural restoration potential, with an emphasis on the fact that restoration should never be considered the first alternative [125]; (**ii**) the cost of relocation vs. an equivalent investment in improving environmental conditions (e.g., ecologically friendly anchoring, sewage treatment, prohibition of trawling and of anchoring of cruise ships, ban on the creation or expansion of harbors and marinas, ban on the removal of *P. oceanica banquette* on beaches, etc.); (**iii**) and of course, the imperative of only replanting (in most cases) in areas formerly colonized by the species concerned; destroying an ecosystem that is believed to be of minor importance, but which plays a role in the functioning of the coastal system, in order to plant a seagrass that was not naturally present there, is not very coherent from an ecological point of view.

Unfortunately, the vast majority (but not all) of seagrass restoration projects in the Mediterranean Sea do not meet these obvious, basic criteria. This perhaps explains the extreme rarity of success stories in the seagrass restoration field. Moreover, is there a single example of medium-term success (say 10–20 years) in the Mediterranean?

Elliott et al. [184] emphasized that the few success stories in restoring habitats concern marginal or semi-enclosed areas such as coastal bays, estuaries, and fringing habitats; they refer less frequently to open coastal and marine habitats. The best option available in the latter is usually to remove the stressor, to prevent other stressors from operating, and to allow the conditions suitable for natural recovery [184,235].

The relative failure of seagrass restoration in the Mediterranean is often compared to successes in other parts of the world ocean, as illustrated by the restoration of *Z. marina*

meadows [245]. Yet, these successes deserve to be re-examined with a critical eye. The losses were partly of natural origin (wasting disease, tropical storms); in the absence of human impact, natural recolonization was often relatively rapid. An accurate comparison of natural and unassisted vs. assisted recolonization is often missing. Was the effort (and money) deployed to try to do better, or faster, than nature really justified? Would not this money and this effort have been more effectively deployed in reducing human impacts? This question of the real cost and benefits balance of seagrass restoration operations is in fact insufficiently addressed by the authors. The myth of man as superior to nature, developed by 18th and 19th century authors (see Boudouresque et al. [269]), is still alive and well present in the 21st century.

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