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SUBMERGED AQUATIC VEGETATION IN RELATION TO DIFFERENT NUTRIENT REGIMES

Carlos M. Duarte
Centro de Estudios Avanzados de Blanes, CSIC
Camí de Santa Bárbara s/n, E-17300 Blanes, Girona, Spain

ABSTRACT

Submerged vegetation respond to increased nutrient loading through a shift from slow-growing seagrasses and large macroalgae to fast-growing macroalgae, and the ultimate dominance of phytoplankton at high nutrient loadings. This shift reflects a change from nutrient to light limitation along the eutrophication gradient. Slow-growing seagrasses and large macroalgae are good competitors when nutrients are limiting because they have relatively low nutrient requirements, are able of efficient internal nutrient recycling, and can access the elevated nutrient pools in the sediment. Fast-growing macroalgae and phytoplankton are superior competitors when light is limiting because they are positioned closer to the water surface, and capture and use light more efficiently. The important ecosystem consequences of altered nutrient regimes derive from the shift in dominant vegetation types. Slow-growing seagrasses and large macroalgae are longevous, decompose slowly, and experience only moderate grazing losses, whereas the production of fast growing macroalgae and phytoplankton is transferred faster to heterotrophs, through increased grazing and decomposition rates. Recovery of submerged vegetation following nutrient reduction plans is a very slow process, which involves the replacement of fast-growing for slow-growing plants. Simulation models predict recovery times to oscillate between a few years for macroalgae and fast-growing seagrasses to centuries for slow-growing seagrasses following nutrient reduction plans.

INTRODUCTION

Estuaries and coastal zones represent only about 1-2% of the surface of the ocean, but their primary production represents a disproportionate 20% of the global production in the ocean (Smith 1981; Charpy-Robaud & Sournia 1990). The much greater areal production of shallow coastal zones and estuaries compared to the open ocean derives from the presence of marine macrophytes and benthic microalgae, in addition to phytoplankton which is present both in oceanic and coastal areas. Marine macrophytes represent about 40% of the primary production of the coastal zone (Charpy-Robaud & Sournia 1990), and are, accordingly, key constituents of these ecosystems. The importance of marine macrophytes as components of the biomass of marine phototrophs is even greater, for they comprise about 2/3 of the oceanic biomass, and their biomass is, per unit area, about

400 times that of phytoplankton (Smith 1981). Hence, marine macrophytes play both a trophic role, as important primary producers in coastal ecosystems, and a structural role, by which they provide habitat and refuge for a number of organisms (Thayer et al. 1984; Duarte 1989). In addition, marine macrophytes provide substrate for epiphytic microalgae, which production often equals or exceeds that of the host macrophytes (Penhale 1977; Capone et al. 1979; Libes 1986; Moncreiff et al. 1992). Benthic microalgae, in contrast, typically sustain relatively low primary production, which may be locally significant (Pinckney & Zingmark 1993), estimated to be, on average, about 10 fold lower than that of macrophytes (Charpy-Robaud & Sournia 1990).

The relative importance of different types of dominant primary producers in coastal ecosystems (i.e. microalgae, and seagrasses) is a key characteristic of ecosystem structure with important functional consequences (Borum et al. 1990; Sand-Jensen & Borum 1991). Although the relative importance of the different types of primary producers is, to a large extent, determined by intrinsic (i.e. time-constant) properties of the system, such as substrate type and bathymetric configuration, it is subject to large-scale variation upon changes in resource, notably nutrient, availability (Sand-Jensen & Borum 1991). Widespread eutrophication of coastal ecosystems during the past decades has resulted in major changes in submerged vegetation, which have been appropriately documented in a number of locations (e.g. Wallentinus 1981; Kemp et al. 1983; Nienhuis 1983; Orth & Moore 1983; Cambridge & McComb 1984; Shepherd et al. 1989; Giesen et al. 1990). Hence, there is an adequate empirical basis to formulate qualitative predictions on the direction of change in submerged vegetation upon nutrient enrichment, and its consequences on ecosystem functioning. In contrast, reports of changes in submerged vegetation upon reduction of nutrient loading are much fewer (e.g. Bokn et al. 1992), and our ability to predict recovery is meagre or nonexisting. Models of submerged vegetation response to changes in nutrient loading will improve if the present empirical knowledge, derived from historical evidence, be strengthened with greater understanding of the causes of these changes.

I provide here an overview of the causal basis for the changes in submerged vegetation upon eutrophication, based on the comparative analysis of functional properties of different types of submerged vegetation. I shall first review, based on historical and experimental evidence, the sequence of changes in submerged vegetation upon increased nutrient loading, and discuss the causes, both direct and indirect, of that sequence. Differences in the structural role and the fate of the production of different types of submerged marine vegetation will then be used to predict the ecosystem consequences of these changes. I will end by discussing whether changes in submerged vegetation upon eutrophication are reversible, and the time scales that might be involved in the recovery process.

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CHANGES IN SUBMERGED VEGETATION UPON INCREASED NUTRIENT LOADING

The changes in submerged vegetation associated to increased nutrient loading are documented by ample historical (e.g. Orth & Moore 1983, Wallentinus 1981; Kemp et al. 1983; Nienhuis 1983; Cambridge & McComb 1984; Shepherd et al. 1989; Giesen et al. 1990) and experimental (Harlin & Thorne-Miller 1981; Kemp et al. 1983; Twilley et al. 1985; Neundorfer & Kemp 1993) evidence. Increased nutrient loading has lead to widespread eutrophication of shallow coastal systems, which was first noticed in the industrialised countries, but has now spread to most of the planet's coastal systems. Hence, opportunities to document the changes in submerged vegetation upon eutrophication have been, unfortunately, many. All studies indicate that eutrophication proceeds towards the dominance of faster-growing autotrophs (e.g. microalgae and fast-growing macroalgae, Wallentinus 1981; Kemp et al. 1983; Cambridge & McComb 1984; Kautsky et al. 1986; Shepherd et al. 1989; Borum et al. 1990; Sand-Jensen & Borum 1991). Increasing nutrient loading leads to the progressive replacement of seagrasses and slow-growing macroalgae by blooming, fast-growing macroalgae and phytoplankton, and a final dominance by phytoplankton at very high nutrient loadings (e.g. Harlin & Thorne-Miller 1981; Wallentinus 1981; Kemp et al. 1983, Cambridge & McComb 1984; Twilley et al. 1985; Kautsky et al. 1986; Borum et al. 1990; Sand-Jensen & Borum 1991; Neundorfer & Kemp 1993). Qualitative changes in submerged vegetation during eutrophication also occur at finer levels, and the replacement sequence during eutrophication can be extended to involve an increasing dominance by dinoflagelates and other bloom-forming phytoplankton taxa with increasing eutrophication (Paerl 1988). The link between nutrient loading and the replacement sequence described has been confirmed by experimental nutrient additions, both to natural ecosystems (Harlin & Thorne-Miller 1981; Kemp et al. 1983; Twilley et al. 1985; Williams & Ruckelshaus 1993) and mesocosms (Neundorfer & Kemp 1993).

The observations available suggest that the change in submerged vegetation is not a continuous, gradual process parallel to the rate of increase in nutrient addition. Instead, changes in submerged vegetation during eutrophication appear to occur as step changes, whereby sudden shifts in submerged vegetation occur which are not directly coupled to increased nutrient loading (Kemp et al. 1983; Nienhuis 1983; Cambridge & McComb 1984). This observation indicates that the changes in submerged vegetation observed cannot be accounted for by direct nutrient effects on submerged vegetation alone, and that there must be indirect and feed-back mechanisms involved (e.g. Kemp et al. 1983; Nienhuis 1983; Neundorfer & Kemp 1993; Williams & Ruckelshaus 1993).

CAUSES OF CHANGE IN SUBMERGED MARINE VEGETATION UPON INCREASED NUTRIENT LOADING

Vegetation responses to eutrophication compound both direct effects of increased nutrient supply and indirect effects. Direct effects include proliferation of microalgae and fast growing macroalgae due to increased nutrient availability (e.g. Kemp et al. 1983; Silberstein et al. 1986; Sand-Jensen & Borum 1991), and a toxic effect of high nitrate concentrations on seagrasses (Burkholder et al. 1992, 1994). Indirect effects involve increased shading of macrophytes by phytoplankton, epiphytes, and free-floating macroalgae (Orth & Moore 1983, Cambridge & McComb 1984; Silberstein et al. 1986; Kautsky et al. 1986; Giesen et al. 1990, Larkum & West 1990, Williams & Ruckelshaus 1993; den Hartog 1994), and altered root metabolism in anoxic sediments (Smith et al. 1988).

Direct effects: Resource requirements and acquisition by marine vegetation

Changes in nutrient and light availability, which are the two resources most often limiting plant growth, are at the root of the changes in submerged vegetation upon increased nutrient loading. Because all autotrophic organisms rely on the same resources (water, nutrients, and light) for growth, they are likely to compete for the limiting resource. The sequence of changes in submerged vegetation may, therefore, be explained by a comparative analysis of the needs, acquisition, and use of these resources by the different types of submerged vegetation involved. The changes in submerged vegetation upon increased nutrient loading suggest, therefore, that phytoplankton and fast-growing macroalgae are superior competitors under abundant nutrient supply, whereas seagrasses and slow-growing macroalgae must be able to out-compete phytoplankton and fast-growing macroalgae when nutrient loading is low. Water is, of course, not limiting in marine environments, and inorganic carbon is assumed to be limiting only rarely (but see Beer 1989; Riebesell et al. 1993; Durako 1994).

The ability to compete for the capture of light is largely dependent on the position submerged plants occupy in the water column. Seagrasses are rooted in the sediments and locate their photosynthetic surfaces at or near the bottom, the longest seagrass leaves being about 1.5 m in length (*Posidonia oceanica* and *Enhalus acoroides;* Duarte, unpubl. data). This position is shared by most macroalgae, that need to be attached to the substrate to avoid hydraulic wash off, though fast-growing macroalgae often grow as free-floating plants in sheltered locations. Phytoplankton, in contrast, are suspended is the water column and, in many

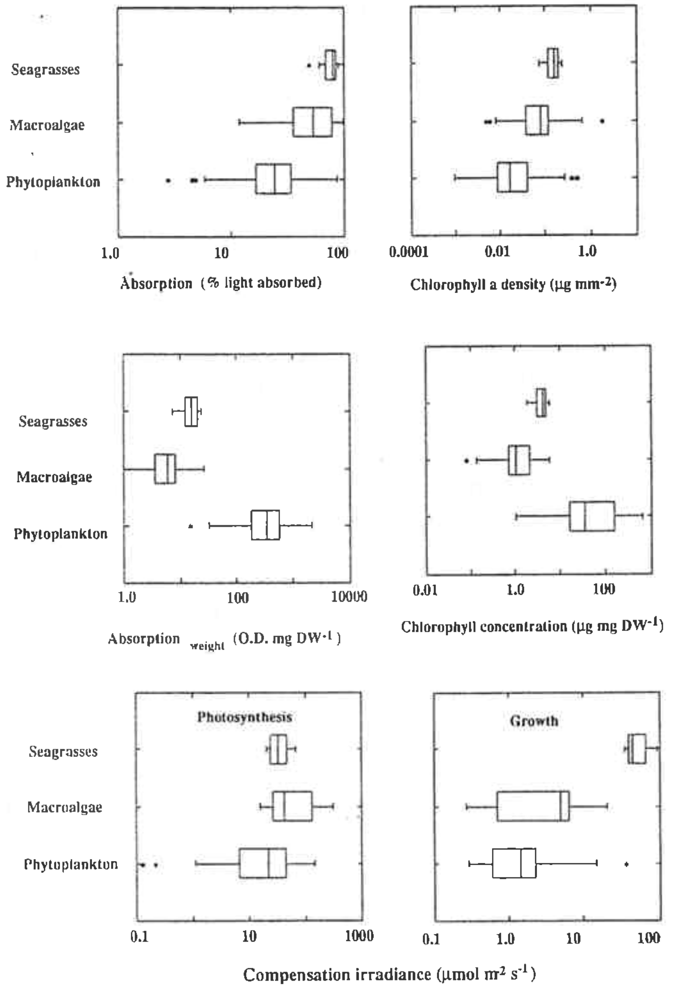

Fig. 1. Box plots showing the distribution of chlorophyll a density and concentration, absorption, and weight-specific light absorption, and light compensation points for photosynthesis and growth for seagrasses, macroalgae, and phytoplankton (data from Kain 1969; Chapman & Lindley 1980; Schoenbeck & North 1980; Phlips & Mitsui 1982; Richardson et al. 1983; Geider et al. 1986; Hanisak & Samuel 1987; Maggs & Guiry 1987; Hillmand & McComb 1988; Sand-Jensen 1988; Dunton & Tomaso 1991; Orfanidis 1992; Enríquez 1993; Olesen & Sand-Jensen 1993; Agustí et al. 1994). Boxes encompass the 25 and 75% quartiles of all the data for each plant type, the central line represents the median, bars extend to the 95% confidence limits, and asterisks represent observations extending beyond the 95% confidence limits

cases may regulate their position there, either by being positive buoyant or motile. Indeed, acute eutrophication leads to the dominance of motile phytoplankton taxa, such as dinoflagellates, that can position themselves higher in the water column, to form red tides and surface scums and prevent light limitation (Paerl 1988). Phytoplankton and free-floating macroalgae are, thus, best able to thrive in turbid waters, whereas seagrasses and attached macroalgae are prone to shading effects.

In addition to the position they occupy, autotrophs differ considerably in their ability to harvest incident light (Agustí et al. 1994). Light absorption by phototrophic organisms increases asymptotically with increasing chlorophyll density, which is smallest in phytoplankton cells and thin macroalgae and greatest in seagrasses and thick macroalgae (Fig. 1, Agustí et al. 1994). Hence, seagrasses absorb a substantial fraction of the incident light (0.75 ± 0.04 (mean ± SE); Enríquez et al. 1992), whereas phytoplankton cells absorb only a minor fraction (0.27 ± 0.026; Agustí et al. 1994) of the incident light (Fig. 1). The asymptotic nature of the relationship between light absorption and chlorophyll density implies that light absorption per unit pigment declines in seagrasses and thick macroalgae. Moreover, seagrasses and thick macroalgae have low chlorophyll concentrations per unit plant weight to counteract self-shading and, hence, their light absorption per unit plant weight is much lower than that of phytoplankton and fast-growing macroalgae (Fig. 1, Agustí et al. 1994). This difference suggests that seagrasses and thick macroalgae should have higher light compensation points and support slower growth rates than phytoplankton and thin macroalgae, because potential carbon turnover increases with increasing light absorption per unit plant weight (Agustí 1991a, b).

Available data supports the suggestion that seagrasses and thick macroalgae tend to have greater light compensation points for photosynthesis and growth than phytoplankton or thin macroalgae (Fig. 1; Enríquez 1993). Moreover, the light requirements are disproportionately greater to support seagrass growth, because of the respiration of non-photosynthetic tissues, which represents 15-50% of the plant's respiration (Fourqurean & Zieman 1991; Kraemer & Alberte 1993; Olesen & Sand-Jensen 1993). The high light requirements of seagrasses and thick macroalgae result in lower photosynthetic efficiency and capacity than those of phytoplankton and thin, fast-growing macroalgae (Fig. 2; Enríquez 1993). Moreover, the efficiency of the photosynthetic transformation of the light energy absorbed, as described by the apparent quantum yield, is smaller for seagrasses and, particularly, thick macroalgae than for phytoplankton and fast-growing macroalgae (Fig. 2, Enríquez 1993).

These comparisons clearly establish that phytoplankton and thin macroalgae have lower light requirements and are able of more efficient use of incident light than seagrasses and thick macroalgae. As a consequence, submerged vegetation shows a gradation in growth potential, from the slow rates of thick macroalgae and, particularly, seagrasses to the fast growth rates of phytoplankton and thin macroalgae (Fig. 2). This gradation represents, in fact, a continuous pattern of

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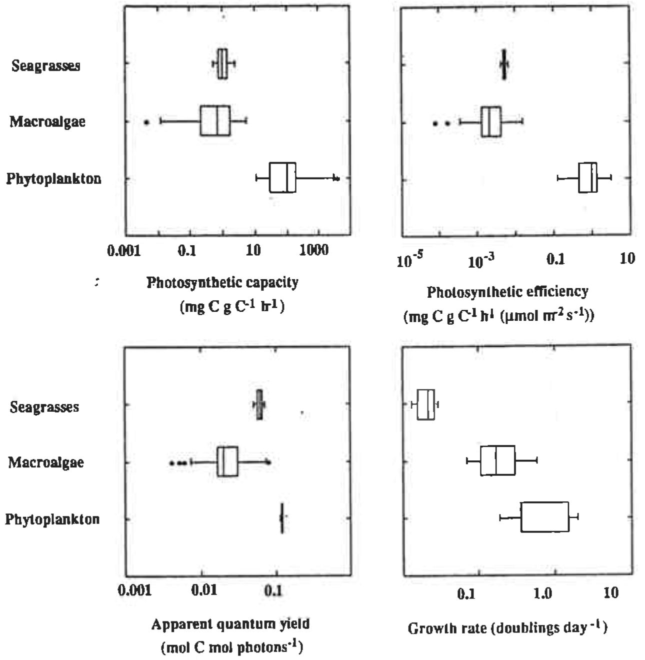

Fig. 2. Box plots showing the distribution of photosynthetic capacity and efficiency, apparent quantum yield, and specific growth rate for seagrasses, macroalgae, and phytoplankton (data from Enríquez 1993). Boxes encompass the 25 and 75% quartiles of all the data for each plant type, the central line represents the median, bars extend to the 95% confidence limits, and asterisks represent observations extending beyond the 95% confidence limits.

reduced growth rate with increasing plant thickness (Nielsen & Sand-Jensen 1990). Hence, the tendency towards the replacement of submerged vegetation by fast-growing organisms with increasing nutrient loading is accompanied by a reduction in plant thickness.

Phytoplankton and free-floating macroalgae are superior competitors for light than benthic plants, and are, therefore, likely to out compete them as light, instead of nutrients, becomes limiting during eutrophication. Conversely, the dominance of benthic plants under low nutrient supply suggests that they must be better competitors when nutrients, instead of light, limit primary production. This is, again, closely related to the relative position they occupy in the water column, which determines whether they have access to nutrient pools in sediments and overlying waters. Sediment nutrient concentrations are often 10-100 fold greater than those in the overlying waters (Sand-Jensen & Borum 1991). The large concentration gradient between sediments and overlying waters leads to a major flux of nutrients from sediments to waters, which can suffice to meet the nutrient requirements of plants located at the sediment-water interface.

Use of sediment nutrients is most prominent among seagrasses. In oligotrophic waters seagrasses appear to acquire virtually all of the nutrients from the sediment's interstitial waters (e.g. Patriquin 1972). Their leaves are, however, also able of substantial nutrient uptake from the surrounding waters, which may, in nutrient-rich waters, provide a large fraction of total nutrient uptake (e.g. Izumi & Hatori 1982; Short & McRoy 1984; Hemminga et al. 1991; Pedersen & Borum 1992). In addition to seagrasses, some benthic macroalgae, notably those within the Caulerpales (Chlorophyceae) are also able to absorb sediment nutrients through their rhizoids (Williams 1984), which are special root-like structures, and other benthic macroalgae can effectively trap nutrients released from the sediments. Seagrasses and these macroalgae are, therefore, dominant components of the submerged vegetation of oligotrophic waters. In contrast, phytoplankton and most macroalgae do not have direct access to sediment nutrients and rely, therefore, solely on nutrients in the water. This also explains why growth of phytoplankton and free-floating macroalgae is most dependent on nutrient loading and resulting concentrations in surface waters. Epiphytic algae depend mostly on nutrient supply from the water, although they may also receive nutrients from their host plants (McRoy & Goering 1974; Penhale & Thayer 1980). Seagrasses and some macroalgae benefit, therefore, from the exposure of their roots and rhizoids to high nutrient concentrations in sediments, thereby allowing them to support highly productive populations in oligotrophic waters. Even so, these plants also experience nutrient limitation (Orth 1977; Short 1987; Powell et al. 1989; Short et al. 1990; Perez et al. 1991; Fourqurean et al. 1992), particularly when growing over carbonaceous sediments in tropical, oligotrophic waters (e.g. Short 1987; Lapointe et al. 1992).

Phytoplankton and thin macroalgae are, however, better competitors for nutrients, once these become available in the water column, than seagrasses and slow-growing macroalgae. This is reflected in significantly (ANOVA, $P < 0.0001$) higher uptake rates for nitrogen and phosphorus for phytoplankton and fast-growing macroalgae compared to seagrasses and slow-growing macroalgae (Fig. 3). Hence, seagrass and slow-growing macroalgae are unable to sequester nutrients as loading increases, leading to the dominance of phytoplankton and fast-growing macroalgae. Competition for nutrients could be alleviated if different types of submerged vegetation differed in the nature of the limiting nutrient. However, this does not appear to be the case, for nitrogen and phosphorus have been shown to limit both macroalgae and seagrasses in regions characterised by silicic and carbonated waters, respectively (Short 1987; Lapointe et al. 1992), and marine phytoplankton has been also shown to be limited both by N and P (Hecky & Kilham 1988). There is mounting evidence for a major role of Fe, and possibly other micro-nutrients, as limiting to phytoplankton growth (Martin et al. 1991). Yet, Fe may also limit benthic plants, at least Caribbean seagrasses (Duarte et al.

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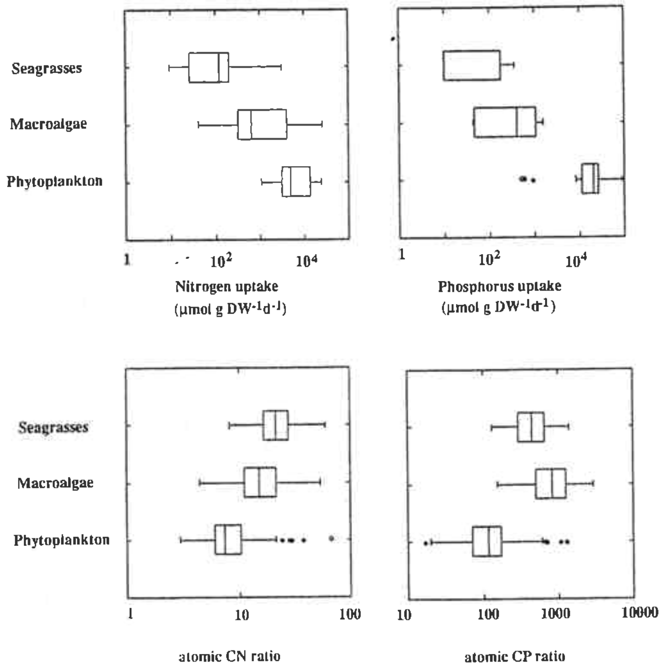

Fig. 3. Box plots showing the distribution of nitrogen and phosphorus uptake rates (data from Duarte, in prep.) and atomic carbon to nitrogen and phosphorus ratios (data from Duarte 1990, 1992) for seagrasses, macroalgae, and phytoplankton. Boxes encompass the 25 and 75% quartiles of all the data for each plant type, the central line represents the median, bars extend to the 95% confidence limits, and asterisks represent observations extending beyond the 95% confidence limits.

unpubl. data), although evalutation of the importance of Fe is hindered by present paucity of data.

The ecological consequences of the differential capacity to acquire nutrients of different aquatic plant types are dependent on their nutrient requirements. Nutrient requirements of different types of submerged vegetation can be compared by considering their nutrient contents and growth rate (Sand-Jensen & Borum 1991). Seagrasses and slow-growing macroalgae have nutrient contents much lower than those of phytoplankton (Fig. 3; Duarte 1990, 1992). Because phytoplankton species also have higher growth rates than other plant types (Fig. 2), their nutrient requirements for growth are much higher than those of seagrasses and most macroalgae. Combination of median nutrient contents (Duarte 1990, 1992) and median growth rates (Fig. 2; from Enríquez 1993) of the different types of submerged vegetation indicates that medium nitrogen and phosphorus requirements of phytoplankton and macroalgae are about 50 and 100 fold higher, and 8 and 1.5 fold higher, respectively, than those of seagrasses.

Hence, seagrasses can grow under smaller nutrient loadings than those required to support fast phytoplankton growth. Thin macroalgae may, however, have tissues depleted in nutrients when growing in oligotrophic waters where their growth rates are also reduced (e.g. Lapointe 1989). Although thin macroalgae have considerable plasticity in nutrient requirements they experience grazing rates much higher than those of seagrasses (Fig. 4, Cebrián & Duarte 1994). Consequently, their abundance may be reduced in oligotrophic waters if their slow growth under low nutrient supply does not suffice to compensate grazing losses. Seagrasses and large kelp macroalgae are long-lived organisms (Duarte 1991a; Steneck & Dethier 1994) and have storage capacity that confer them a considerable capacity to regulate their internal nutrient economy (e.g. Gagne et al. 1982; Hemminga et al. 1991; Pedersen & Borum 1992; Walsh & Hunter 1992). Seagrasses can reabsorb a substantial fraction of the nitrogen and phosphorus of mature leaves before these are shed (Harrison & Mann 1975; Thayer et al. 1977; Walker & McComb 1988; Borum et al. 1989; Umebayashi 1989; Pedersen & Borum 1992, 1993). The nutrients are then allocated to support the growth of new leaves. Internal nutrient recycling has been reported to provide about 25% of the annual nitrogen requirements of seagrasses (Hemminga et al. 1991; Pedersen & Borum 1993), and to be important for kelps (Schmitz & Lobban 1976). The fraction of nutrient demands supplied through internal recycling is probably much higher for seagrasses growing in oligotrophic waters (e.g. 70%, Patriquin 1972), than for those in nutrient-rich environments (Hemminga et al. 1991).

Hence, the successional sequence of submerged vegetation during eutrophication is largely dependent on an associated shift from nutrient to light limitation. Phytoplankton and free-floating macroalgae are superior competitors under light limitation and seagrasses and thick macroalgae are better competitors under nutrient limitation. Yet, changes in the relative abundance of different vegetation types cannot be accounted for on the bases of their relative growth potential alone, because the balance between losses and gains should be considered. Phytoplankton, epiphytes, and ephemeral macroalgae could, in principle, still dominate oligotrophic environments, albeit with reduced growth rates. This is, however, precluded by the much greater grazing losses they experience compared to seagrasses (Fig. 4), which can only be compensated for by fast growth rates.

Indirect and feed-back effects

The depth to which seagrasses and benthic macroalgae are able to colonise depends closely on water transparency (Nielsen et al. 1989; Duarte 1991b). Seagrasses are able to colonise down to the depth receiving, on the average, 11% of surface light (Duarte 1991b). Leathery and thin and crustose macroalgae colonise down to depths receiving 0.12-1.5% and < 0.003-0.05% of surface light, respectively (Markager & Sand-Jensen 1992). The increased shading to seagrass-

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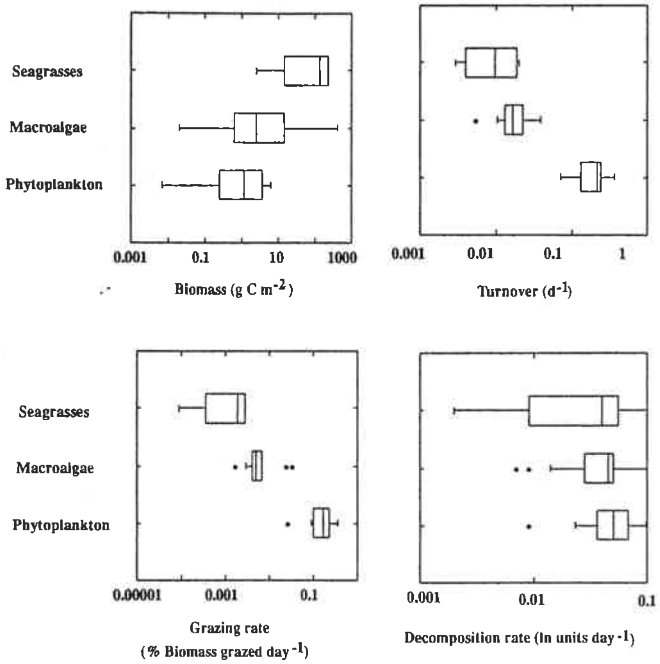

Fig. 4. Box plots showing the distribution of biomass, biomass turnover rate, grazing rate (data from Cebrián & Duarte 1994) and decomposition rate (data from Enríquez et al. 1993) for seagrasses, macroalgae, and phytoplankton. Boxes encompass the 25 and 75 % quartiles of all the data for each plant type, the central line represents the median, bars extend to the 95% confidence limits, and asterisks represent observations extending beyond the 95% confidence limits.

es and benthic macroalgae by phytoplankton and epiphytes with increasing nutrient loading results in a shallower depth limit, reducing macrophyte cover (e.g. Kautsky et al. 1986). The net consequence is that there is a negative relationship between nutrient concentration and the depth limit of benthic macrophytes (Nielsen et al. 1989), which could be used to predict the areal loss of macrophytes upon eutrophication. The extent of the areal loss of benthic vegetation as their depth limits become shallower during eutrophication depends on bathymetric configuration. Gently sloping littorals lead to a greater areal loss for a given reduction in light attenuation than steep littorals. Indeed, some of the most spectacular cases of catastrophic seagrass decline following increased nutrient loading have been observed in shallow coastal zones (e.g. Lake Grevelingen, Nienhuis 1983; Cockburn Sound, Cambridge & McComb 1984; Wadden Sea, Giessen et al. 1990). The effect of increased nutrient loading on shading to benthic plants may be, however, effectively buffered by the presence of herbivores grazing on phytoplankton and epiphytes for some length along the gradient of eutrophication (Borum 1987; Sand-Jensen & Borum 1991; Neckles et al. 1993, Williams & Ruckelshaus 1993).

Seagrasses leaves (Duarte 1991a) and thalli of thick macroalgae (e.g. Drew et al. 1982; Kautsky et al. 1986; Steneck & Dethier 1994) live over months or years and ensure, therefore, an adequate coupling between oxygen production and respiration, compared to phytoplankton and fast-growing macroalgae which undergo population blooms and subsequent collapses. The increased frequency of blooms of phytoplankton and fast-growing macroalgae during eutrophication are associated with subsequent high respiration rates and oxygen depletion in sediments and bottom waters (Sand-Jensen & Borum 1991). Hence, oxygen production and respiration becomes increasingly uncoupled in time as vegetation change in response to increased nutrient loading (Sand-Jensen & Borum 1991). The oxygen deficit in sediments and shallow waters following blooms of phytoplankton and macroalgae leads to reducing sediment conditions and enhanced nutrient fluxes to the overlying waters, which accelerate the eutrophication process.

Sediment anoxia impairs seagrass growth by reducing oxygen supply to the roots and their ability to acquire nitrogen (Smith et al. 1988; Kraemer & Alberte 1993), and further accelerates seagrass mortality (Pérez et al. 1994). Low oxygen availability in sediments and bottom waters also leads to decimation of animal populations, some of which are important grazers of phytoplankton and epiphytes (Sand-Jensen & Borum 1991). Release of grazing pressure on phytoplankton and epiphytes, in turn, accelerates the decline of seagrasses and slow-growing macroalgae by increasing the shading from phytoplankton and epiphytes. Loss of seagrass meadows and benthic microalgae films favour sediment resuspension, thereby leading to coastal erosion and increased turbidity, in a self-accelerating manner (Fig. 5). Increased resuspension further accelerates the transfer of nutrients from sediments to the water column, thereby speeding up phytoplankton growth.

The replacement sequence of submerged vegetation upon increased nutrient loading involves, therefore, a cascade of direct, and indirect effects interacting in a self-accelerating manner. Indirect effects include increased internal nutrient loading, and increased shading of benthic plants, increased seagrass mortality and reduced growth as sediments approach anoxic conditions (Fig. 5). Feed-back effects are many, grazing on microalgae and fast-growing macroalgae may buffer their proliferation in response to increased nutrient loading until the grazer population collapses. Most feed-back effects, however, speed up vegetation changes. In particular, seagrass demise involves ever-increasing turbidity due to enhanced sediment resuspension and phytoplankton growth as benthic plants decline (Fig. 5). The importance of self-accelerating processes in the response of submerged vegetation to eutrophication implies that these changes may not be

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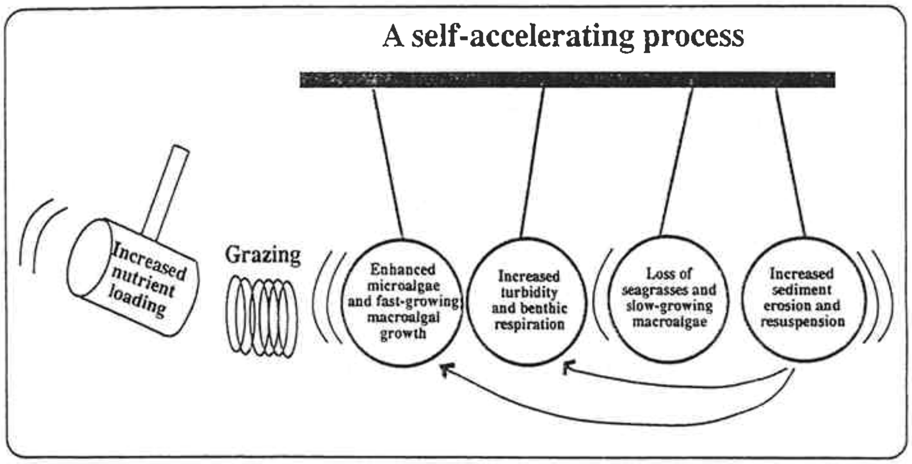

Fig. 5. A cartoon depicting a conceptual model of the effect of increased nutrient loading on submerged vegetation, stressing the self-accelerating nature of the process and the buffer mechanisms operating.

stopped once initiated (Sand-Jensen & Borum 1991), and that they are maintained and amplified in the system through a "domino effect" until the cover of submerged angiosperms and slow-growing macroalgae is lost (e.g. Nienhuis 1983; Orth & Moore 1983; Giessen et al. 1990).

Effect of changes in submerged marine vegetation on ecosystem structure and carbon flow

The replacement sequence of submerged vegetation with increasing nutrient loading alters ecosystem structure, without necessarily altering total primary production (Borum et al. 1990; Sand-Jensen & Borum 1991). Seagrasses have slower growth rates than phytoplankton and ephemeral macroalgae (Fig. 2), but compensate the slow growth rates by having much higher biomass (Fig. 4, Cebrián & Duarte 1994), thereby maintaining areal primary production approximately constant during eutrophication (Borum et al. 1990; Borum et al. 1994).

Hence, the consequences of vegetation changes during eutrophication of coastal ecosystems cannot be attributed to altered primary production, and must be associated to qualitative changes dependent on the differential roles of the different types of primary producers in the ecosystems (Sand-Jensen & Borum 1991). The vegetation replacement sequence during eutrophication is associated with a decline in biomass from seagrass-dominated to phytoplankton-dominated systems (Fig. 4), which has important ecosystem implications. The large biomass of seagrasses and slow-growing macroalgae implies that their tissues may be

CHALLENGES FOR RESEARCH

Predicting submerged vegetation changes upon eutrophication

The preceding discussion seeks to provide a comprehensive picture of the current knowledge regarding the response of submerged vegetation to eutrophication, as well as to increase understanding of the causes and consequences of these responses. This understanding suffices to allow qualitative predictions of the changes of submerged vegetation and associated ecosystem properties upon eutrophication. Qualitative predictions are, however, of little use to managers responsible for coastal ecosystems and legislators responsible for setting tolerable nutrient loadings. Hence, there is a social demand for quantitative models that predict how much nutrient loading may increase before the replacement sequence described here is triggered.

The diversity of processes involved in the response of submerged vegetation to eutrophication (Fig. 5) renders prediction of these changes very difficult. The present lack of predictive capacity implies that our ability to forecast the response of submerged vegetation to nutrient loading is meagre (Williams & Ruckelshaus 1993), and the development of models to provide the required answers is still a distant goal. It is clear, however, that vegetation response to eutrophication is not proportional to the changes in nutrient loading, and the development of non-linear models that account for the self-accelerating process causing the "domino effect" described is a challenge for future research.

More modest, and yet useful, models are already available (Nielsen et al. 1989; Duarte 1991a), that allow simple predictions of the areal loss of seagrasses and benthic macroalgae upon eutrophication-derived reduction in water transparency. Development of such simple empirical models may provide useful tools for coastal managers while quantitative, process-based predictive models become available.

Predicting recovery upon reduction of nutrient loading

Far more distant still is the availability of models that predict the consequences of reduced nutrient loading for submerged vegetation. Moreover, the question of whether changes in submerged vegetation due to eutrophication are reversible has seldom been addressed. Yet, there is an increasing need for such models at present, when different governments (e.g. Denmark, The Netherlands), have implemented ambitious plans to reduce nutrient loadings.

Changes in submerged vegetation upon eutrophication involve the replacement of slow-growing organisms by faster-growing ones so that colonisation times of the replacing vegetation are increasingly reduced with eutrophication. Conversely, the inverse process implies a replacement of fast-growing organisms by slower-growing ones, which should involve increasingly longer lag-times between the reduction of nutrient loads and the recovery of slow-growing submerged vegetation. These lagged responses are inherent of the process of colonisation by seagrasses, which involves the production of new patches by seedlings and the occupation of the space by subsequent patch growth (Duarte & Sand-Jensen 1990a, b). Colonisation of the denuded areas upon implementation of nutrient reduction plans depends on the advection of propagules from neighbour reproductive populations. These populations, however, may be very far away, for eutrophication may lead to the loss of seagrasses over vast coastal areas, such as the present decline over the Wadden Sea (Giessen et al. 1990), and production of colonising patches by seedlings is, accordingly, very slow. Recovery times for macroalgae may perhaps be faster. Macroalgal sporelings may have greater dispersal potential than the larger propagules of angiosperms (Deysher & Norton 1982), both because of their smaller size and because of their massive release (e.g. 10^4-10^6 propagules for an individual *Sargassum* sp., Umezaki 1984, Kendrich & Walker 1991). In addition, drifting macroalgal fragments may be important in macroalgal recolonisation (Dayton 1985; Deysher & Norton 1982, van der Hoek 1987), whereas there is no solid evidence of a comparable potential for seagrasses.

Models allowing the prediction of seagrass recovery are lacking at present, and the scant information available indicates that seagrass recovery is a very slow process, involving time-scales ranging from a few years to centuries (Birch & Birch 1984; Meinesz & Lefevre 1984; Clark & Kirkman 1989; Duarte & Sand-Jensen 1990a; Quammen & Onuf 1993). Modelling seagrass recovery has not been attempted as yet, probably because the detailed data on seagrass growth rate, architecture, branching patterns, and reproduction, needed to produce an appropriate model (cf. Bell et al. 1979, Bell & Tomlinson 1980, Callaghan et al. 1990) are not available. Our goals must be set to more modest targets, such as the prediction of the time scale involved in the recovery of seagrass from eutrophication-derived decline.

Seagrass recovery from catastrophic decline requires patch initiation from seeds and subsequent patch growth (Duarte & Sand-Jensen 1990a). Patch formation rates do not bear a simple relationship to reproductive effort because only a few of the seedlings sprouted from seeds survive to develop new patches (c.f. Duarte & Sand-Jensen 1990a). Reports of net seagrass patch formation rates are extremely sparse, the few reports available ranging from $5 \cdot 10^{-3}$ patches m^{-2} y^{-1} for a *Cymodocea nodosa* population (Duarte & Sand-Jensen 1990a) to about $3 \cdot 10^{-4}$ patches m^{-2} y^{-1} for a colonising *Posidonia oceanica* population (Meinesz & Lefevre 1984). These patch formation rates, however, may represent low, rather than average, values, for seedling production of some species can be quite phenomenal (> 1000 seedlings m^{-2} y^{-1} for a *Zostera marina* population, Robertson & Mann 1984). Established patches grow through elongation of rhizome apices in their periphery (Duarte & Sand-Jensen 1990a), at rates ranging from about 1 cm y^{-1}in

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I examined the time scales involved in seagrass recovery from eutrophication by simulating this process for a wide combination of patch formation and elongation rates (i.e. independent variables). The simulation model (Appendix 1) describes recovery as a non-linear process similar to growth of organisms, best represented by a logistic growth curve. The predicted increase in seagrass cover with time could be described as a function of patch elongation and patch formation rate by the regression equation fitted to the model's output.

$$\log \% \text{ cover} = 2 * [1.5 \cdot \log \text{time (years)} + 1.24 \cdot \log \text{patch elongation (m } y^{-1}) + 0.61 \cdot \log \text{patch formation (patches m}^{-2}\ y^{-1})]$$

$R^2 = 0.92$; $N = 328$; $F = 392$; $P < 0.0001$

which indicates that seagrass recovery increases faster with increasing patch elongation rate than with increasing patch formation rate. Hence, the time scale for seagrass recovery decreases faster with increasing patch elongation than with increasing patch formation rate as describe by the regression equation,

$$\log \text{Time (years)} = 0.125 - 0.682\ (\pm 0.018) \log \text{patch elongation (m } y^{-1}) - 0.338\ (\pm 0.008) \log \text{net patch formation rate (patches m}^{-2}\ y^{-1})$$

$R^2 = 0.99$; $N = 98$; $F = 1032$; $P < 0.0001$

More important, the model results indicated that the time scale necessary for meadow (i.e. 95% cover) formation ranged from < 1 year for small, fast-growing species to about four centuries for large, slow-growing species (Fig. 6). These results indicated that the recovery of large, slow-growing seagrass species (which are often the climax species within their distributional regions; Duarte 1991a) is an extremely slow process. For instance, the model predicts that recovery (to 95% cover) of the large, slow-growing Mediterranean seagrass *Posidonia oceanica,* whose rhizomes elongate at about 3 cm y^{-1}, in the Bay of Villefranche (France), where it was observed to produce $3 \cdot 10^{-4}$ new patches $m^{-2}\ y^{-1}$ (Meinesz & Lefevre 1984), should require about three centuries (280 years). In contrast, the time required for the fast-growing seagrass *Cymodocea nodosa* to develop a meadow in the Alfacs Bay (NW Mediterranean), where $4.5 \cdot 10^{-3}$ new patches $m^{-2}\ y^{-1}$, growing at an average rate of 1.5 m y^{-1}, were formed (Duarte & Sand-Jensen 1990a), is expected to be slightly over 6 years. Small seagrass species often tend to have faster elongation rates (Duarte 1991a) and areal reproductive outputs (cf. Johnson & Williams 1982; Hootsmans et al. 1987) than large species (Pergent & Pergent-Martini 1990; Duarte 1991a), thereby suggesting an exponential increase in the time needed for recovery as plant size increases.

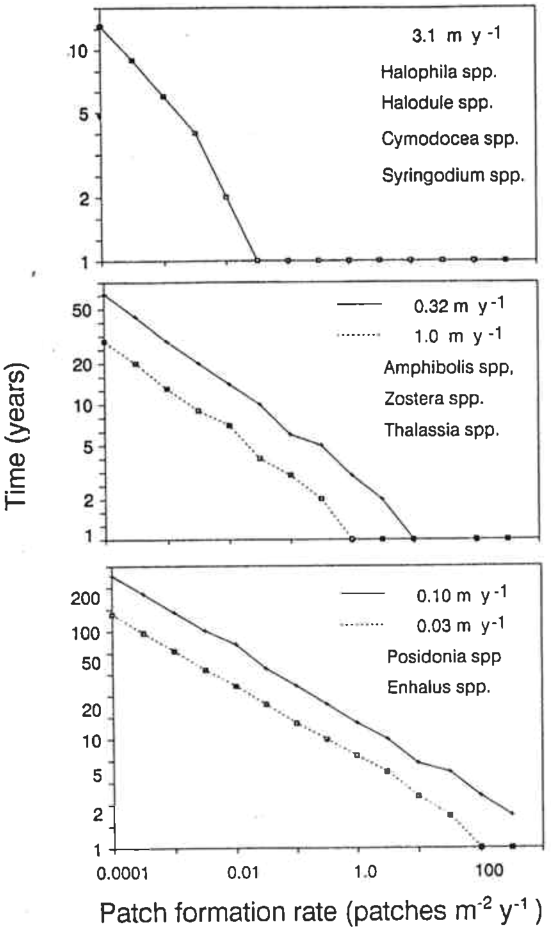

Fig. 6. The simulated time scale for the development of seagrass populations (the time to develop 95% cover) as a function of net patch formation rates (x axis) and the different rates of elongation (inside boxes).

The simple model developed confirms the notion that recovery of rooted vegetation upon reduced nutrient loading may be a long process (e.g. Clark & Kirkman 1989), for small, fast-growing seagrasses may recover within one or a few years after disturbance, but large, slow-growing seagrasses require several centuries to recover. Thus, loss of meadows of large seagrasses, which may be a fast process (Cambridge & McComb 1984; Robblee et al. 1991), will likely have ecosystem consequences lasting for decades or even centuries. It is clear, therefore, that the ecosystem consequences of eutrophication associated to the shift in submerged vegetation may last for many years after nutrient reduction plans are implemented.

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CONCLUSIONS

Decades of observations of shifts in submerged vegetation upon increased nutrient loading had provided a basis to postulate the importance of shading to benthic plants as a result of promoted microalgal growth as the main causal factor involved (Kemp et al. 1983; Sand-Jensen & Borum 1991), and to identify the importance of positive feed-back effects in this process (Sand-Jensen & Borum 1991). The experimental confirmation of the identity of the causal factors and main processes observed (Harlin & Thorne-Miller 1981; Kemp et al. 1993; Twilley et al. 1985; Neundorfer & Kemp 1993; Williams & Ruckelshaus 1993) had, however, failed to provide a basis for quantitative predictions. The discussion above offers the comparative analysis of resource capture and requirements by different types of submerged vegetation as an additional basis for understanding.

The replacement sequence of submerged vegetation associated with increased nutrient loading involves a progressive reduction in the thickness of the dominant organisms, from slow-growing benthic plants with high biomass to fast-growing macroalgae and phytoplankton. Reduced thickness increases the efficiency of light capture and use (Enríquez 1993; Agustí et al. 1994), and leads to faster growth rates (Nielsen & Sand-Jensen 1990). Fast growth rates, in turn, are associated to faster carbon and nutrient flow (Enríquez et al. 1993; Cebrián & Duarte 1994). The fast growth rate of thin phototrophs implies, however, high nutrient requirements, whereas the thick tissues of slow-growing organisms allow storage and efficient internal nutrient recycling. Hence, thick organisms dominate under low nutrient loadings, where nutrients are limiting. The path of increased carbon turnover with increasing nutrient loading leads to fast changes in the nature of the dominant phototrophs, accelerated further by feed-back processes acting as a *"domino effect"*. Conversely, reduced nutrient loading requires progressively longer time-lags for the recovery of thick, slow growing organisms, implying that loss of the more longevous plants, such as *Posidonia oceanica,* may not be recoverable within operational time despite implementation of costly nutrient reduction plans.

Hence, the changes associated to increased nutrient loading could be modelled as a series of functional changes dependent on the progressive shift towards thinner phototrophs. The associated functional changes could be modelled as a function of the shift in the thickness of the dominant plants (e.g. Nielsen & Sand-Jensen 1990; Enríquez 1993). I believe that this approach would yield significant improvement in our predictive capacity, by shifting from a simplistic, typological description of submerged vegetation to one that recognises the great functional variability within each of the main types of submerged vegetation.

APPENDIX 1

The time scales involved in seagrass recovery from eutrophication were simulated for a wide combination of patch formation and elongation rates. These rates were set to vary, at 0.5 base-10 logarithmic intervals, between 0.01 and 10 m^{-2} y^{-1} (i.e. 7 different rates) in patch elongation rate, and between 316 and 0.0001 patches m^{-2} y^{-1} (i.e. 14 different rates) in net patch formation rate, thereby encompassing the range of values observed in nature (e.g. Duarte 1991a). The time scale for recovery was simulated as the time required by the modelled seagrasses to occupy 95% of the space. Because this is a subjective boundary, which some seagrass meadows may never reach due to small-scale perturbation, I also examined the time required to reach sparser seagrass cover.

The simulation was performed on a landscape scaled to receive 100 new patches y^{-1} (i.e. representing a simulated area of 1 m^2 and 10^4 m^2 for plants with net annual production of 100 and 0.01 new patches m^{-2} y^{-1}, respectively). Sampling within the simulated landscapes was established at a scale such that the probability of formation of a new patch in each sampling unit for a model iteration (i.e. "year") be 1%. This was achieved by splitting the landscape into 10^4 units (i.e. a 100 · 100 grid), each unit representing a sampling area of 10^{-4} m^2 and 1 m^2 for plants with net annual production of 100 and 0.01 new patches m^{-2}, respectively. The proportion of the 10^4 sampling units containing plants was used, at each model iteration (i.e. "year"), to estimate percent seagrass cover. New patches were randomly seeded within the landscape, such that establishment of new patches in sampling units already occupied by a patch does not increase plant cover. The model was initiated by seeding each landscape with 100 randomly-distributed patch-developing seedlings, which were than allowed to grow at each of the 7 selected horizontal elongation rates for a time increment (i.e. "year") before computing plant cover. If plant cover exceeded 95%, used here to represent an established meadow, the model was stopped. Otherwise a new iteration was initiated by seeding the landscape with 100 additional randomly-distributed patch-developing seedlings, which were again allowed to grow, together with the patches present at the previous iteration, for one more time inverval. The model was run in 14 different landscapes scaled to represent the selected ranges of net new patch formation rates. Variability in elongation and patch formation rates was introduced by sampling random, normally distributed values, with mean equal to the simulated average values, and a coefficient of variation of 25 and 50%, of elongation and patch formation rates, respectively, because sexual effort is subject to strong high interannual variation (e.g. Durako & Moffler 1987; Gallegos et al. 1992). I used the Polar Marsaglia method to generate the normal distributions (Morgan 1984).

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