

# 12

## How long time does it take to recolonize seagrass beds?

The time scales for seagrass recolonization after events of disturbance are important information for seagrass managers, because, based on this information, they can decide what actions need to be taken for each scenario. Seagrass recolonization potential vary considerable among species. The potential for seagrass colonization is a function of both rhizome elongation, which determines patch growth, and reproductive effort, which sets the potential for formation of new patches. Additionally, environmental conditions are important factors in the recolonization times.

By Alexandra H. Cunha (CCMAR), Carlos M. Duarte (IMEDEA) and Dorte Krause-Jensen (NERI)

Seagrass landscapes are often patchy with patches from less than one meter to several kilometres wide. Patch-forming mechanisms operate at spatial and temporal scales controlled by intrinsic and extrinsic factors. The dynamics of seagrass patches is the basis for the maintenance of this structure and it is important to understand the changes that occur in these meadows. The potential for seagrass colonization is a function of both rhizome elongation, which determines patch growth, and reproductive effort, which sets the potential for formation of new patches. Clonal propagation is considered to be the most important process for the maintenance of seagrass meadows. Recruitment from sexual reproduction depends on the flowering probability and survival of the seeds, which are very variable between species. The environmental conditions play here an important role that is not quite understood yet.

It is difficult to estimate the recovery of a seagrass meadow based on their growth capacity, but some simulation techniques have been used to produce models. These models are based on the growth of the horizontal rhizome and the rate of formation of new patches assuming the rate of patch formation to be constant. The predicted recovery times are particularly short for fast-recovering species (e.g. *Cymodocea nodosa* – within 1 year) but can exceed a century for *Posidonia oceanica* due to the slow rate of patch formation of this species.

The aim of this chapter is to provide an overview of the recolonization capacity of European seagrass beds on long and short time scales and on large and small spatial scales. We searched for examples that would contribute to the

understanding of the capability of seagrass to recolonize new areas.

### How do seagrasses recolonize?

Gaps within seagrass meadows formed by natural events, such as storms or by anthropogenic disturbances, such as anchor scars, are primarily recolonised by the extension of the rhizomes of the plants located in the periphery of the gaps. The effectiveness of this process is limited by the horizontal extension rates of the species present. Hence, gaps in the order of 1 m<sup>2</sup> can be closed within one or a few years, whereas gaps tens of meter across require a decade or longer to be recolonised. Horizontal rhizome extension (i.e. clonal growth) is not an effective mechanism for the recolonization of larger gaps, which must necessarily involve sexual reproduction to initiate new patches within the denuded area.

Seagrass patches can also be established from drifting fragments, if they are anchored or trapped within the area to be recolonised. Also, following storms, or intense anthropogenic activities such as clam digging or boat anchoring, detached pieces of flowering shoots can float and release seeds far from the original area. Whenever an entire meadow is lost, due, for instance to disease related decline, recolonization is dependent on the arrival of propagules as seeds or viable vegetative fragments from neighbouring populations. Among the European seagrasses, only *Posidonia oceanica* has buoyant seeds able of long-range (10's of km) dispersal. The seeds of the remaining species are negatively buoyant, and the seeds of *Cymodocea nodosa* are produced at the base of



Figure 12.1 – Runners of *Cymodocea nodosa* in Ria Formosa, southern Portugal. Seagrass patches grow by the horizontal expansion of the rhizomes that extend out of the patches centrifugally. Photo: Alexandra H. Cunha.

the shoots and are often positioned at, or just below, the sediment surface. These seeds are, therefore, not likely to disperse far. The dispersal range of seagrass seeds is a very poorly studied aspect of their reproductive ecology, and robust estimates of dispersal events are only available for *Zostera marina* populations, for which 95 % of the seeds are retained within 30 m from the source, and robust estimates of dispersal events are only available for *Zostera marina* populations.

Once in the sediment, the seeds of some seagrass species can remain dormant for some time, with a documented dormancy period of a few months for *Zostera marina* and 7-9 months for *Cymodocea nodosa*, thereby building a rather ephemeral seed bank. Indeed, seed survival for more than one year appears to be a rare situation in seagrasses. While high seed production (e.g. > 50,000 seeds m<sup>-2</sup>yr<sup>-1</sup> for some *Zostera marina* stands) and dense seed banks (e.g. > 1000 seeds m<sup>-2</sup> for *Cymodocea nodosa*, and *Zostera marina*) have been reported in some meadows, seedling density is always comparatively low (typically about 1 to 10 % of the seeds produced) providing evidence of high seed losses. These losses are due to many factors including lack of viability, physical damage, export to unsuitable areas and burial. Moreover, seeds are also lost through predation, as documented by the experimentally estimated 65 % loss of *Zostera marina* seeds to predators. Seagrass germination does not appear to be too demanding, so that germination rates are typically high under field conditions. Seedling mortality is very high with a reported survival probability of only a few percent of the germinated seedlings over the first year for most species, although it may occasionally be very high as the exceptionally high seedling survival rates reported

for *Posidonia oceanica* seedlings established on dead rhizome mats.

Successful recruitment from sexual reproduction is a rare event in most seagrass species, particularly in *Posidonia oceanica*, where seedlings have been reported only in a few meadows. Low flowering probability and low survival rates of seeds are major bottlenecks. Even when sexual reproduction culminates in the establishment of a new plant, this process is still an ineffective way to propagate because of the short dispersal distances that most species seem to exhibit. The inefficiency of sexual reproduction highlights the importance of clonal propagation as the main process responsible for the maintenance of seagrass meadows.

### Small scale recolonization in seagrass meadows

Small scale recolonization in seagrass meadows depends on rhizome growth and patch formation rates. Seagrass patches grow by the horizontal extension of the rhizomes that extend out of the patches centrifugally (Fig. 12.1).

These rhizomes, which colonise unvegetated substrata, produce longer internodes and thereby grow faster than rhizomes growing in the interior of the meadow. The growth of the colonizing rhizomes is supported by the translocation of resources from the older shoots. The available data on rhizome elongation rates shows a considerable variability among and within species (Table 12.1). Species with low elongation rates as *Zostera marina* may attain a high potential for colonization by balancing with a high reproductive effort.

Besides the species capacity for rhizome growth, patch growth is subject to considerable variability among and within patches. The growth rate of seagrass patches is initially slow but accelerates as the patches grow larger due to the proliferation of branching. In addition, seagrasses modify their surroundings by reducing currents, stabilizing sediments and reducing sediment resuspension

Table 12.1. Rate of horizontal elongation rate (m year<sup>-1</sup>) of European seagrass species

Species	Rate of horizontal
<i>Zostera marina</i>	0.1 – 0.9
<i>Zostera noltii</i>	0.44 - 1.68
<i>Cymodocea nodosa</i>	0.09 – 2
<i>Posidonia oceanica</i>	0.02 – 0.08

within the patch. Also as the patch grows, a positive feedback in seagrass growth takes place such that seagrass patches form a “mutually sheltering” structure as they grow.

The rate of formation of new seagrass patches has been examined for a few seagrass populations (Table 12.2).

### Patch growth of *Zostera marina*

*Zostera marina* has declined extensively during the last decades following eutrophication of coastal regions of Western Europe. Sharply declining mortality with increasing patch age and size was observed in a population of *Zostera marina* growing in a protected embayment in Limfjorden, Denmark. This observation was associated to improving anchoring, mutual physical protection and physiological integration among the shoots as the patches grow larger. Here, the patch size distribution was dominated by small patches, which were formed by seedlings at high rates during spring (0.16 to 0.76 m<sup>-2</sup>). The seedlings were subjected to high mortality and only 24% survived. The lateral growth rate of established patches was low (16 cm yr<sup>-1</sup> on average) and, therefore, acreage expansion will be faster in systems with many small patches than in systems with few large patches. In large scale systems, successful recovery will be dependent on seed production, seed establishment and subsequent patch development.

### Patch growth of *Zostera noltii*

Patch growth of *Zostera noltii* has not been investigated as yet. However, this species combines a very high branching rate with a moderately fast rhizome elongation rate suggesting that it must be capable of fast patch growth. The use of patch growth models to simulate *Zostera noltii* patch growth suggests that patch growth is fast and compact due to the high branching rate. Observations of fast recovery of gaps created by disturbance in *Zostera noltii* stands support the conclusion that recolonization rates are fast for this species.

### Patch growth of *Cymodocea nodosa*

In the Mediterranean a *Cymodocea nodosa* community growing over highly mobile sandy sediments demonstrates that patch development proceeds by colonization by seedlings (0.047 m<sup>-2</sup> yr<sup>-1</sup>) and subsequent patch development by the surviving seedlings (<10%). Seedling distribution was highly aggregated and tended to be greater in areas where previous patches had died. There was considerable seedling mortality in the first year after germination (>70%). Rhizome development, necessary for patch formation from established seedlings, was observed in less than 50% of the seedlings. Patch growth was subject to considerable variability among and within patches, which demonstrates the influence of the environmental conditions. Difference in growth among patches of different sizes are attributed to a positive feed back effect accelerating patch growth as patch size increases.

### Time scales for recolonization in seagrass meadows

It is difficult to provide an estimate of the recovery rate of seagrass species based on their growth capacity. However, estimates of the time scales for seagrass recovery have been produced using simulation techniques as well as estimates derived from projections of observed patch growth rates. In one such model, the interplay between the horizontal growth and the rate of formation of new patches was combined to provide a first-order estimate of the likely colonization time of different seagrass species. The model results predict recovery times ranging from < 1 year to centuries depending on species. The predicted recovery times for fast-growing species (*Zostera noltii* and *Cymodocea nodosa*) are particularly short, so that even with a moderate rate of new patch formation, a meadow can be established - provided suitable habitat is available - within 1 or a few years. In contrast, the recovery time for *Posidonia oceanica* involves several centuries, which would be in a permanent stage of overall decline if the return time of disturbance is shorter than a century. Extrapolations derived from the

Table 12.2. Examples of rates of formation of seagrass patches.

Species	Rate of formation	Source
<i>Zostera marina</i>	1000 patches ha <sup>-1</sup> yr <sup>-1</sup>	(Olesen & Sand-Jensen 1994)
<i>Cymodocea nodosa</i>	45 patches ha <sup>-1</sup> yr <sup>-1</sup>	(Duarte & Sand-Jensen 1990)
<i>Posidonia oceanica</i>	3 patches ha <sup>-1</sup> yr <sup>-1</sup>	(Meinesz & Lefèvre 1984)

observed growth rate of seagrass patches concur with model estimates to indicate that recolonization time scales for *Posidonia oceanica* are in the order of several centuries. Hence, any large-scale loss of *Posidonia oceanica* must be considered almost irreversible on managerial time scales.

Some seagrass populations exposed to periodical disturbance (e.g. transit of sand waves, etc.) are permanently in a stage of local loss and recovery resulting in a characteristic patchy landscape. Whether the substrate is devoid of seagrass, supports a dynamic patchy landscape or a continuous seagrass meadow depends on the frequency and magnitude of the disturbance relative to the capacity to resist disturbances and the recovery time of the species. Such dynamic equilibria have been demonstrated for *Cymodocea nodosa* growing on a Mediterranean bay swept by sand waves 10 – 20 cm in height. The progression of the sand waves causes the mortality of the buried patches as the rhizomes become exposed and colonised by drilling organisms following the passage of the sand wave, but the time interval in between the passage of consecutive sand waves was sufficient to allow the formation and development of new patches. *Posidonia oceanica* even survives larger (> 30 cm), frequent (> 1 yr<sup>-1</sup>) sand waves without experiencing mortality. Hence, a persistent patchy landscape is only possible under combinations of disturbance magnitude and frequency causing only partial mortality and allowing the partial recovery of the species involved.

#### *Zostera marina*

Nature provided a large-scale test on the recolonization capacity of eelgrass when the worldwide wasting disease eliminated the majority of the European eelgrass populations in the 1930s. Fortunately, the process proved to be at least partly reversible. Assessments of eelgrass area distribution through the latter half of the 19th century provide evidence from many areas that considerable recolonization had occurred within 2-3 decades. However, recolonization after the wasting disease has not led to a complete reestablishment of the former distribution and abundance of eelgrass. In many areas various kinds of anthropogenic disturbances hinder full recolonization and cause further decline of especially deep populations (see chapter 5 for details).

#### *Zostera noltii*

Quantitative observations of recolonization dynamics in *Zostera noltii* are few if not non-existing. However, indications on the recolonization capacity following local and larger-scale disturbance have been conducted at Ria Formosa (S. Portugal). Clam digging often creates gaps within *Zostera noltii* populations. However, these have been observed to be recovered within a few months, and there are indications that the disturbance stimulates flowering and seed production, which may further contribute to the fast recolonization. The migration of sand bars has also been shown to disturb *Zostera noltii* at larger scales (ha) in the Ria Formosa. Recovery from such large-scale disturbance was slower, but still relatively fast, in the order of a few years (see chapter 5 for details).

#### *Posidonia oceanica*

Within the European seagrass flora, *Posidonia oceanica* is the species with the lowest recolonization capacity. The slow rhizome elongation rate (a few cm per year) and the sparse flowering of this species, where the meadows may not flower in several years and when they do, this involves only a small fraction of the shoots, are conducive to a low recolonization capacity. Small (m<sup>2</sup>) gaps within *Posidonia oceanica* meadows can remain visible over several years, and large-scale recovery is indeed very slow requiring time scales of centuries (500 – 800 years, depending on patch formation rate). Yet, large-scale decline appears to be widespread in the Mediterranean Sea, involving a number of factors, such as constructions along the shoreline (e.g. ports, wave breakers, etc.), enhanced organic and nutrient inputs from land and from aquaculture activities, coastal erosion and mechanical damage by trawling boats and anchors. The deterioration of sediment conditions due to enhanced organic inputs may slow recolonization even further, as rhizomes cannot extend into anoxic sediments. Recolonization rates can be somewhat accelerated by measures to improve the growth conditions for seagrasses including action on the sources of deteriorated water and sediment quality and measures to stop mechanical damage.

#### *Cymodocea nodosa*

Within the European seagrass flora, *Cymodocea nodosa* is the species with the fastest rhizome growth (up to 2 m year<sup>-1</sup>) and this species may flower profusively. However, the very low dispersal capacity of the seeds implies that

recolonization processes are largely dependent on horizontal spread as well as new patch formation from occasional seeds or vegetative fragments that may colonise the area. Observations on the dynamics of *Cymodocea nodosa* landscapes indicate that gap recolonization occurs within a year, and the meadow development takes place in less than a decade.

## Conclusion

European seagrasses differ greatly in recolonization time scales due to the vast differences in sexual reproduction, seed dispersal and horizontal elongation rates. Whereas, recolonization of *Zostera* species and *Cymodocea nodosa* seems to be a relatively rapid phenomenon, extending over months for gap recolonization, to a few years for large-scale recolonization, recolonization of *Posidonia oceanica* is much slower involving time scales of a decade for gap recolonization to several centuries for large-scale recolonization. In managerial terms, loss of *Zostera* species and *Cymodocea nodosa* area can be considered reversible provided adequate measures are implemented to facilitate recovery, whereas loss of *Posidonia oceanica* should be considered as an irreversible process. Hence, conservational efforts, which

must prevent losses of all European seagrasses, must be particularly strict to protect *Posidonia oceanica* meadows.

## References

- Duarte CM, Sand-Jensen K (1990) Seagrass colonization: patch formation and patch growth in *Cymodocea nodosa*. Marine Ecology Progress Series 65:193 – 200
- Hemminga MA, Duarte CM (2000) Seagrass Ecology. Cambridge University Press.
- Olensen B, Sand-Jensen K (1994) Patch dynamics of eelgrass *Zostera marina*. Marine Ecology Progress Series 106:147-156
- Ramage DL, Schiel DR (1999) Patch dynamics and response to disturbance of the seagrass *Zostera novaezelandica* on intertidal platforms in southern New Zealand. Marine Ecology Progress Series 189: 275-288
- Vidondo B, Duarte CM, Middelboe AL, Stefansen K, Lutzen T, Nielsen SL (1997) Dynamics of a landscape mosaic: size and age distributions, growth and demography of seagrass *Cymodocea nodosa* patches. Marine Ecology Progress Series 158:131-138