

Chapter 11

Dynamics of Seagrass Stability and Change

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I. Introduction

To the casual observer, seagrass meadows often appear to be uniform landscapes with limited structure. Belying this appearance, seagrass meadows contain considerable structure and dynamics (cf. den Hartog, 1971). Seagrass meadows, at any one time, consist of a nested structure of clones, possibly fragmented into different ramets, each supporting a variable number of shoots. Thus, although apparently rather static, seagrass meadows are highly dynamic landscapes maintained through the continuous recruitment of new clones to the meadow, and the growth and the turnover of the shoots they contain. Therefore, the intense dynamics of seagrass ecosystems results from the combination of processes operating at various scales, which—if balanced—maintain a rather stable ecosystem. Often, however, the various processes responsible for meadow dynamics are either unbal-

anced or out of phase due to either natural causes or anthropogenic effects. Such imbalances result in changes in the meadows, which are sometimes readily evident, such as the case in catastrophic seagrass declines or are so subtle as to even elude quantification, such as may be the case in the gradual decline of slow-growing seagrass species (e.g. Marbà et al., 2003).

A proper understanding of these dynamics require, therefore, a basic understanding of contribution of the different relevant processes conforming the seagrass meadow. These processes are those affecting clonal growth, from the dynamics of apical meristems and the resultant shoots—the basic units of seagrass meadows—to that of the patches. Sexual reproduction is the primary mechanism of patch initiation, along with the dispersal of seagrass fragments, and the survival and growth of the patches is under strong environmental control. These processes and mechanisms will be discussed in this chapter to offer an overview of the processes responsible for the dynamics of seagrass meadows.

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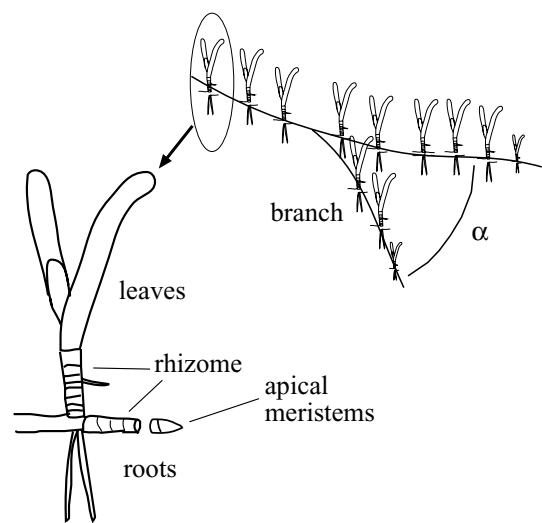


Fig. 1. Schematic representation of a shoot, the basic module of seagrass clones, containing leaves, grouped into leaf bundles, roots and a piece of rhizome, and a branching rhizome. α denotes the branching angle.

II. Components of Seagrass Meadows: from Apical Meristems to Meadows

Seagrasses are clonal plants, whereby the plant growth occurs through the reiteration of a basic set of modules, connected by rhizome material to develop the clone (Marbà and Duarte, 1998; Hemminga and Duarte, 2000). This basic module consists of a shoot, bearing a leaf bundle in all species except some *Halophila* species that have a leaf pair at each shoot (den Hartog, 1970), and a set of adventitious roots and a rhizome piece connecting them to neighboring shoots (Fig. 1). The reiteration of these modules is achieved through cell division at the apical rhizome meristem, which provides, therefore, the basis for seagrass clonal growth (Tomlinson, 1974). In addition, to produce new modules, the apical rhizome meristem may divide, producing a branch also containing an apical rhizome meristem, which extends the clone in a different direction (Fig. 1). Hence, an adequate representation of clonal growth patterns requires characterization of the size of the clonal modules and their organs, the spacing in between consecutive modules along the rhizome, the rhizome elongation rate and its branching rate, and angle (Fig. 1; Marbà and Duarte, 1998). There has been, therefore, considerable effort to quantify these properties across the seagrass flora (Tables 1 and 2).

Table 1. Mean and range of components of clonal growth of seagrass species. Based on data compiled by Marbà and Duarte (1998).

Trait	Mean	Min	Max
Rhizome elongation (cm year ⁻¹)	79	2	3.56
Horizontal rhizome branching rate (% of internodes)	5.8	0.06	25.97
Horizontal rhizome branching angle (degrees)	47	19	81

The components of clonal growth all range greatly across the seagrass flora (Table 1, range of variation of clonal properties across the seagrass flora), including significant plasticity within species (Pérez et al., 1994; Marbà and Duarte, 1998). However, much of this variability can be explained through allometric relationships between these components and module size, as represented by either shoot weight or rhizome diameter (Duarte, 1991; Marbà and Duarte, 1998; Hemminga and Duarte, 2000). Hence, small seagrasses show faster clonal growth rates than large species (Table 2), which tend to

Table 2. Average rhizome elongation rates of seagrass species. Based on data compiled by Marbà and Duarte (1998).

Species	Rhizome elongation (cm year ⁻¹)
<i>Amphibolis antarctica</i>	20
<i>Amphibolis griffithii</i>	4
<i>Cymodocea nodosa</i>	40
<i>Cymodocea rotundata</i>	210
<i>Cymodocea serrulata</i>	153
<i>Enhalus acoroides</i>	3
<i>Halophila decipiens</i>	215
<i>Halophila hawaiiiana</i>	89
<i>Halophila ovalis</i>	356
<i>Heterozostera tasmanica</i>	103
<i>Halodule uninervis</i>	101
<i>Halodule wrightii</i>	223
<i>Posidonia angustifolia</i>	12
<i>Posidonia australis</i>	9
<i>Posidonia oceanica</i>	2
<i>Posidonia sinuosa</i>	4
<i>Phyllospadix scouleri</i>	17
<i>Phyllospadix torreyi</i>	26
<i>Syringodium filiforme</i>	123
<i>Syringodium isoetifolium</i>	109
<i>Thalassia hemprichii</i>	54
<i>Thalassia testudinum</i>	69
<i>Thalassodendron ciliatum</i>	16
<i>Thalassodendron pachyrhizum</i>	3
<i>Zostera marina</i>	26
<i>Zostera noltii</i>	68

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grow slowly (Duarte, 1991; Marbà and Duarte, 1998; Hemminga and Duarte, 2000). On the basis of the existence of such allometric relationships, the seagrass flora has been described as composed of scale models of a generic design (Marbà and Duarte, 1998). Whereas this statement holds if examining individual properties, the simultaneous variation in average clonal properties across species renders clonal patterns complex, thereby resulting in contrasting growth strategies across species.

The simplest models of clonal growth could not elucidate these differences for they portrayed clonal growth as a simple radial growth process, with circular-shaped clones extending at a constant radial growth rate equivalent to the average rhizome elongation rate of the modeled species (Duarte, 1995; Kendrick et al., 1999). However, comparison of the resulting prediction of colonization rates with observed dynamics provided evidence that clonal growth does not proceed at a constant rate, but that it accelerates over time (Kendrick et al., 1999). More elaborate models of clonal growth used all components of clonal growth, as represented by their average value and observed within-species variability, to examine the development of clonal networks (Marbà and Duarte, 1998; Sintes et al., 2005). Models using clonal growth rules to simulate clonal growth provided evidence that, as suggested by field observations (Vidondo et al., 1997; Kendrick et al., 1999), this is a strongly non-linear process (Marbà and Duarte, 1998; Sintes et al., 2005). The radial growth of seagrass clones accelerates from very low values at the early stages of growth to high rates (Marbà and Duarte, 1998; Sintes et al., 2005), equaling the extension rates of runners (i.e. rhizomes extending outside seagrass patches), by the time they reach highly compact structures (Fig. 2). The efficiency of space occupation, as described by the increase in patch size achieved for a given rhizome production, declines sharply with increasing clonal size (Sintes et al., 2005). The applicability of these models, developed using *Cymodocea nodosa* as the model species, to other species is yet to be assessed.

Whereas fast-growing seagrasses have been assumed to display a guerrilla strategy compared to the more compact, 'phalanx' growth strategy assumed for larger, slow-growing species, analysis of model results indicate that these expectations do not hold (Marbà and Duarte, 1998). The broad branching angles of the fast-growing, small seagrass species (e.g. *Zostera noltii*) lead to a compact growth, following a

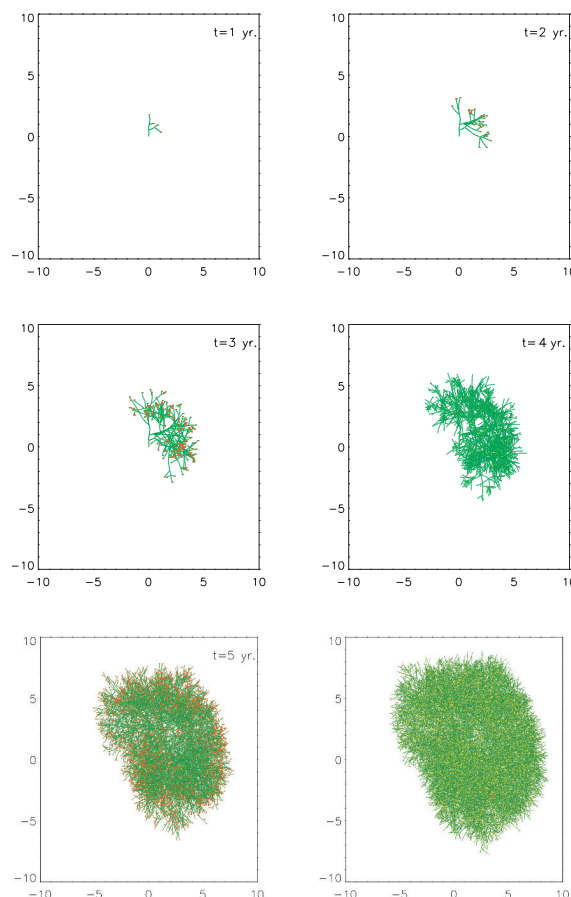


Fig. 2. The shape of modelled *Cymodocea nodosa* clones of different ages. From Sintes et al. (2005)—with permission.

spiral pattern around the origin of the clone, whereas the narrow branching angles of large-slow-growing seagrasses project them at relatively larger distances for a given investment in rhizome material, generating a guerrilla-like pattern but over a long period of time (Fig. 3).

Present depictions of clonal growth patterns cannot, however, be used to infer the resulting structure of the meadows, for these models examine the growth of individual clones and do not consider possible interferences from neighboring clones. Moreover, there is evidence that there is a limit to the maximum density of seagrass stands (e.g. Duarte and Kalff, 1987; Marbà and Duarte, 2003), so that the presence of neighboring clones is expected to reduce the growth of adjacent clones. Indeed, models of seagrass clonal development can only reproduce the internal density of seagrass clones if an exclusion

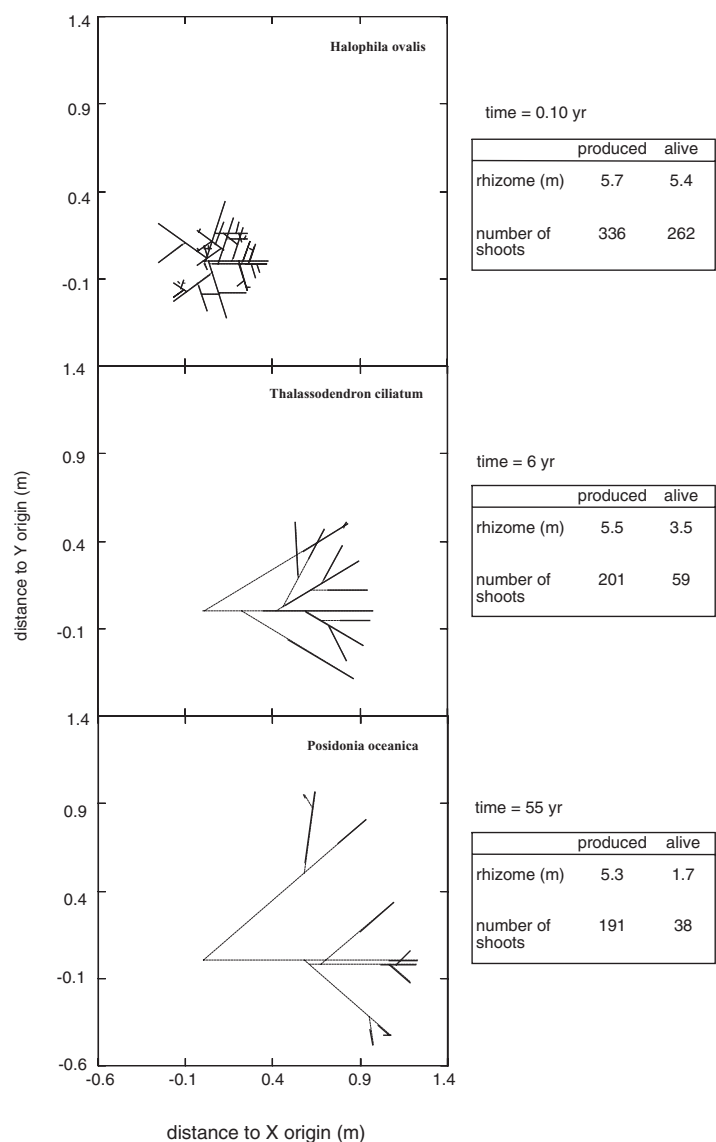


Fig. 3. The simulated spread of clones of different seagrass species predicted on the basis of their basic growth rules: horizontal rhizome elongation rate, and branching rules (probability and angle). The graphs depict the clonal topography after producing ca. 5 m of rhizome for three contrasting seagrass species (*Halophila ovalis*, *Thalassodendron ciliatum*, and *Posidonia oceanica*). The time required to develop the networks, and the rhizome length, and number of shoots produced and surviving since initiation of clonal spread are indicated. Dashed lines show the spatial distribution of the rhizomes and shoots produced, and continuous ones the distribution of surviving rhizomes and shoots. Reproduced from Marbà and Duarte (1998)—with permission.

area, or per capita space, which is unlikely to be occupied by another shoot, is defined around each shoot (Sintes et al., 2005), thereby supporting empirical evidence for architectural-determined seagrass density (Marbà and Duarte, 2003). The role of density-dependence in regulating clonal growth and space occupation in seagrasses is, however, insufficiently developed at present. Hence, whereas the expected dynamics of colonizing clones are adequately represented by existing knowledge and rate estimates, the dynamics of clones within established meadows is not sufficiently understood as yet to allow reliable models of meadow development and dynamics to be formulated. Moreover, the role of environmental factors, prominently hydrodynamics in shaping the landscape produced (cf. Bell et al., Chapter 26), is

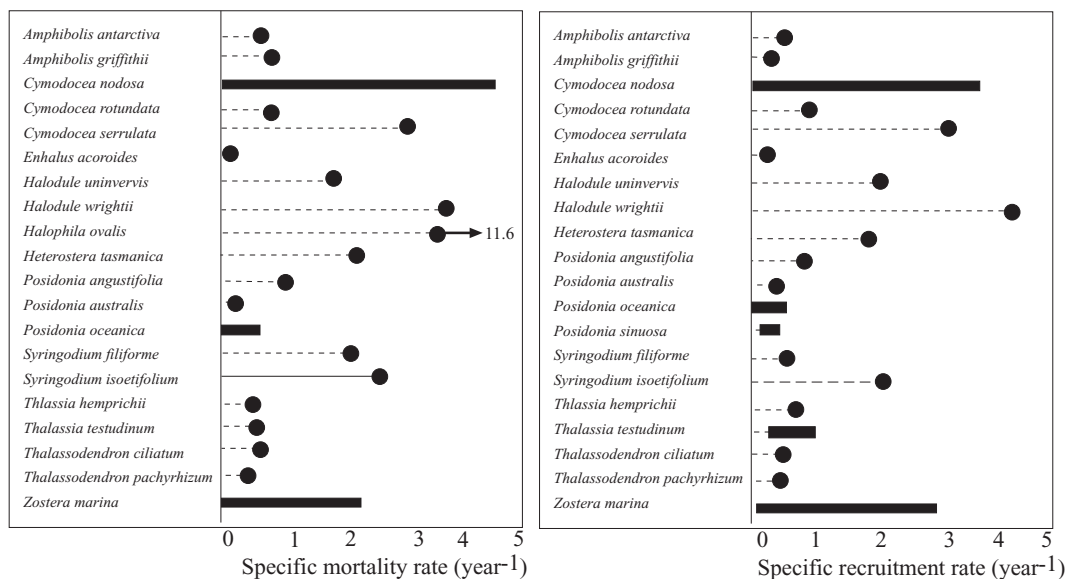


Fig. 4. Reported shoot mortality and recruitment rates for seagrass species. Solid circles represent average values, and bars extend across reported ranges. Data from tables in Hemminga and Duarte (2000).

also not captured as yet by models of how clonal growth develops into meadows.

III. Shoot Dynamics

A. Shoot Recruitment: Vegetative and Sexual

Shoot recruitment is the addition of new individuals to the population occurring by the vegetative production of new shoots through clonal growth or by the recruitment of new genets through production and germination of seeds or fragments. Up-rooted shoot modules may also act as recruitment units (Ewanchuk and Williams, 1996; Reusch, 2001; Campbell, 2003) although the successful establishment and survival of such vegetative fragments inside established vegetation has yet to be documented. Vegetative shoot recruitment proceeds at highly variable rates and is largely a species characteristic although individual species also show plastic response of clonal growth to ambient conditions. Hence, vegetative shoot recruitment does not proceed at constant rates in time and space and experimental studies have demonstrated reduced rates of shoot recruitment in nutrient and light limited stands (Gordon et al., 1994; Pérez et al., 1994; Agawin et al., 1996; Ruíz and Romero, 2001). In dense stands light also tends to impose an upper limit to shoot

recruitment such that rates may be constrained by the density of neighbouring shoots, thereby avoiding overcrowding of the populations (Duarte and Kalff, 1987; Olesen and Sand-Jensen, 1994a). Variability in clonal growth also has a seasonal pattern, particularly in temperate regions, with shoot formation rates proceeding slowly during winter when growth is restricted by adverse growth conditions and rapidly in early summer concomitant with increasing temperature and light (Bigley and Harrison, 1986; Marbà et al., 1996a). Accordingly, shoot formation rates are influenced by resource availability imposing a limit to overall rates of seagrass growth but the substantial plasticity observed may also be an important component of their capacity to acclimate to growth under a range of environmental conditions.

The high variability across species in rates of vegetative shoot formation scales to size such that the time interval between the production of consecutive shoots on the horizontal rhizome is much longer (months) in large seagrass species than in small species (days) (Duarte, 1991; Marbà and Duarte, 1998; Marbà and Walker, 1999; Hemminga and Duarte, 2000). Hence, the average specific vegetative recruitment rates of new shoots into seagrass populations proceed at rates spanning more than 10-fold from the large seagrass species *Enhalus acoroides* (0.26 year^{-1}) to the small species *Halodule wrightii* (4.81 year^{-1} ; Fig. 4). The variability

within a species can be as large as that across the seagrass flora, and there can be considerable variability between years and sites in the rate of recruitment of new shoots into populations (Durako, 1994; Marbà et al., 1996b). Hence, for the relatively large species *Thalassia testudinum*, characterized by moderate rates of vegetative shoot formation, annual recruitment can vary from 0.01–1.30 year⁻¹ among populations (Peterson and Fourqurean, 2001). Despite the very low rates of vegetative shoot production in the large seagrass species, however, the much longer shoot life-span of these species ensure a close balance between shoot recruitment and losses in stable populations.

Vegetative rather than sexual recruitment is generally considered the primary mechanism to the maintenance of shoot density within closed seagrass vegetation. Firstly, the sexual reproductive effort is low in many seagrass species, the proportion of shoots that flower being generally less than 10%, and seed set occur irregularly in many populations (Duarte et al., 1997b; Durako and Moffler, 1985; Marbà and Walker, 1999; Campey et al., 2002). Secondly, large plants suppress the growth of small ones, such that the entry of new sexual recruits inside areas occupied by adult genets can be expected to occur only when established individuals are lost and vacate space. Most information of seedling recruitment and establishment come from studies performed outside established vegetation where it is less problematic to discern sexual recruits from shoots derived from already established clones. However, these studies suggest low survival rates of seeds and newly established seedlings (Hootsmans et al., 1987; Duarte and Sand-Jensen, 1990a; Harrison, 1993; Kirkman, 1998; Kaldy and Dunton, 1999; Balestri and Cinelli, 2003) supporting the contention that successful sexual recruitment events must be rare within closed vegetation.

Even though vegetative shoot formation is the dominant reproductive mode in seagrass meadows, large differences in recruitment strategies among species (Inglis, 2000) and considerable variation in spatial and temporal extent of seed production suggest that sexual recruitment can play a potential role in meadow maintenance, particularly in populations where the risk of adult mortality is high, leaving open space available for seedling establishment and growth (see Orth et al., Chapter 5). In the *extant*, studied seagrass *Zostera marina*, the reproductive effort is highly plastic and populations adopting an

annual growth strategy, typically in physically harsh environments, produce significant number of seeds (>20,000 seeds m⁻²) and regenerate completely from seeds each year (Harlin et al., 1982; Phillips et al., 1983; Phillips and Backman, 1983; van Lent and Verschuure, 1994). Also, the ability to accumulate *reserves* of persistent seeds inside the parent meadow of some of the small, shorter-lived seagrass species producing poorly-dispersed seeds (e.g. *Cymodocea nodosa*; Terrados, 1993 and *Halophila* spp; McMillan, 1988; Kuo et al., 1993; Preen et al., 1995; Kenworthy, 2000; also see Ackerman, Chapter 4 and Orth et al., Chapter 5) may promote meadow persistence following natural senescence of plants or disturbances by recruiting new sexual propagules. Hence, the relative importance of sexual and asexual shoot recruitment to meadow maintenance may vary considerable among species and environments. While sexual recruitment can be critical for meadow maintenance in highly disturbed and extreme environments inhabited by small shorter-lived seagrass species, the quantitative importance of sexual recruitment in meadows of larger and longer-lived species is low relative to asexual recruitment and seeds primarily contribute to the establishment of new patches.

B. Shoot Mortality

Specific shoot mortality rates range greatly both across seagrass species (Hemminga and Duarte, 2000) and across meadows for any one species (Marbà et al., 1996b; Peterson and Fourqurean, 2001), from lowest values of 0.06 year⁻¹ (i.e. 6% of shoots dying in a year) for a stand of the long-lived Mediterranean seagrass *Posidonia oceanica* to a maximum estimated mortality rate of 4.47 year⁻¹ for *Cymodocea nodosa* (Fig. 4). These shoot mortality rates incorporate two additive components, a baseline mortality corresponding to an internally-controlled mortality rate necessary to maintain shoot turnover, and a component derived from stresses and disturbances to the meadows.

Shoot mortality is not only a prominent component of the dynamics of seagrass meadows, but is indeed a necessary one. In an established, steady meadow, the continuous recruitment of seagrass shoots resulting from branching processes cannot be sustained without a parallel mortality of shoots, as crowding would otherwise impare recruitment. Shoot mortality is, however, insufficiently

understood, and the causes of shoot mortality have not been elucidated as yet. Shoot mortality is a necessary component of the maintenance of stable seagrass meadows, so that the presence of a stress factor need not be invoked to account for shoot mortality. These thoughts suggest that, to some extent, shoot mortality should be considered a component of clonal integration, such that a clone may selectively 'decide' to cease the activity of a particular leaf-producing meristem, thereby causing shoot death. Whereas the activation of seagrass meristems in response to disturbance, such as increased branching rates (i.e. shoot production) in response to clipping of apical rhizome meristems (Terrados et al., 1997), have been examined, the internal controls on loss of meristematic activity have not been addressed, as yet. More importantly, there is a need to examine what factors may cause the death of apical meristems, which would reduce shoot recruitment. The understanding and capacity to predict meristematic activity may provide the capacity to detect stress and forecast mortality before this is reflected in shoot density changes.

Hence, most knowledge on the controls on shoot mortality derives from examination of stress and disturbance factors. Reduced water and sediment quality leads to shoot mortality, often resulting in catastrophic seagrass loss through multiple factors. Deterioration of water quality leads to seagrass mortality through light limitation and unbalanced plant carbon budgets (e.g. Gordon et al., 1994; Ruiz and Romero, 2001). Shoot mortality as a consequence of reduced light penetration has been reported at the depth limit of seagrass meadows (Krause-Jensen et al., 2000), and confirmed by shading experiments (Gordon et al., 1994; Ruiz and Romero, 2001). Increased nutrient inputs have also been shown to be associated to high mortality rates (Pérez et al., 1994). Deterioration of sediment conditions, such as increased sediment anoxia and sulfide production has been shown to lead to seagrass mortality, although the responses vary greatly across species (Terrados et al., 1999). Water column hypoxia, also derived from excessive organic inputs, has also been identified as a factor affecting the health of leaf-bearing meristems, and eventually causing shoot death (Greve et al., 2003). Sediment disturbance, such as excessive burial and sediment erosion, also causes shoot death by killing meristems, altering clonal integration, and, when extreme, creating topographical barriers (Marbà and Duarte, 1994, 1995;

Duarte et al., 1997a). Physical disturbance is also an important source of shoot mortality, through uprooting of the plants during storms or due to human activities such as anchoring, dredging, anchor damage, and trawling (Duarte, 2002). Biological disturbance may also generate substantial seagrass mortality (e.g. Orth, 1975).

C. Shoot Demography

It is possible to estimate the age of individual shoots of most seagrass species because there is a relatively constant rate of production of new leaves on a shoot, called the **plastochron interval**. Each leaf leaves a distinctive scar on the short shoot at the node, so it is possible to count the number of leaves produced over the lifespan of an excavated shoot and multiply this number of leaves by the plastochron interval to estimate the age of the shoot (Patriquin, 1973; Duarte et al., 1994). Once recruited into the population, shoots of different species have different average lifespans. Shoots of the small, fast-spreading species, like *Halophila* spp., have an average lifespan of only a month or so, and a maximum age of a few months (Table 1). In contrast, the shoots of the larger, slower-spreading species like *Posidonia* spp. and *Thalassia* spp. have average life expectancies of a few years, with some shoots surviving for decades. A genetically individual plant may be much older than individual short shoots, since most seagrasses exhibit monopodial or sympodial growth. As a rhizome grows through the soil and produces new shoots, each successive shoot is necessarily younger than the previous shoots. Older shoots may eventually senesce, but their progeny shoots may continue thriving and extending away from the point where a seedling originally produced the genetically individual plant. Theoretically, genetic individuals could be as old as the origin of the species, even though individual shoots can only survive a few decades at most.

Seagrasses, as angiosperms, are all capable of sexual reproduction through flowering and seed production (although sexual structures have not been observed for all species, e.g. Jewett-Smith et al., 1997). As long as seeds result from the fertilization of an ovule by pollen from another genetically distinct individual, the plant originating from that seed is genetically distinct from others in the population. Once a seedling becomes established in a seagrass meadow, it begins to grow up by the production of

photosynthetic leaves, but also out by the production of new plant modules consisting of a length of rhizome, associated roots, and a shoot. The branching pattern created by the production of new modules varies from many-branched plants that expand almost equally in two dimensions (e.g. *Posidonia oceanica*) to plants that extend almost exclusively linearly through space (e.g. *Thalassia testudinum*). Eventually, through the action of either senescence of modules or disturbance, these individuals can become physically separated so that what was once one plant can become many isolated plants—but all of these plants are genetically identical—i.e. they are parts of the same genetic individual (i.e. genet).

So, when studying the dynamics of seagrass populations, it is important to keep in mind that what appears above the sediments as a shoot is likely connected to many more shoots underground. And, merely because two shoots do not share a common connection somewhere under the sediments is no indication that these shoots are genetically different. In fact, there is molecular evidence for genetically identical shoots of *T. testudinum* separated by over 3 km in an otherwise genetically diverse, continuous seagrass bed (Davis et al., 1999). A more thorough discussion on this topic is provided in Waycott et al. (Chapter 2, this volume).

New genets can enter a population not just through successful seedlings, but also as adult plant fragments that may drift into a population from some distant source (Setchell, 1929). Seagrasses can float and survive for extended periods out of the sediment; apparently viable modules of the tropical seagrass *Thalassia testudinum* can occasionally be found on the temperate beaches of the North Carolina in the US (JWF, pers. observ), over 1000 km from the nearest known *T. testudinum* populations. Seagrass shoots can survive for months in the water column, but the ability of detached shoots to survive when transplanted decreases with time in the water column, limiting the potential of drifting adult plants to establish new seagrass beds (Ewanchuk and Williams, 1996). Floating seagrass shoots not only have some potential to become reestablished and expand via asexual reproduction, but they can also carry viable seeds (Harwell and Orth, 2002; Orth et al., Chapter 5) and epiphytes (Worcester, 1994) to distant locations. The role of vegetative fragments as vectors for colonization has likely been underestimated in seagrass ecology, as these are rare events, that chal-

lenge direct observation, although direct evidence of widespread establishment by fragments has been recently reported (Campbell, 2003).

Although there are mechanisms to provide genetically unique recruits to seagrass populations, the importance of these mechanisms in producing new shoots in seagrass beds is considered low compared to the asexual ramification of plant modules by clones already extant in populations (Tomlinson, 1974). For most species, observations of successful seedling recruitment are rare (Orth et al., Chapter 5). However, the study of sexual recruitment in established populations is complicated by the difficulty in distinguishing whether shoots are derived from a single seed or from fragmentation of a larger clone (cf. Waycott et al., Chapter 2). Moreover, it is possible that the perception that successful seedling recruitment is a rare event may be dependent on insufficient observational effort, as this process may occur over significant spatial and temporal scales that challenge conventional sampling strategies.

D. Predicting Population Dynamics Using Shoot Demography

Most monitoring programs are inefficient at detecting and predicting change in shoot density, because such change can occur either precipitously (e.g. Robblee et al., 1991) or be too gradual to be detected within the typically broad error margins of density and cover estimates used in most monitoring programs (Heidelbaugh and Nelson, 1996). There is, therefore, a demand for approaches to quantify the components of seagrass population dynamics with the aim of allowing an evaluation of their status and an ecological forecast of possible future trends. Recently, the analysis of age structure data to infer population growth rate has been applied to seagrass beds using what has come to be known as the 'reconstructive technique' (Duarte et al., 1994), which has been applied to multiple species since (e.g. Kenworthy and Schwarzschild, 1998; Marbà and Walker, 1999; Guidetti, 2001; Peterson and Fourqurean, 2001).

Population dynamics reflect the balance between immigration, emigration, recruitment, and mortality, and the various factors that affect these gains and losses. For any closed population, the population growth rate per individual (r) is the difference

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between the per capita birth rate (Recruitment, R) and death rate (Mortality, M):

$$r = R - M \quad (1)$$

Knowing R and M , then, would allow for predictions of r . In concept, it should be a simple procedure directly to observe the production of new shoots and the death of others from a regularly-visited portion of a seagrass meadow. In practice, however, these observations have proven difficult to make because of the multiple visits required, the substantial time required to mark shoots in very dense, often deep stands, and the extended life span of many of the target seagrass species (e.g. *Posidonia* spp, *Thalassia* spp, cf. Hemminga and Duarte, 2000).

Within the limits imposed by some simplifying assumptions, it is possible to estimate R and M by analyzing the age structure of a population of seagrass shoots. The model generally used by seagrass ecologists (cf. Duarte et al., 1994; Peterson and Fourqurean, 2001) to estimate M from age structure data is:

$$N_x = N_0 e^{-Mx} \quad (2)$$

where N_x is the number of shoots in age class x and N_0 is the number of shoots recruited into the population (cf. Duarte et al., 1994). But, the rather restrictive assumptions of applying this model to seagrass shoot age structure data (Jensen et al., 1996; Kaldy et al., 1999; Ebert et al., 2002) require caution and an understanding of the implications of violations of these assumptions in application. Most importantly, this analysis assumes a stable age distribution (and, therefore, that $R = M$), a condition which cannot be verified a priori, and age-independence of R and M . This approach has been successfully applied (constrained by the same assumptions) to a wide variety of organisms, for example: mosses (Økland, 1995); marsh plants (Sutherland and Walton, 1990); bamboo (Taylor and Zisheng, 1993); mangroves (Duarte et al., 1998); terrestrial trees (Szeicz and MacDonald, 1995; Kelly and Larson, 1997). In fisheries research, analyses such as these are called 'catch curve' analyses (Ricker, 1975; Quinn and Deriso, 1999) and have been widely applied [e.g. larval sciæenids (Flores-Coto et al., 1998); tropical gobies (Kritzer, 2002)].

In the case where $r \neq 0$, and therefore $R \neq M$, application of Eq. (2) is not appropriate (Ebert et al., 2002). Instead, a more general model of the form:

$$N_x = N_0 e^{-(M+r)x} \quad (3)$$

is appropriate (Fourqurean et al., 2003). But, since the methods explicitly assume that M and R have remained constant over the lifespan of the oldest individuals in the population, how can this method logically be used to predict changes in r for the population? In reality, using a regression approach to estimate N_0 and R assumes that M and R have had no trend over the lifespan of the oldest shoots in the population, with year to year random variation around some mean value of M and R . So not only does the regression approach result in an estimate of the long-term mean R , but it provides statistical confidence limits for this estimate (Fig. 5). Hence, whereas the reliability of the estimates of R and M are dependent on the validation of the assumptions, which are always cumbersome, relevant information can still be extracted which is informative of the demographic dynamics of the populations. Similarly, forecasts derived from the examination of past demographic dynamics have to be taken with caution, provided that there is no guarantee that the underlying rates will remain constant in the future. This is however, a limitation inherent to any forecasting approach.

Besides this estimate of a long-term average recruitment rate, the age structure also yields an estimate of the recruitment for the year the population was sampled (R_0):

$$R_0 = \ln N_t - \ln N_{x>0} \quad (4)$$

where N_t is the total number of shoots in the population and $N_{x>0}$ is the number of shoots older than 1 year (Duarte et al., 1994; Short and Duarte, 2001).

From each age distribution, then, come two estimates of R (R_0 , which is an estimate of the current recruitment rate, and the long term mean R). If one assumes no trend in M over the lifespan of the oldest shoots in the population, then a comparison of these two estimates can predict whether r (Eq. 1) for the current year is different from the average r over the lifespan of the oldest individuals in the population. Because the regression analysis provides confidence limits about the long-term mean R , such differences

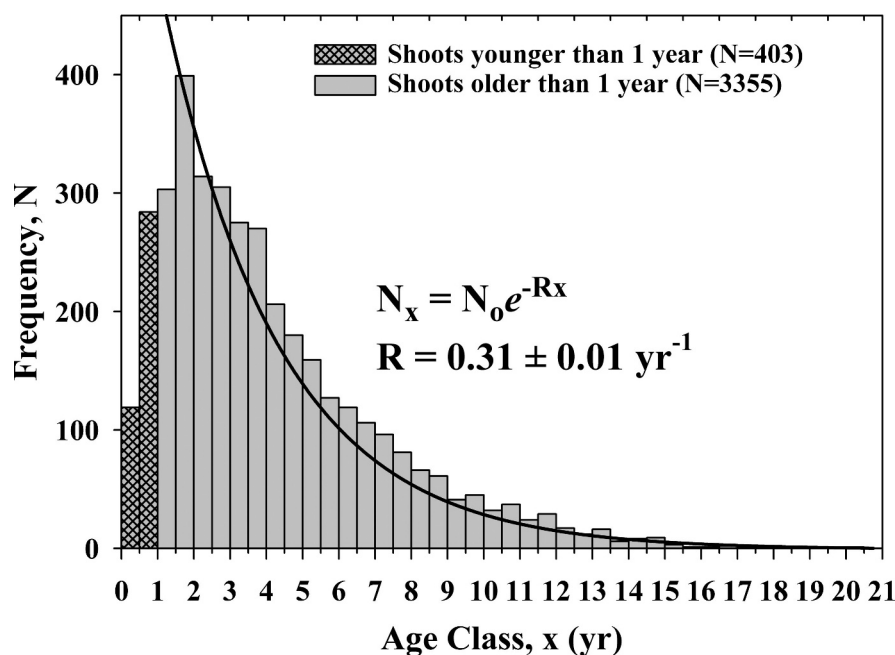


Fig. 5. Graphical depiction of the techniques used to calculate demographic information from age structure data. These data are ages of 3,758 short shoots (N_t) of *Thalassia testudinum* collected from south Florida in 2001. The current year's recruitment, $R_0 = \ln(3,758) - \ln(3,355)$, or 0.11 year^{-1} . The exponential decay model indicates the long-term average R to be $0.31 \pm 0.01 \text{ year}^{-1}$, indicating that recruitment in the year the shoots were collected (R_0) is significantly less than the long-term average recruitment. If the size of the population has been stable over the lifespan of the oldest shoots in the population (20 year in this case), then the long-term average $R =$ long-term average M , and therefore we should expect this population to shrink by 20% this year (i.e. $r = R_0 - M$, or $0.20 \text{ year}^{-1} = 0.11 - 0.31 \text{ year}^{-1}$).

can be tested statistically—but it should be noted that the accuracy of the prediction of the long-term mean R is dependent on the number of age classes, so that the method will derive more robust estimates for long-lived species (Fourqurean et al., 2003).

In addition to the comparison of present recruitment (R_0) relative to the long-term mean recruitment, ecologists can, through a residual analysis of the age class distribution against the assumed exponential decline in shoot number with increasing age (cf. Durako and Duarte, 1997), detect particularly bad and good years for the population in the form of fewer or greater shoots than expected for a particular age class. These inferences are more robust as the sample size used to build the age distributions increases, and reasonable estimates can be obtained at sample sizes in excess of 200–300 shoots. Examination of seagrass shoot age distributions provide useful assessments of the status of the stands and ecological forecasts, which inform of the likely trends in the population—but not numerical predic-

tions, which predict the actual population size—of the future trends of the stands, assuming that the relation between the present year's R_0 and the long-term mean R were to persist. Improved forecasts or predictions require direct estimates of dynamic population parameters.

By following the 'birth' and death of shoots in tagged populations, direct estimates of M , R , and r can be derived (Short and Duarte, 2001), free of the assumptions required to derive estimates from age distributions. Direct censuses, however, are demanding of time and effort, for shoots have to be tagged individually in the field and relocated repeatedly. Moreover, individual tagging is difficult for small, fragile species, such as *Zostera noltii*, as well as in adverse environments, such as very deep or very turbid ones, and is easiest for longer-lived species, such as *Posidonia oceanica* and *Thalassia testudinum*. Large-scale assessment of seagrass population dynamics through direct censuses is, however, possible, as demonstrated by Marbà et al. (2003).

IV. Clones and Patch Dynamics

A. Processes of Patch Formation

The spatial structure of seagrass populations is highly variable among sites ranging from extant, nearly continuous meadows to meadows that are highly fragmented and arranged into a mosaic of discrete patches. Patchy seagrass vegetation often reflects processes of recovery from disturbances, whether natural or human-induced, that occurred at different times in the past, as well as the particular hydrodynamic conditions of the seagrass habitats (cf. Bell et al., Chapter 26). Seagrass meadows have, therefore, not only spatial but also temporal dynamics involving the continuous recruitment, expansion, and mortality of patches. Hence, knowledge of these dynamic properties is essential to gain insight into the dynamics and persistence of seagrass populations.

Patches may result from fragmentation or colonization processes. Loss of seagrass cover may lead to fragmented beds resulting in a patchy, rather than continuous meadow distribution. Alternatively, patches may result from a colonization process, where propagules, whether established seeds or vegetative fragments initiate clonal growth, thereby producing a patch. Patch formation through seedling establishment has been well documented (e.g. Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994b; Vidondo et al., 1997), although estimates of patch formation rates are still few. In contrast, patch formation through the anchoring of detached vegetative fragments has received limited attention (e.g. Campbell, 2003), although it may be an important process for seagrass patch formation.

Seedling establishment is a precondition but not a sufficient condition for patch formation, as available evidence suggests that many seedlings may die without ever producing patches (e.g. Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994; Olesen et al., 2004). For instance, a study of a *Cymodocea nodosa* population growing in a patchy lagoon showed that only small fractions of established seedlings initiated patch formation through clonal growth (Duarte and Sand-Jensen, 1990a). Failure to initiate clonal growth was attributed, in this particular population, to nutrient limitation (Duarte and Sand-Jensen, 1996).

B. Patch Growth and Loss

Seagrass patch growth proceeds by the horizontal extension of rhizomes at the patch edge and the subsequent branching and vegetative production of new shoots at the rhizome apex to fill out the open space between expanding rhizomes. The branching frequency and the angle between the horizontal rhizome and the rhizome branches that are formed on it are, therefore, important determinants of the capacity to spread in two dimensions (Marbà and Duarte, 1998). However, the main controlling factor on the patch growth rate is the elongation of horizontal rhizomes, extending the patch through its periphery. Realized patch growth rates may be lower than the potential rates set by rhizome extension rate whenever sediment dynamics and hydrodynamics interfere with plant growth or create disturbance (cf. Bell et al., Chapter 26).

The elongation rate of horizontal rhizomes is species specific (Table 2) and range from about 2 cm year⁻¹ in the large slow-growing species as *Enhalus acoroides* and *Posidonia oceanica* to more than 300 cm year⁻¹ in small fast-growing species as *Halophila ovalis* (Duarte, 1991; Marbà and Duarte, 1998). The close, negative scaling between rhizome elongation rates and seagrass module size, suggests that shoot size is a strong predictor of patch extension through clonal growth for the different seagrass species.

The maximal rate of rhizome growth sets the upper rate of patch extension possible although this capacity is not necessarily realized in natural patches. Seagrasses display considerable plasticity in formation rates and size of modules (Duarte, 1991). Variability in rhizome growth often has a distinct seasonal pattern, particularly in temperate and subtropical climates, where rhizome growth is minimized during **winters** as a result of low light and temperature conditions. Rhizome growth can also be expected to respond to resource **availability**, e.g. through enhanced elongation rates in deep growing stands, thereby reducing internal self-shading by increased distance between neighboring shoots (Olesen et al., 2002). This response pattern does not apply to all species, however, and experimental evidence is needed to evaluate the adaptive significance of seagrass rhizome growth to various environmental conditions.

Patch growth may also be affected by intrinsic factors and has been found to accelerate with patch size and age (Duarte and Sand-Jensen, 1990a; Vidondo et al., 1997). In a study of *Cymodocea nodosa* the rate of lateral extension increased with patch size and shoot number in an exponential manner whereas isolated single shoots survived for several years without developing into patches (Vidondo et al., 1997). Such positive effects of increasing patch size are probably linked to reduction of water movement and increased sediment stabilization as patches grow in size (Fonseca et al., 1983). Moreover, the gradual formation of physiologically integrated shoot systems through clonal growth enhances the potential translocation of resources from older shoots on the rhizomes to the apical shoots at patch edge (Terrados et al., 1997). Such a growth pattern has not, however, been found for *Zostera marina* (Olesen and Sand-Jensen, 1994b) or for *Z. novazelandica* (Ramage and Schiel, 1999), presumably because of the slower horizontal growth of these species resulting in densely packed patches near edge and relatively high nutrient availability at the study sites.

Whereas patch extension is governed by the capacity for rhizome growth there are no constraints on patch recession or mortality. Net growth of patches can be substantially lower than expected from the potential rhizome growth due to loss processes caused by physical and biological disturbance agents. Hence, sediment reworking by burrowing animals can cause disruption of the patch edge (Philipart, 1994; Townsend and Fonseca, 1998) and the erosion of patches at windward margins represents significant disturbances to inhibit expansion of seagrass patches or to cause recession (Fonseca and Bell, 1998). Restriction of patch expansion by the exposure to high flow velocity and the predominantly growth of patches in the shelter, greatly influence the shape and heterogeneity of patches (Fonseca et al., 1983). Accordingly, patch edges are expected to be highly dynamic as confirmed by the high rates of shoot mortality and recruitment found at patch margin compared to inside the patches (Duarte and Sand-Jensen, 1990b).

Disturbances above a certain magnitude are also a common source of patch mortality and even large meadows can disappear during extreme storm events (e.g. Orth and Moore, 1983; den Hartog, 1987). The mortality risk is size-dependent and patch losses are often confined to the smaller patches below a certain threshold size, presumably defined by the species in-

involved and the disturbance regime within the study area (Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994b; Vivondo et al., 1997; Ramage and Schiel, 1999). These negative effects of size are probably linked to lack of mutual protection and firm anchorage leading to higher susceptibility to physical disturbances and nutrient stress in small patches. Consequently, patch formation from seeds is typically very inefficient due to high seed and seedling mortality and often less than 10% of newly established seedlings survive past their first year (Churchill, 1983; Duarte and Sand-Jensen, 1990a; Harrison, 1993; Kaldy and Dunton, 1999) although higher survival probabilities have been reported in some populations of *Zostera marina* (24%, Olesen and Sand-Jensen, 1994b) and for *Enhalus acoroides*, and *Thalassia hemprichii* (19 and 22%, Olesen et al., in press). Moreover, the probability of newly established patches to reach a large size is low as small patches are subject to rapid turnover as indicated by positively skewed patch size distribution that is frequently found in patchy seagrass stands (e.g. Vidondo et al., 1997). The production of sexual and vegetative propagules remains the term that maintain the positive side patch production, of the patch dynamics, thereby ensuring the recovery and formation of seagrass meadows.

C. Resulting Patch Dynamics

The spatial and temporal dynamics of seagrass patches is strongly influenced by the magnitude and frequency of physical disturbances in a given area and by the capacity of the species involved to persist and recover from disturbances. Some seagrass populations experience continuous patch extinction and replacement, which maintain the vegetation in a permanent state of colonization and promote the development of a mosaic of patches of different age and developmental stages (Duarte and Sand-Jensen, 1990a; Olesen and Sand-Jensen, 1994b; Vidondo et al., 1997). When in balance, such populations will maintain a dynamic equilibrium with a uniformity of patch distribution in time and space such that an overall landscape equilibrium of patches applies. This has been demonstrated for *Cymodocea nodosa* growing on highly mobile sediments where the time interval between the passage of consecutive sub-aquatic sand dunes allowed a close balance between loss of vegetation caused by erosion and burial

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and the formation and development of new patches (Marbà and Duarte, 1995).

The dynamic properties of seagrass patch formation and subsequent growth and survival are essential to the recolonization process in denuded areas. The more than 10-fold span across species in rhizome elongation rates and reproductive effort, defining an upper limit for patch formation from seed, suggests contrasting capacities to recover from disturbances (Duarte et al., 1997b; Marbà and Duarte, 1998; Marbà and Walker, 1999). Small seagrass species exhibit potential fast patch growth and clonal growth of these species is held responsible for much of the temporal dynamics observed following small-scale disturbances (Williams, 1990; Duarte et al., 1997b). Sexual reproduction is, however, still essential for the recovery of small seagrasses (e.g. Kenworthy, 2000). Nevertheless, some of the larger seagrass species (e.g. *Zostera marina*) with slow elongation rates can achieve high colonization potential by having high reproductive effort (Verhagen and Nienhuis, 1983). In contrast the combination of very slow clonal growth and poor ability to set seeds in other large species (e.g. *Posidonia oceanica* and *P. sinuosa*) suggest these to be restricted to slow patch growth and an extremely slow recovery process (Duarte, 1995).

Small seagrass species also tend to produce more seeds per ground area than large species and have the ability to build up persistent seed banks whereas large species typically produce seed with no or limited dormancy (Kuo and den Hartog, Chapter 2). However, the rate of patch formation from seeds does not necessarily bear a simple relationship to seed production but is also influenced by loss processes acting on seeds and seedlings and by the seed dispersal capacity (Orth et al., Chapter 5). In a recent study (Olesen et al., 2004), the importance of contrasting reproductive strategies to recovery dynamics was studied over 2.5 years on a mixed-species Philippine seagrass meadow by following patch formation, growth, and mortality in a disturbed gap area (1200 m²). Different species were involved in sexual vs. colonization as the large species *Thalassia hemprichii* and *Enhalus acoroides* with slow clonal growth but relatively high production of large, broadly dispersed seeds were the major contributors to colonization in areas devoid of vegetation. Although seedling turnover was rapid the high frequency of sexual recruitment (*T. hemprichii* 0.052–1.31 m⁻² year⁻¹ and *E. acoroides* 0.043–0.081 m⁻²

year⁻¹) allowed the successful formation and development of new patches and subsequent patch extension through clonal growth. In contrast the small fast-growing species *Cymodocea rotundata* and *Halodule uninervis* with limited seed dispersal ensured rapid clonal extension (>1.5 m year⁻¹) of surviving patches in areas where disturbances had only removed part of the existing flora. Hence, the scale of area affected by disturbance and its interaction with the reproductive strategy of the contrasting species involved is fundamental to the recovery dynamics of seagrass communities.

V. Gap Dynamics

In seagrass species that form extensive meadows, intense but localized disturbances can cause scars in the meadow that are akin to canopy light gaps in forests. Gap dynamics is a key component of seagrass dynamics (Bell et al., 1999), as gaps are produced often through physical and biological (e.g. Nakaoka and Aioi, 1999) disturbances. In such gaps, the death of later-successional, better competitor species through many different mechanisms can provide small gaps that allow space for the recruitment of new individuals into the forest. As there is often an inverse relationship between competitive ability and colonization potential, the first colonizers to these gaps are generally species that will, through time, be replaced by the original superior competitor (see Pickett and White, 1985 for a detailed treatment of forest light gaps). In *Thalassia*-dominated seagrass beds of the tropical Western Atlantic, small scale physical disturbances caused by wave action or herbivory can remove the dense *Thalassia* canopy and provide room for calcareous macroalgae and faster-growing seagrasses like *Halodule wrightii* and *Syringodium filiforme* to become established (e.g. den Hartog, 1971; Patriquin, 1973). These features tend to erode at one end and fill in at the other, thereby slowly moving through space in a direction determined by the predominant wave and current regime. At the trailing edge of these 'blowouts', the rapidly colonizing species are replaced by *Thalassia testudinum*, as new ground for the early successional species is cleared at the leading edge by continued erosion. Disturbances like this allow for the coexistence of competitively inferior species in a landscape dominated by a superior competitor. The blowouts in seagrass meadows are very similar to the

wind-induced migrating wind-throws responsible for the 'wave-regenerated' evergreen high-latitude forests, in which gaps in the forest generated move slowly upwind at a rate of 1–3 m year⁻¹ as old trees succumb to wind fall and younger trees recruit into the space cleared by the wind falls (e.g. Cooper, 1913; Sprugel, 1976). As gap formation and closure are not synchronized in the meadow, a mosaic of different stages of gap dynamics may be encountered in a meadow, maintaining a mosaic of species diversity in the meadow (Duarte et al., 2000). There are, of course, exceptions to this simplified successional pattern, as pioneer species may sometimes develop strategies, such as the formation of a three-dimensional canopy, preventing their exclusion (Fourqurean et al., 1995).

The closure of gaps is primarily dependent on clonal processes, through the extension of rhizomes of the plants at the periphery of the patches onto the gap, as demonstrated by multiple examinations of gap dynamics, including experimental approaches (e.g. Williams, 1987; Rasheed, 1999), as well as observations of recovery of gaps following disturbance, such as those produced by propellers (e.g. Andorfer and Dawes, 2002; Kenworthy et al., 2002).

VI. Dynamics of Seagrass Meadows at Different Time Scales

A. Disturbance

As seagrass meadows provide a variety of ecosystem services, there is much focus on the range and time scales of their variability. At a given site, this variability reflects the frequency and magnitude of disturbances relative to the capacity of the species to resist and recover. Disturbances can be natural or human-induced and are defined here as factors preventing seagrasses from reaching their maximum potential abundance. Natural disturbances most commonly responsible for seagrass loss include extreme climatic events (such as hurricanes) and biological interaction such as diseases, grazing, and bioturbation, while the most common human-induced disturbances are eutrophication, leading to reduced water clarity and quality, and dredging, filling, and certain fishing practices causing direct physical damage (see review by Short and Wyllie-Echeverria, 1996). Changes in light conditions, temperature, and water level, due to climate changes, are

also likely to affect the world's seagrass meadows both directly and indirectly and cause large-scale variations, but this aspect is not treated separately here (for further discussion see Walker et al., Chapter 23, and Ralph et al., Chapter 24). Tolerance toward disturbances as well as growth and recolonization potentials differ among species and various seagrass species therefore show different temporal and spatial dynamics.

While individual seagrass shoots have a life span of weeks or decades depending on species, meadows, and clones may in extreme cases persist for centuries or millennia (Reusch et al., 1999; Hemminga and Duarte, 2000). Hence, studies on temporal dynamics of seagrasses tend to focus on different attributes depending on the time scale of interest. Seasonal studies often involve a small spatial scale and focus on attributes such as shoot density or biomass while long-term studies generally involve large spatial scales with focus on population attributes such as presence/absence or area cover. The following sections give examples of changes in abundance of seagrasses on seasonal and inter-annual time scales and discuss long-term perspectives. For further discussions on landscape dynamics of seagrass meadows, the reader is referred to the chapters by Bell et al., Chapter 26 and Walker et al., Chapter 23.

B. Seasonal Fluctuations

The biomass of seagrasses may change markedly over an annual cycle. A large-scale compilation of data from 14 seagrass species shows that, on average, 70% of the intra-annual variability in biomass of seagrasses reflects seasonal responses (Duarte, 1989). As seasonal variability in seagrass biomass is mainly regulated by changes in light and temperature associated with the solar cycle (Sand-Jensen, 1975; Perez and Romero, 1992; Alcoverro et al., 1995), it changes with latitude. In fact, there seems to be a latitude-dependent upper boundary to seasonal biomass variability rather than a simple linear coupling between the two parameters (Fig. 6; Duarte, 1989). Hence, temperate seagrass communities tend to show greater seasonality but also a wider range of seasonal responses than tropical and subtropical communities, which maintain a more stable biomass throughout the year. However, there is still substantial seasonal variability in some tropical and subtropical communities. In subtropical south

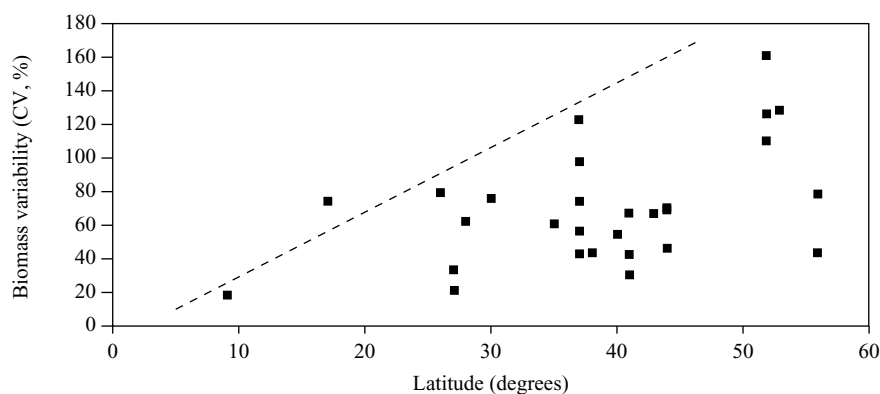


Fig. 6. Relation between the degree of biomass variability (as the coefficient of variation of mean annual biomass), and the latitudinal position of seagrasses. Broken line represents the suggested latitude-dependent boundary to biomass seasonality. Data represent 14 different seagrass species. Redrawn from Duarte (1989) with permission.

Florida, USA, (ca. 24° N) abundance and growth of *Thalassia testudinum* in summer and winter, respectively, are 30% higher than and 30% lower than the mean even at this relatively low latitude, but the seasonal variability decreases toward the equator and increases toward more northern latitudes (Fourqurean et al., 2001).

The seasonal forcing of light and temperature acts differently on different seagrass species. Growth patterns of the four Western Mediterranean seagrass species (*Cymodocea nodosa*, *Zostera noltii*, *Z. marina*, and *Posidonia oceanica*) thus exhibit species-specific differences in the timing and magnitude of seasonal fluctuations even though they experience the same seasonal forcing (Marbà et al., 1996a). These differences may be related to variations in the capacity of plants for storing and allocating resources among ramets. Both processes are positively related to plant size and should enable large seagrass species to grow more independently of environmental conditions than small species (Marbà et al., 1996a). In accordance with these expectations, the largest of the three seagrass species in the Adriatic Sea, *P. oceanica*, shows lower seasonal variation in biomass, shoot density, leaf area index (LAI), shoot weight, and above/belowground biomass than the two smaller species, *Z. marina* and *C. nodosa* (Guidetti et al., 2002). Hence, seasonal forcing seems to be buffered by the availability of internal resources stored in the belowground parts of *P. oceanica* but to be amplified by the lower capacity for storage and allocation in *C. nodosa* and *Z. marina* (Guidetti et al., 2002).

Seasonal variations in temperature may also impose species-specific threshold effects. For instance, the carbon balance of *Zostera marina* becomes negative at high temperature (Marsh et al., 1986) and high temperatures may therefore generate abrupt changes in seasonal growth pattern. At the southern distribution limit of *Zostera marina* in the Gulf of California, USA, where summer water temperatures exceed 25°C, eelgrass thus has an annual life cycle involving growth in winter and dieback in summer (Meling-Lopez and Ibarra-Obando, 1999).

Other seagrass parameters in addition to abundance also show a seasonal pattern that is most likely a direct consequence of the seasonality in carbon balance caused by light and temperature patterns. Growth rate is obviously seasonal, but so are leaf emergence rates (Peterson and Fourqurean, 2001) and flowering and asexual shoot production also show marked seasonal patterns.

C. Inter-Annual and Long-Term Fluctuations

Disturbances, whether natural or human-induced, local or regional, episodic or persistent, may blur the 'natural' seasonal pattern caused by changes in light and temperature and thereby create differences in distribution patterns between years. Whether variations in seagrass populations operate on short or long time scales depends on the intensity and persistence of disturbances, the recolonization potential of the population and the extent of negative feedback effects following the loss of seagrass biomass.

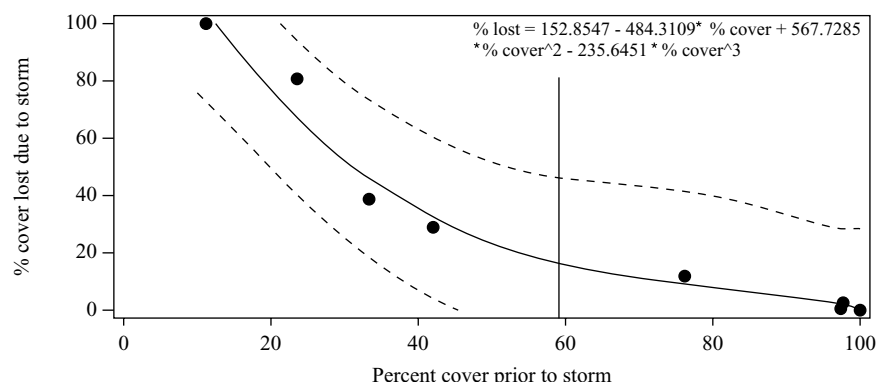


Fig. 7. Percent seagrass cover lost due to the March 1993 storm as a function of cover prior to the storm. Vertical line indicates 59% cover (see Fonseca and Bell, 1998), the theoretical level at which the transition from connected to discontinuous cover takes place. Regression is a cubic fit with 95% confidence limits. Redrawn from Fonseca et al. (2000) with permission.

Physical processes such as wave exposure and tidal currents are among the natural factors that influence the inter-annual variability of seagrass features on both shoot and landscape scales. For example, episodic sediment redistribution by hurricanes is reflected in the growth pattern of *Thalassia testudinum* as changes in length of short shoot internodes (Marbà et al., 1994b), and migrating subaqueous sand dunes induce similar changes in the growth pattern of *Cymodocea nodosa* (Marbà and Duarte, 1994; Marbà et al., 1994a).

On the landscape scale, high exposure and current regimes tend to reduce seagrass cover and increase the fragmentation of seagrass beds (Fonseca and Bell, 1998). A threshold seagrass cover of about 60%, which separates patchy seagrass meadows from large, uniform ones, also separates meadows that suffer structural losses during high-energy periods from those that are more stable (Fonseca and Bell, 1998). Patchy, high-energy beds therefore tend to be more vulnerable to the additional effects of extreme storm events such as hurricanes (Fig. 7; Fonseca et al., 2000). An extreme example of seagrass decline on the landscape scale occurred in Queensland, Australia, when a cyclone and two major floods struck the same area within a period of a few weeks and caused a loss of 1000 km² of seagrasses. Shallow populations were uprooted while deep populations died as a result of light deprivation caused by increased water turbidity. After 10 months, no recolonization was detected, but after 2 years marked recolonization from seeds had occurred in deep water (Preen et al., 1995).

As the intensity of physical exposure declines with depth, benthic habitats represent gradients of reduced physical harshness as well as reduced energy input to photosynthesis from shallow to deep water. So with increasing depth, seagrasses experience the contrasting influence of reduced mechanical disturbance, facilitating size development and long-term survival, and reduced light availability, restricting photosynthesis, and plant growth. As a consequence, intermediate water depths often show maximum levels of biomass or cover while shallow waters on wave-swept shores or deep, calm, more shaded waters exhibit reduced biomass (Dring, 1982; Krause-Jensen et al., 2003). In Øresund, Denmark, eelgrass shoot density responds to the vertical gradient by generating many small shoots in the exposed and illuminated shallow waters and fewer but larger shoots with increasing depth (Fig. 8; Krause-Jensen et al., 2000), and these differences create a higher inter-annual variability in shoot density in the shallow-water meadows as compared to the deep-water meadows (Middelboe et al., 2003).

While such patterns toward a greater variability of shallow, compared to deep stands hold within a species, deep seagrass meadows can exhibit intense dynamics whenever formed by fast-growing species. Indeed, *Halophila* species often produce extensive, sparse meadows toward the depth limits to tropical and subtropical stands (e.g. Josselyn et al., 1986; Williams, 1988). These deep stands also experience intense dynamics, due to both intrinsic factors, such as the annual life strategy and rapid rhizome growth of some of these small, fast-growing

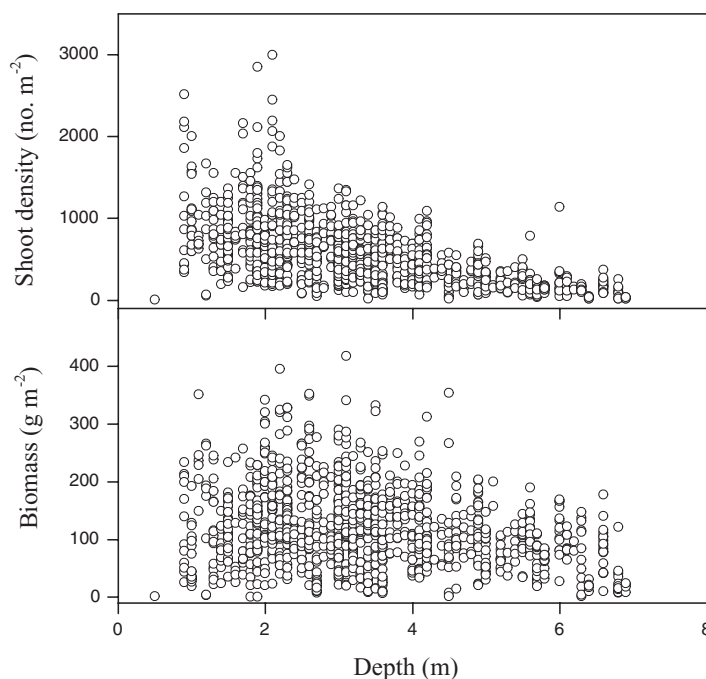


Fig. 8. Eelgrass shoot density (upper panel) and biomass (lower panel) as functions of water depth in Øresund, Denmark. Redrawn from Krause-Jensen et al. (2000) with permission.

species combined with extreme disturbances, such as severe storms and hurricanes reaching down to those depths (e.g. Williams, 1988; Kendall et al., 2004).

Diseases are another category of natural disturbances that may markedly affect the distribution of seagrasses. The world-wide wasting disease that struck *Zostera marina* in the 1930s is the most notable natural event causing long-term and large-scale decline in seagrass communities (Rasmussen, 1977; Short and Wyllie-Echeverria, 1996). Many populations, especially along the Atlantic coasts of Europe, the USA and Canada were completely eradicated (Muehlstein, 1989). The causative agent of the disease is thought to be the slime mould *Labyrinthula* sp. which has also more recently caused diseases to occur locally (e.g. Short et al., 1987).

Information on recolonization after the eelgrass wasting disease in the 1930s is scattered and mostly qualitative but indicates that large meadows were re-established during the 1950s and 1960s (Rasmussen, 1977). A recent study based on aerial photos from the period 1940s–1990s shows that shallow Danish eelgrass meadows subjected to the wasting disease exhibited a time lag of more than 10 years before substantial recolonization began, probably reflecting

long distances to seed-producing populations and extreme climatic events during that period. After the initial time lag, the eelgrass area increased rapidly and large recoveries had taken place in the 1960s (Fig. 9; Frederiksen et al., 2004). This time scale of 30–40 years corresponds well with model predictions of *Zostera marina* recolonization (Duarte, 1995). However, the distribution area of Danish eelgrass meadows still constitutes only about 25% of the area found around 1900 (Petersen, 1914; Boström et al., 2003). Increased coastal erosion in the period without eelgrass may have made some of the shallow habitats less suitable for eelgrass growth (Rasmussen, 1977) and thereby created a negative feedback loop of seagrass decline. Moreover, reduced water clarity has markedly reduced the potential vertical distribution range as compared to around 1900 (Ostenfeld, 1908; Boström et al., 2003).

Although only few types of herbivores graze directly on seagrasses, grazing may be yet another natural factor regulating seagrass meadows on both small and large scales, especially in subtropical and tropical regions. In the Mombassa Lagoon, Kenya, sea urchin grazing controls the density of the slow-growing seagrass *Thalassodendron ciliatum*

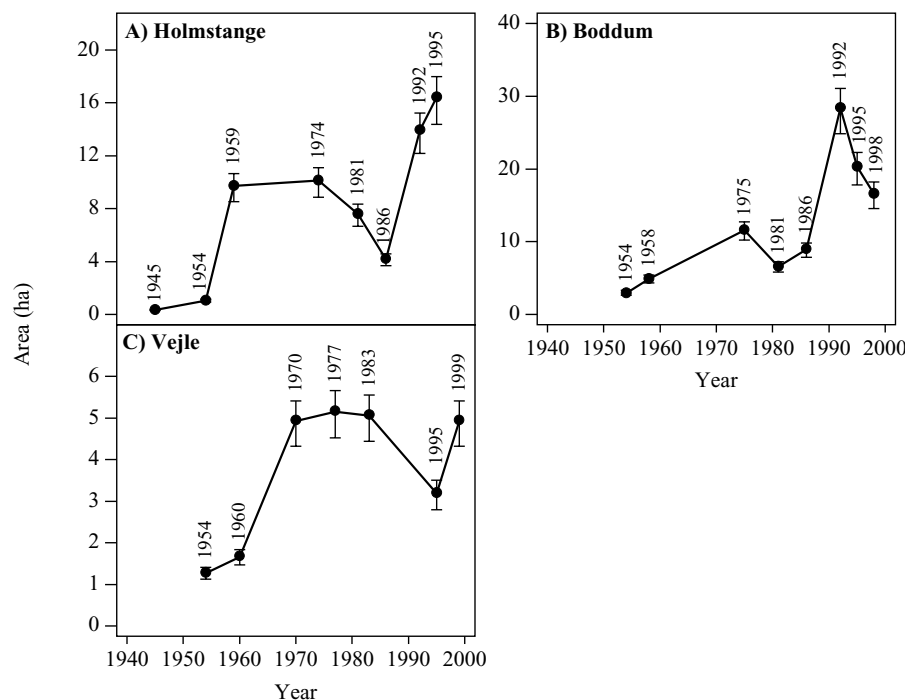


Fig. 9. Long-term changes in eelgrass area distribution at 3 sites subjected to the wasting disease in the 1930s. Eelgrass area distribution was assessed from aerial photos and digital image analysis. Error bars indicate maximum error of interpretation and represent the range between the minimum and the maximum estimate of seagrass cover as evaluated through digital image analysis. Redrawn from Frederiksen et al. (2004) with permission.

and thereby contributes to generating a patchy seagrass landscape with mixed meadows. An example from the outer Florida Bay and the Florida Keys shows that unusually dense populations of sea urchin (> 300 individuals m^{-2}) overgrazed and completely denuded a population of *Syringodium filiforme*. The large-scale loss of seagrass biomass initiated community-wide cascading effects that altered resource regimes and species diversity. The loss of seagrass canopy and subsequent death and decay of the belowground biomass destabilized the sediments. As the sediments eroded, turbidity significantly increased, reducing light availability and significantly reducing the sediment nutrient pool and depleting the sediment bank of *S. syringodium* seeds (Rose et al., 1999; Peterson et al., 2002). Explosions in populations of herbivores, such as sea urchins, have been reported from many ecosystems and may be the result of the removal of apex predators by fishing (Jackson et al., 2001).

Seagrasses also constitute the primary food for endangered grazers such as turtles and sea cows,

and these giant grazers may introduce marked fluctuations in the biomass and structure of seagrass meadows. In Moreton Bay, Australia, dugongs often graze in large herds at the same location for weeks or months and may thereby reduce the above-ground biomass of seagrasses by up to 96% (Preen, 1995). But following even intense grazing, recovery is usually rapid (months) because the distance between surviving tufts of seagrasses is generally small (< 1 m). Grazing may also influence the species composition of seagrass communities, e.g. by favouring pioneer species (Preen, 1995). In fact, the cessation of the plowing of the seafloor by the once abundant grazers must have profoundly altered the ecology of the formerly grazed seagrass beds, and some authors argue that this may have increased the vulnerability of seagrass meadows to recent disturbances (Jackson et al., 2001).

Reduced water clarity caused by increased nutrient inputs or suspended sediments is now the most serious cause of global seagrass decline, and has eradicated several tens of thousands of hectares

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of seagrass globally (Short and Wyllie-Echeverria, 1996). The newly published World Atlas of Seagrasses provides a global synthesis of the distribution and present status of seagrass meadows and documents that seagrasses are being steadily destroyed by the run-off of nutrients and sediments from land and by boating, land reclamation, dredging, and some fishing methods (Green and Short, 2003). Along with increased eutrophication, negative cascading effects upon the loss of seagrass biomass are common. These involve, for example, increased resuspension of sediments and thereby increased turbidity that further reduces seagrass abundance (Duarte, 1995). Moreover, the occurrence of anoxia during warm calm periods becomes more frequent as eutrophication increases (Rabalais and Turner, 2001) and may seriously affect seagrasses (Terrados et al., 1999; Greve et al., 2003) and cause diebacks (Rask et al., 2000; Plus et al., 2003).

One example of seagrass decline upon increased eutrophication is from the Dutch Wadden Sea. Both the fact that littoral eelgrass gradually disappeared after the mid-1960s and the fact that sublittoral eelgrass beds failed to recover from the wasting disease have been interpreted as responses to increased turbidity caused by eutrophication (Giesen et al., 1990). Florida Bay also experienced a serious loss of seagrasses over a decade (1984–1994), which was partly due to increased turbidity (Hall et al., 1999) and in Chesapeake Bay losses of *Zostera marina* and *Ruppia maritima* were also related to increased turbidity as a result of eutrophication (Orth and Moore, 1983). In Waquoit Bay, Massachusetts Short and Burdick (1996) related housing development and nitrogen loading to eelgrass habitat loss over the period 1987–1992 (Fig. 10). The effect occurred largely via ground water and resulted in a gradual fragmentation and loss of the meadows.

Examples of recolonization upon reduction of eutrophication are limited. The seagrass cover in Cockburn Sound, Western Australia, was markedly reduced between 1976 and 1981 as a response to eutrophication, but reductions in nutrient loads in the 1980s did not lead to recolonization (Walker et al., Chapter 23). It is likely that alterations in shelf-environments during the period without seagrasses have rendered the area unsuitable for seagrass growth (Kendrick et al., 2002). In contrast, *Posidonia coriacea* and *Amphibolis griffithii* have recolonized former seagrass areas in Success Bank, Western Australia, at surprisingly high rates in-

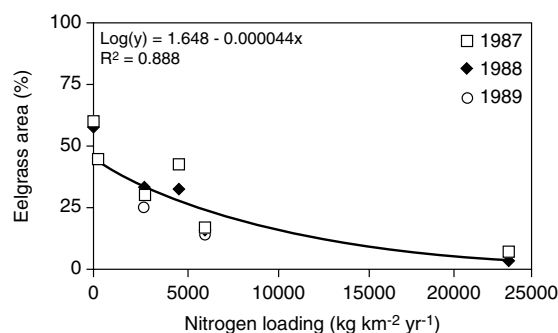


Fig. 10. Comparison of nitrogen loading rates and eelgrass area in the Waquoit Bay estuary's sub-basins over the first three years of study. The log of eelgrass area is regressed against loading. From Short and Burdick (1996), with permission from the Estuarine Research Federation.

volving both vegetative and sexual reproduction (Kendrick et al., 1999; Walker et al., Chapter 23). An extremely rapid eelgrass recolonization was also observed in the Archipelago of Southern Funen, Denmark. This area experienced an 80% reduction in the distribution area of eelgrass following an anoxic event during a warm summer period, but recovered completely within 3 years through a combination of vegetative growth of surviving shoots and germination of seeds (Rask et al., 2000). An even faster recolonization of *Z. marina* after anoxia-induced mortality was observed in the Thau Lagoon, French Mediterranean Sea (Plus et al., 2003).

Rapid recolonization seems possible if the disturbance causing the seagrass decline is limited in time and space and if seedlings originating from the sediment bank or from neighbouring populations experience suitable growth conditions the following year. By contrast, recovery of seagrass populations from catastrophic decline on the landscape scale requires patch initiation from seeds transported from distant populations and subsequent patch growth. The survival chances of these initial patch stages are low, and the formation of new extended patches may, therefore, be a protracted process. Simulation models show that small species with large recolonization potentials may recover within a few years after a disturbance, while large species with small recolonization potentials may require centuries to recover if the process is at all reversible (Duarte, 1995). Colonization may be further delayed or impeded by negative cascading effects (Duarte, 1995).

In many cases, declines of seagrass meadows are not detected before marked losses have occurred

either because surveys have been lacking or methods have been inefficient. Recording of depth limits is a relatively simple way of detecting declines in seagrass populations and as turbidity-related reductions in seagrass cover often affect the deep-water meadows most markedly, the method should be relatively sensitive. Methods involving measurements of population change based on rates of shoot recruitment and mortality have also proved sensitive and may allow early alerts (Duarte et al., 1994; Peterson and Fourqurean, 2001). A large-scale study of the Mediterranean climax species *Posidonia oceanica* thus showed that shoot recruitment does not balance shoot mortality, and the study predicted that shoot density will decline by 50% within 2–24 years if the present disturbance and rate of decline persist (Marbà and Duarte, 1997). These perspectives are serious, especially because meadows of *P. oceanica* represent a very old ecosystem dating back more than 6,000 years, and slow growth rates imply that recolonization may take centuries if the process is reversible at all (Duarte, 1995; Marbà et al., 2002).

VII. Prospect: Forecasting Seagrass Dynamics

The recent declines in seagrass populations worldwide (Green and Short, 2003; Walker et al., Chapter 23; Ralph et al., Chapter 24) accentuates the need for protecting these valuable ecosystems. As anthropogenic inputs to the coastal zone are the primary cause of the declines (Short and Wyllie-Echeverria, 1996), measures should be taken to reduce these inputs. The many examples of negative cascading effects upon the loss of seagrass biomass emphasize the need for taking action at an early stage.

Moreover, the accumulated knowledge on the mechanism of change and the dynamics in seagrass meadows should be formalized in models forecasting the dynamics of seagrass meadows, and their recovery times. Such models should include predictions of the closure of gaps within meadows. These forecasts are increasingly demanded by managers and our capacity to deliver them is still meagre. Much progress has been made in understanding the dynamics of seagrass meadows since the earlier accounts (den Hartog, 1971). However, although reliable models of clonal growth are now being developed, the prediction of recolonization rates at the landscape scale is cumbersome (cf. Bell et al.,

Chapter 26), as the contingencies of patch formation by sexual propagules or vegetative fragments dispersed into the area is essentially non-predictable. Rare events of long-range dispersal of seeds or vegetative fragments, which cannot be predicted, may play a pivotal role in the recolonization of areas away from any adjacent seagrass source (cf. Orth et al., Chapter 5, this volume). Indeed, current knowledge also indicates that the expectation that knowledge on rhizome extension and patch initiation could suffice to predict seagrass dynamics, by upscaling these processes to the landscape scale (e.g. Duarte, 1995), is unsupported, as evidence of the emergence of complex dynamics as these processes are brought to increasing scales accumulates (e.g. Sintes et al., 2005; Kendrick et al., 2005).

However, the combined knowledge on seagrass reproduction and dispersal (e.g. Orth et al., Chapter 5), and clonal growth, reviewed above, now allows predictions on the recolonization time scales inherent for different species, which range from one or a few years for the fastest growing species, to several centuries for the slowest-growing ones. As yet, this knowledge has not been formalized into models delivering, at least, predicted seagrass dynamics under plausible scenarios of growth and new patch initiation.

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