Nonlinear processes in seagrass colonisation explained by simple clonal growth rules

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The development of single clones of the seagrass *Cymodocea nodosa* was analysed using a growth model based on the formation of structures limited by diffusive aggregation. The model implemented the measured clonal growth rules (i.e. rhizome elongation and branching rates, branching angle, and spacer length between consecutive shoots) and shoot mortality rate for *C. nodosa* at Alfacs Bay (Spain). The simulated patches increased their size nonlinearly with time displaying two different domains of growth. Young patches showed a rapid increase with time of the length of rhizome network and the number of living shoots, which depended on rhizome branching rate, and increased the radial patch size (R_g) algebraically with the number of living shoots as $R_g \propto N_s^{1/D_f}$, being D_f the fractal dimension of the patch structure. Patches older than 4 years increased the production of rhizome network and the number of living shoots much more slowly, while their radial patch size behaved as $R_g \propto N_s^{0.5}$ resulting from an internal patch compactation. Moreover, the linear growth rate of the simulated patches changed up to 30 fold during patch development, increasing with increasing patch size until patches reached an intermediate size. The modelled patch development was found to closely reproduce the observed patch structure for the species at the Alfacs Bay (Spain). Hence, the growth of *C. nodosa* patches initially proceeds with a growth mode controlled by the branching pattern (branching frequency and angle) of the species, producing sparse and elongated patches. Once patches exceed 4–5 years of age and contained >500 shoots, becoming dense and circular, they shift to a growth model typical of compact structures. These results explain previously unaccounted evidence of the emergence of nonlinear patch growth from simple clonal growth rules, and highlight the importance of branching frequency and angles as critical determinants of the space occupation rate of seagrasses and probably other clonal plants.

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Rhizomatous plants are widespread components of a broad range of ecosystems, both terrestrial and aquatic (Silvertown and Lovett Doust 1993). They typically exhibit highly organised clonal growth, progressing according to a set of simple rules (Bell and Tomlinson 1980), which are adequately represented by the length of the rhizome piece in between consecutive shoots (hereafter called spacer length), the rhizome elongation and branching rates, and the branching angle (Bell and Tomlinson 1980). The possibility to describe the clonal growth of rhizomatous plants from a few, simple growth rules has been used to model space occupation by clonal plants (Routledge 1990, Oborny and Cain 1997, Marbà and Duarte 1998). These modelling exercises have

allowed the description of network development (Bell 1979, Bell and Tomlinson 1980, Brouns 1987, Callaghan et al. 1990, Molenaar et al. 2000), the forecast of the spatial distribution of the clones in favourable and unfavourable environments in response to their foraging behaviour (Sutherland and Stillman 1990, Cain 1994, Cain et al. 1996), and the test of the adaptive advantages of rigid or plastic growth in clonal plant populations (Oborny 1994).

The rhizomatous architecture has been particularly successful in the colonisation of shallow coastal areas by angiosperms, represented by a group of a few (about 50) rhizomatous species, collectively known as seagrasses, which develop productive ecosystems (Duarte and Chiscano 1999) covering about 0.6×10^6 km^2 worldwide (Duarte 2000, Hemminga and Duarte 2000). Seagrasses develop highly dynamic landscapes (Fonseca et al. 2000, Robbins and Bell 2000), often comprised of a mosaic of temporally dynamic patches (Duarte and Sand-Jensen 1990a, b, Olesen and Sand-Jensen 1994a, Marbà and Duarte 1995). Patch establishment is mostly driven by sexual reproduction and patch spread which depends, because of the low reproductive effort of most seagrass species (Hemminga and Duarte 2000), on clonal growth. The species-specific growth rules driving clonal growth are relatively well established (Duarte and Sand-Jensen 1990a, Marbà and Duarte 1998) and can be predicted from plant size (Duarte 1991, Marbà and Duarte 1998). The predictability of clonal growth rules led to the expectation that the growth of seagrass patches, and therefore, colonisation rates would be predictable as a simple radial expansion process (Duarte 1995, Kendrick et al. 1999). However, examination of patch dynamics for the seagrass *Cymodocea nodosa* (Ucria) Aschers in situ has provided evidence that patch growth is a self-accelerative process (Vidondo et al. 1997), a behaviour that has also been observed during the earliest stages of patch life in clones of land plants (Cain 1990), using simple clonal growth models (Marbà and Duarte 1998), and which seems to apply to the space occupation by a range of seagrass species (Kendrick et al. 1999). In particular, Vidondo et al. (1997) found the horizontal extension rate of *Cymodocea nodosa* patches to increase with patch size and patch age (Vidondo et al.1997). In fact, the acceleration of horizontal growth rate of *Cymodocea nodosa* patches with patch size showed a complex, nonlinear behaviour, with a fast initial increase to reach relatively uniform linear extension rates in larger patches (Fig. 5 in Vidondo et al. 1997). There is, therefore, evidence that the clonal growth of seagrasses (Vidondo et al. 1997, Marbà and Duarte 1998) and terrestrial rhizomatous plants (Cain 1990) involves non-linear processes that render the prediction of space occupation using simple radial growth models inaccurate. This observation has important implications. In particular, the colonisation rates of seagrass meadows predicted by simple radial growth models are very slow, involving time scales ranging from decades to centuries (Duarte 1995). However, self-accelerating clonal growth, such as reported by Vidondo et al. (1997), Marbà and Duarte (1998), and Kendrick et al. (1999), may result in significantly faster space occupation rates than predicted by current models.

The nonlinear behaviour of the growth of rhizomatous clones is particularly intriguing, since such behaviour must be contained within the simple, essentially linear, growth rules that control clonal growth (Bell and Tomlinson 1980, Marbà and Duarte 1998). The formation of patterns reaching a high level of complexity from simple rules is also a subject of intense research in nonlinear physics, which has resulted in the formulation of a range of models (e.g. Eden model, Jullien and Botet 1985; diffusion-limited aggregation – DLA-model, Bunde and Havlin 1996) explaining the emergence of complex behaviour from simple growth rules.

Here, we simulate the development of single clones of *Cymodocea nodosa*, for which extensive knowledge on its clonal growth rules is available (Duarte and Sand-Jensen 1990a, b, Terrados et al. 1997, Marbà and Duarte 1998). We do so using a growth model based on the formation of structures limited by diffusive aggregation, to demonstrate that the complex, nonlinear space occupation by single clones of this species results from emergence of complex behaviour arising from simple growth rules. The parameters describing clonal growth in the model (Table 1) are all ecologically relevant: the rhizome elongation rate sets the upper limit for the horizontal spread of the clone; the branching rate is closely linked to the capacity of the clone to occupy the space forming a dense network; the branching angle is an important determinant of the efficiency of space occupation and the resulting growth mode of the clone (Stevens 1974, Marbà and Duarte 1998), and the spacer length (i.e. length of the piece of rhizome in between consecutive shoots) is an important determinant of the per-capita space and resources available (Marbà and Duarte 2003). An exclusion area (Table 1) around each shoot is required in the model to avoid crowding, consistent with the general positive correlation between shoot size and the inverse of shoot density observed in seagrasses (Duarte and Kalff 1987, Marbà and Duarte 2003). Because these growth rules represent the most parsimonious set of parameters required to model clonal growth, the model developed should be applicable to rhizomatous plants in general, provided the parameters required are available. Empirical observations on patch growth of *C. nodosa* in Alfacs Bay (Spain, Vidondo et al. 1997) were used to validate the model. The model output was analysed to assess the occurrence of domain shifts in the growth process and a sensitivity analysis of the model was conducted to identify the drivers of the complex behaviour observed.

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Methods

We formulated a numerical model to study the development of seagrass patches. The model uses simple parameters (Table 1) to simulate the development of clonal networks, and allows the examination of the evolution of the relevant variables describing patch growth, such as the total length of the rhizome network, the patch radius, and the internal density of shoots and rhizome apices. The input parameters, characterised by their average and standard deviation, including a cut-off at the minimum and maximum observed values (Table 1), were derived from empirical observations at Alfacs Bay (Spain), and were sampled, at each time step in the model, from the corresponding gaussian distribution, thereby accounting for variability in these rules.

The simulation starts by placing a seed (a shoot holding an apical meristem) at an origin coordinate r_0, and assigning to it a unitary, randomly oriented vector director u, setting the direction of rhizome extension. A per capita area of radius ρ (i.e. spacer length or distance between consecutive shoots) was assigned to each shoot, and an exclusion area of radius $\sigma < \rho$ defined whereby any invading shoot will be strongly penalised, thereby preserving stand density and avoiding the same position to be simultaneously occupied by more than one shoot. The exclusion area was estimated by fitting this parameter to achieve the shoot density reported in natural stands of the species. The robustness of the empirically fitted exclusion area is supported by the observation that the resulting density of rhizome apices, which is independent of the fitting procedure, also matches field observations. The model iterates the clonal growth process according to the following steps:

1) A rhizome, that originates in the apex, is proposed to grow from r_0 to $r = r_0 + \rho u$. The proposal will be accepted while the exclusion area principle is preserved. Then, the apex is relocated to the new position r where a new shoot will develop. In this process the direction of growth u does not change.
2) A new branch (with a growing apex) may develop at r with probability ν_b per unit time (Table 1). Thus, the probability that a particular meristem will branch at any one iteration is given by the

product $\nu_b \times \rho \times \nu^{-1}$, where ν is the rhizome elongation rate (cm apex^{-1} yr^{-1}). A new branch will extend along a new vector director u' forming an angle ϕ with u, randomly, along the right or left side of u. Only one branch is possible, as defined by the probability ν_b evaluated only at the time the rhizome apex occupies a particular position.
3) During this process, time is increased as $\Delta t = \rho/(\nu N_a(t))$, being ρ the spacer length and $N_a(t)$ the number of apices at time t.
4) Within this time step, $\mu_r \Delta t$ shoots are selected at random, since seagrass shoot mortality (μ_r) is believed to be an age-independent event (Duarte et al. 1994), and are removed from the patch.

This process is iterated to result in patch growth. At regular time intervals the total number of apices $N_a(t)$, shoots $N_s(t)$, and the total length of the rhizome network L(t) are computed as descriptors of clonal growth. The size of the growing patch at any time t is measured through the evaluation of the radius of gyration $R_g(t)$, defined as:

$$R_g^2(t) = \frac{1}{N_s(t)} \sum_{i=1}^{N_s(t)} (r_i(t) - \langle r(t) \rangle)^2 \tag{1}$$

where $r_i(t)$ is the position of the i-th shoot at time t, and $\langle \ldots \rangle$ denotes the position of the centre of mass of the patch. The radius of gyration, a property used to characterise the linear dimension of objects in most growth models developed in the context of physics (Stanley and Ostrowski 1986), is equivalent to the circular-equivalent radius weighed for the internal distribution of shoot density of the patch. The use of the radius of gyration to characterise patch size is particularly useful at the initial stages of growth, when the patches present highly irregular shapes and internal densities (Fig. 1). The density of the patch is calculated through the evaluation of the average number of shoots and apices in a square cell of size 20×20 cm^2, comparable to the field estimation of shoot density.

The model simulated 15 years of clonal growth, slightly above the oldest age reached by *Cymodocea nodosa* patches in the field, which was 10.5 years (Vidondo et al. 1997), equivalent to about 650 time steps in the model, where the growth of each rhizome

Table 1. *Cymodocea nodosa* growth rules and shoot mortality rates, measured at Alfacs Bay (Ebro Delta, Spain), used in the numerical model.

Parameter	Unit	Symbol	Value	Reference
Spacer length	cm	ρ	3.7 ± 0.1	Terrados et al. 1997
Rhizome elongation	cm yr^{-1} rhizome apex^{-1}	ν	160 ± 5	Duarte and Sand-Jensen 1990a
Branching rate	branches yr^{-1} rhizome apex^{-1}	ν_b	2.30 ± 0.05	Unpubl.
Branching angle	degrees	ϕ	46 ± 15	Marbà and Duarte 1998
Shoot mortality rate	ln units yr^{-1}	μ_r	0.92 ± 0.08	Duarte and Sand-Jensen 1990b
Radius of exclusion area*	cm	σ	0.7	This study

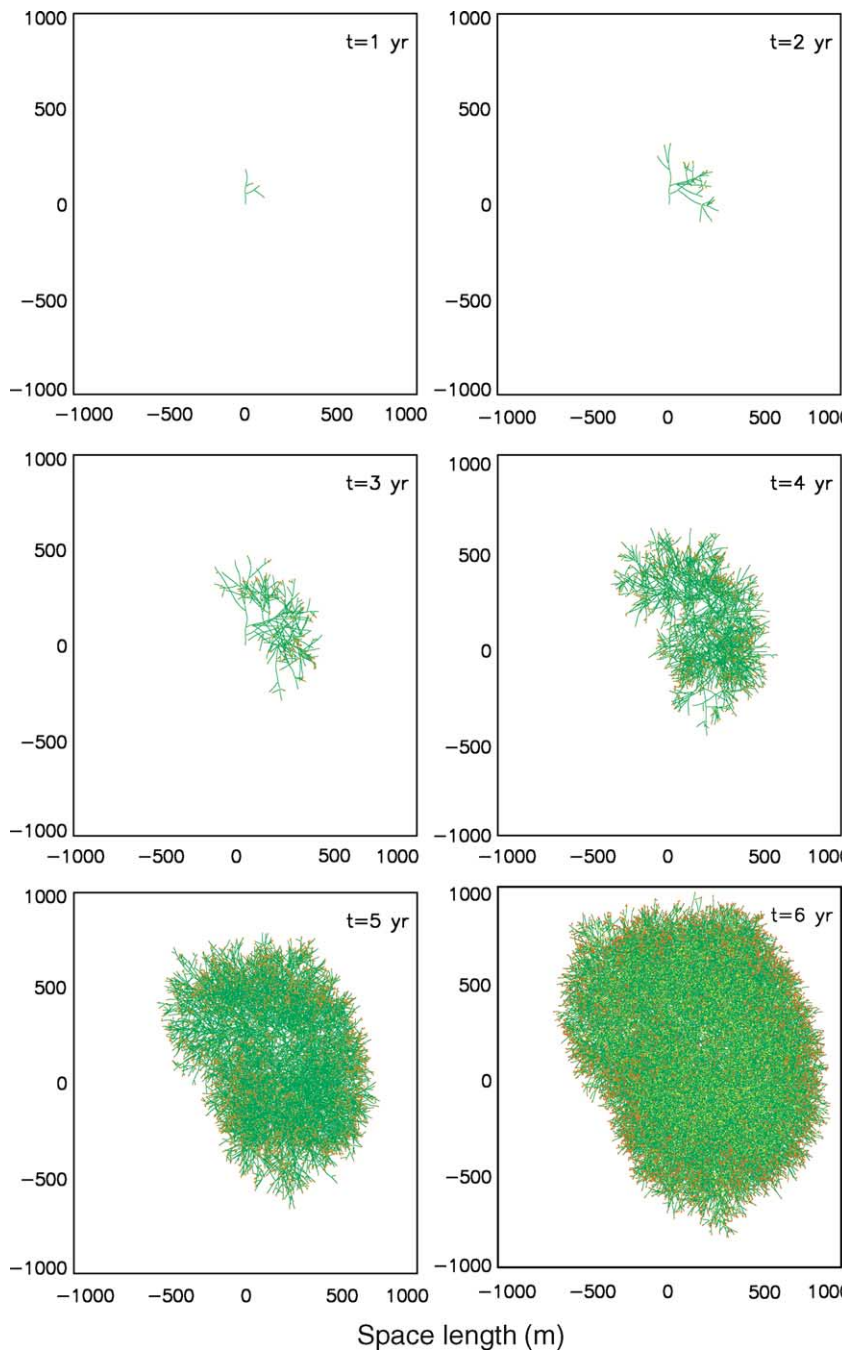*Parameter estimated with the model.

Fig. 1. Snapshots of the shape of modelled *Cymodocea nodosa* at different patch ages (1 to 6 yr). The green colour denote the living rhizomes and the red spots indicate the position of the apices, mainly concentrated along the outside contour.

apex was evaluated within any one time step, requiring a memory storage capacity of 512Mb to follow the fate and growth of the 3 million shoots and 40 000 apices the 15 year old patch contained. The model output was averaged over 50 replicated complete runs to yield estimates of the average clonal structure at each time step. We implemented a link cell method (Allen and Tildesley 1987) to efficiently determine the available space for new shoots to be placed. The model was written in Fortran, and was run on a workstation.

The clonal growth rules of the seagrass *Cymodocea nodosa* have been extensively documented, showing variability among stands (e.g. $CV_{\text{rhizome elongation rate (cm yr}^{-1}\text{ apex}^{-1})} = 107\%$, $CV_{\text{rhizome branching rate (branches} \times 100 \text{ rhizome internode}^{-1})} = 81\%$; Marbà and Duarte 1998) and providing the parameters necessary to model this process (Table 1). A sensitivity analysis was conducted to examine the relative bearing of the different rules (Table 1) on the clonal growth. This analysis consisted in the evaluation of the model output obtained when

varying the branching frequency, branching angle and spacer length beyond the range of values reported for the species (Table 1).

Results

The simulated patches increased initially as an elongated unit, then the directions of growth expanded, as a consequence of branching processes, after about 3 years, to eventually yield a circular, compact shape after about 6 years (Fig. 1). The shoot and apex density in the patches increased rapidly to reach asymptotic values of about 1400 and 50 m^{-2}, respectively, for patches of about 5 years of age (Fig. 2).

The total length (L, in m) of the rhizome network increased nonlinearly with time, with a shift from rapid to slower growth after some 3–4 years (Fig. 3a). The rapid initial rate of increase is best described by an equation of the form:

$$L \propto e^{(2.31 \pm 0.07) \times \text{Age (years)}} \qquad (2)$$

Similarly, the number of living shoots in the patch (N_s (t)) increased nonlinearly with patch age, with a very fast rapid increase in clonal size, described by an exponential equation of the form:

$$N_s(t) \propto e^{(2.31 \pm 0.07) \times \text{Age (years)}} \qquad (3)$$

up to 3–4 years of age, and then a much slower growth in clonal size thereafter (Fig. 3b). The rate of increase in the number of apical meristems in the clone showed a similar behaviour (Fig. 3b).

The radial patch size (R_g, in m) also increased nonlinearly with patch age, with an initial, fast increase described by the equation:
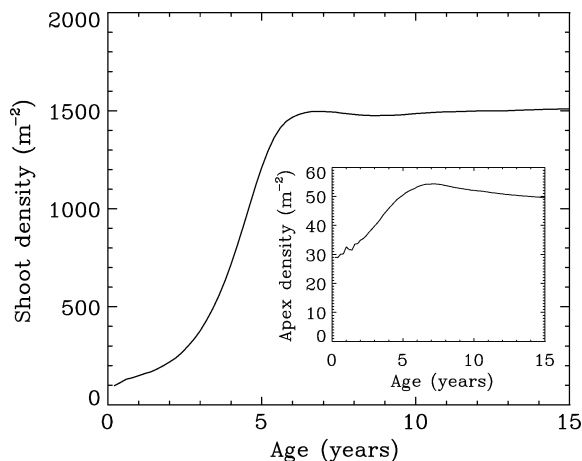

Fig. 2. Time course of the shoot and rhizome apex (insert plot) density of modelled *Cymodocea nodosa* patches. The steady-state values correspond, approximately, to 1500 shoots m^{-2} and 50 apices m^{-2}, respectively.
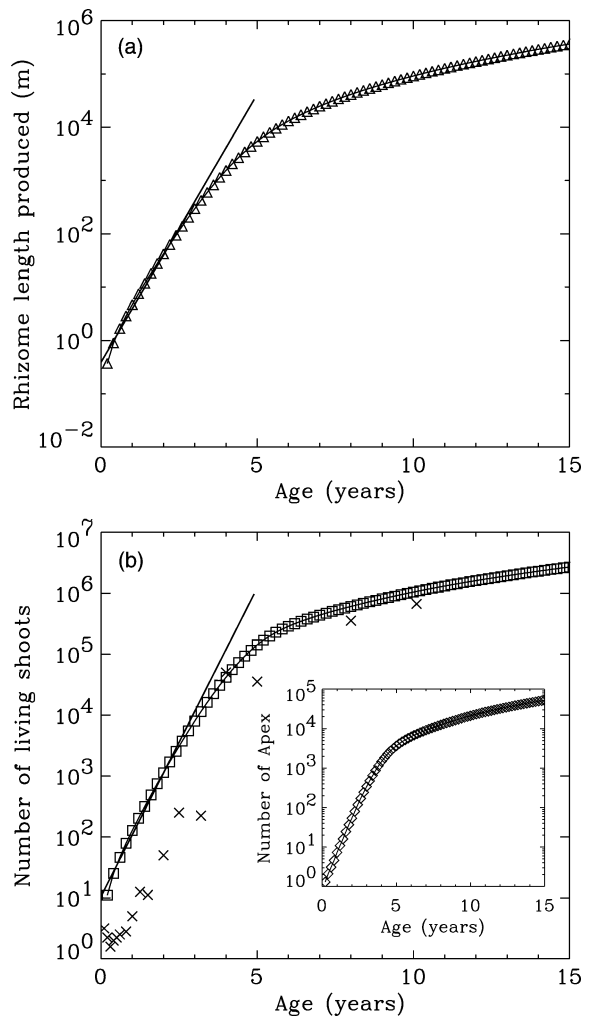

Fig. 3. (a) Semi-logarithmic plot of the time course of the total rhizome length (L) produced by modelled *Cymodocea nodosa* patches. The solid line represents the fitted exponential growth of the form: ln (L) = $-0.94 + 2.31$ (± 0.07) patch age; (R^2 = 0.98, p < 0.001) for the early stage (t < 3 yr) of the patches. (b) Semi-logarithmic plot of the time course of the number of living shoots (N_s) and rhizome apices (insert) produced by modelled *Cymodocea nodosa* patches. The solid line represents the fitted exponential growth of the form: ln (N_s) = 2.36 + 2.33 (± 0.07) patch age; (R^2 = 0.99, p < 0.001) for the early stage (t < 3 yr) of the patches. ($\times$) symbols correspond to the empirical observations of patches growing in the Ebro delta by Vidondo et al (1997).

$$R_g \propto e^{(1.38 \pm 0.14) \ \text{Age (years)}} \qquad (4)$$

and a reduction in the increase in radial patch size with age after 2–3 years (Fig. 4). The change in radial patch size (R_g) with the number of living shoots (N_s) showed a sigmoidal pattern, suggesting the occurrence of different domains of patch growth (Fig. 5), which can be summarised by a power law of the form $R_g \propto N_s^{\alpha}$. The computed exponent (α) for patches containing less than 1000 shoots is $\alpha = 0.6 \pm 0.05$, whereas the exponent

describing the pattern for larger patches (above 100 000 shoots) is $\alpha = 0.5 \pm 0.01$ (Fig. 5), with a transition zone in between characterised by a low increase in patch size despite increasing number of shoots, indicative of internal patch compactation.

The linear growth rate of the patches increased with increasing patch size up to patches containing about 500 shoots, to reach patch growth rates equivalent to the maximal horizontal extension rate of the rhizomes at about 1.6 m year^{-1} (Fig. 6).

Model validation and sensitivity analysis

The modelled increase in the number of living shoots with patch age closely reproduced the empirical observations reported by Vidondo et al. (1997), with a correlation coefficient of 0.98 (p < 0.001) between the modelled and the observed number of living shoots (Fig. 3b). The modelled increase in linear growth rate of the patches with increasing patch size closely reproduced (r = 0.76, p < 0.001) the observed values reported by Vidondo et al. (1997) for this species (Fig. 6).

During the early stages of patch growth (patch age < 3 years), the outgrowing branches basically grow independently, so that the process can be described by a set of two ordinary differential equations:

$$\frac{dN_a}{dt} = \nu_b N_a$$

$$\frac{dN_s}{dt} = -\mu_r N_s + N_a$$

The solution with the initial conditions $N_a(0) = N_s(0) = 1$ can be derived as

$$N_a = e^{\nu_b t}$$

$$N_s = \left(1 - \frac{1}{\mu_r + \nu_b}\right) e^{-\mu_r t} + \frac{1}{\mu_r + \nu_b} e^{\nu_b t}$$

showing both the change in the number of shoots $N_s(t)$ and the number of apices $N_a(t)$ to be dominated by the frequency of horizontal branching ν_b, thus,

$$N_s(t) \propto N_a(t) \propto e^{\nu_b t}.$$

This is also the case for the overall length of the clonal network produced, which is proportional to the number of shoots. The slopes obtained from the analysis of the model for the rhizome length (Fig. 3a) and the number of shoots (Fig. 3b) produced are 2.31 ± 0.07 (Eq. 2) and 2.33 ± 0.07 (Eq. 3), respectively. The modelled slopes are in agreement with the value of the branching rate $\nu_b = 2.30$, used in the simulation (Table 1), consistent with the key importance of the branching rate in determining the early patch growth rate inferred analytically.

During this early growth period, the radial patch size grows exponentially with time, as described by Eq. 4, with a slope of 1.38 ± 0.14 (Fig. 4). Since the radial size scales with the number of shoots as $R_g \propto N_s^\alpha$, and $R_g \propto \exp(\nu_b \alpha\, t)$, then the slope derived is consistent with the expected slope at early stages of growth where α was found to be 0.6 so that $\nu_b \alpha = 1.38$. The radial growth rate, defined as dR_g/dt, scales with the number of shoots as $dR_g/dt \sim N_s^\alpha$ (Fig. 6), with an exponent $\alpha = 0.60 \pm 0.13$ during the early growth of the patches, which is in close agreement with the theoretical expected exponent for a diffusion-limited growth process.

The sensitivity analysis conducted confirmed the dominant importance of the branching frequency on the growth process (Fig. 7). A 10 fold reduction in
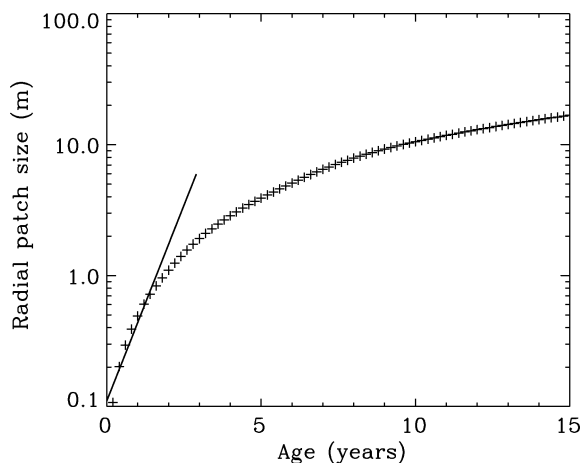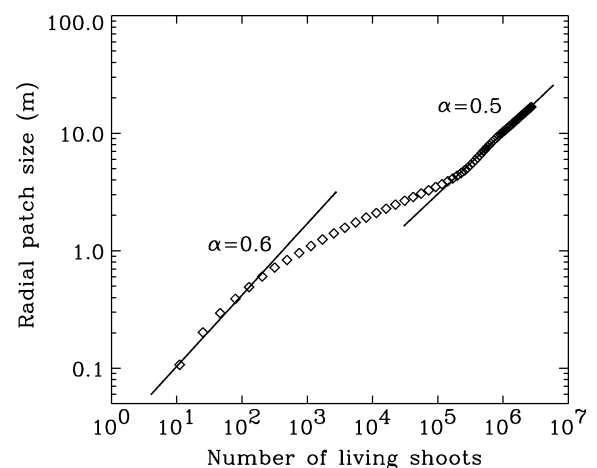

Fig. 4. Change of the radial patch size (R_g) with patch age of modelled *Cymodocea nodosa* patches. The solid line represents the fitted regression equation: ln (R_g) = $-2.20 + 1.38(\pm 0.14)$ patch age ($R^2 = 0.87$, p < 0.001).

Fig. 5. Log-log plot of the radial patch size (R_g) with the number of living shoots (N_s). The solid lines were fitted to the early (diffusion-limited) and advanced (compact) stage of the patches using a power law relationship of the form $R_g \sim N_s^\alpha$. Values represent the fitted exponent, α.

branching frequency resulted in a 10 000 fold reduction in the number of shoots produced after 10 years, and a 10 fold increase in branching frequency leading to the development of one million shoots in 2, rather than the 15 years with the frequency reported in Table 1 (Fig. 7a). Patch growth was robust against major ($>$three fold) changes in the branching angle (Fig. 7b), with a reduction in the number of shoots produced only becoming apparent at branching angles broad enough ($>90°$) as to revert the direction of growth at each branching event (Fig. 7b). Changes in the spacer length did not result in significant changes in patch growth if the exclusion area changed proportionally (Fig. 7c). However, a doubling of the spacer length, maintaining the exclusion area unchanged did not alter the growth pattern but resulted in a two fold increase in the internal density of the patch (Fig. 7c), which exceeded that of the values observed in the field (Vidondo et al. 1997).

Discussion

Patch size and growth during patch development

The simple diffusional growth model based on measured clonal growth rules (i.e. rhizome elongation and branching rates, branching angle, and spacer length) and shoot mortality rate, predicted the emergence of nonlinear space occupation during the growth of *Cymodocea nodosa* patches. The size, shoot density and growth of simulated patches increased nonlinearly with time displaying two different domains of growth (Fig. 2–4). Young patches showed a rapid increase in the length of rhizome network (L) and the number of living shoots
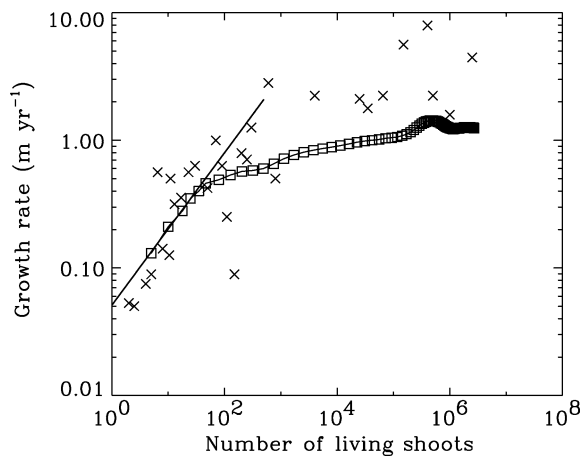

Fig. 6. The relationship between the number of living shoots (N_s) and the patch growth rate (m yr^{-1}) of modelled *Cymodocea nodosa* patches. The solid line represent the equation log (growth rate) $= -1.29 + 0.60$ (± 0.13) log (N_s) ($R^2 = 0.76$, p < 0.001) fitted to small (less than 1000 shoots) patches. ($\times$) symbols correspond to the empirical observations of patches growing in the Ebro delta by Vidondo et al. (1997).
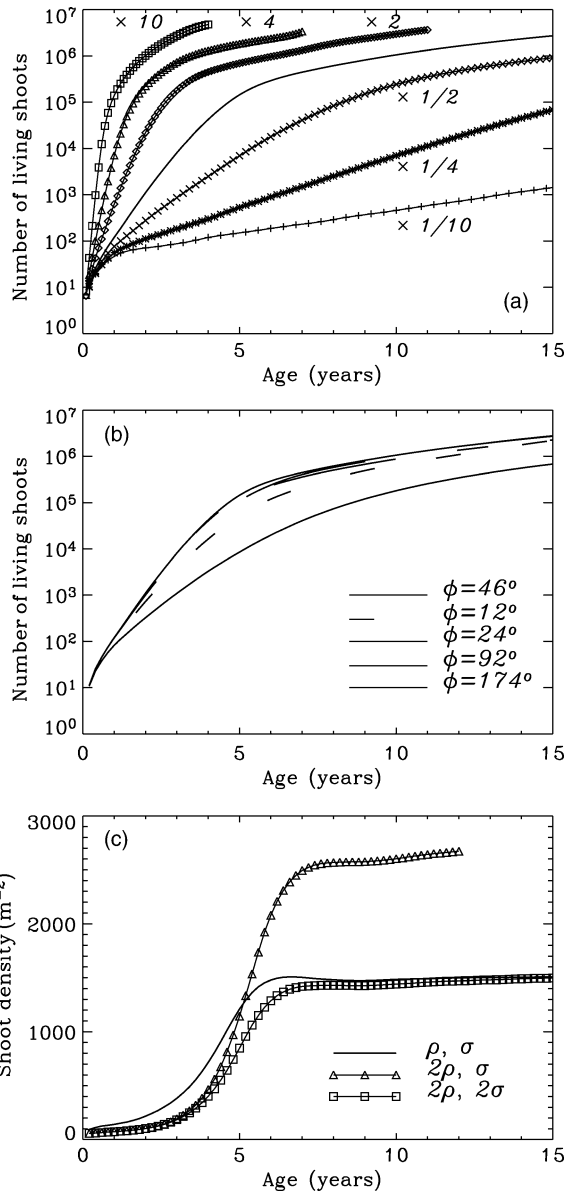

Fig. 7. Sensitivity analysis of the model varying (A) branching rate (v_b) as 10 v_b, 4 v_b, 2 v_b, v_b, $v_b/2$, $v_b/4$, $v_b/10$, (B) branching angle (ϕ) as 12°, 24°, 46°, 92°, 174°, and (C) spacer length (ρ) both maintaining the exclusion radius (σ) invariable (2ρ, σ) and keeping the exclusion radius proportional to spacer length (2ρ, 2σ).

(N_s) as $L \propto N_s \propto e^{\text{(branching rate)} \times \text{Age}}$ with time. During this period, the radial patch size (R_g) increased algebraically with the number of living shoots as $R_g \propto N_s^{1/D_f}$, being D_f the fractal dimension of the patch structure. Older patches increased the production of rhizome network and the number of living shoots much more slowly, while their radial patch size behaved as $R_g \propto N_s^{0.5}$ resulting from an internal patch compactation during growth.

The results presented here also indicate that patches of different ages show linear growth rates with a 30 fold variation (Fig. 6), despite a uniform underlying rhizome extension rate. These findings invalidate the early believe that seagrass patch growth could be modelled as a simple radial process (Duarte 1995, Kendrick et al. 1999), which led to emphasis on the measurement of linear rhizome extension rates (Marbà and Duarte 1998), and explain the observations of accelerated space occupation by clonal growth (Kendrick et al. 1999).

The modelled patch growth of *Cymodocea nodosa* closely reproduces the patch structure observed in the field, predicting a rapid increase in shoot density to reach an asymptotic shoot density comparable to the values observed in the field (Duarte and Sand-Jensen 1990b). Most importantly, the complex behaviour observed for this species in nature, where the growth rate of the patches increased nonlinearly with increasing patch size (Vidondo et al. 1997), was also observed in the modelled patches (Fig. 6). Indeed, there was a close agreement between modelled and observed (from Vidondo et al. 1997) patch behaviour (Fig. 3b, 6), which clearly demonstrates that the properties leading to the emergence of nonlinear behaviour are, to a large extent, contained within the simple rules defining clonal growth.

There are, however, some deviations between model results and empirical patterns (Fig. 6), revealing that nonlinear patch growth might also be affected by factors other than simple growth rules. For instance, *Cymodocea nodosa* ramets are physiologically integrated over distances at least 80 cm (Terrados et al. 1997, Marbà et al. 2002), and internal resources in *C. nodosa* clones are mainly mobilized towards the rhizome apex, indicative that developed ramets support clonal spread (Duarte and Sand-Jensen 1996, Marbà et al. 2002). Hence, as patch size increases, the amount of resources in the clone available for translocation should also increase, which might further accelerate the spread of the clone. Rhizome growth acceleration in natural patches, however, is expected to attain a threshold that would depend on the life span of rhizome connections. In addition, patch growth may be altered by physical disturbance (Brodie et al. 1995, Marbà and Duarte 1995). Indeed, the *C. nodosa* patch population studied by Vidondo et al. (1997) colonizes submerged dunes that migrate across the seagrass bed, and patch growth is stimulated in the direction of dune migration (Marbà and Duarte 1995). The modelled clonal growth represents a minimum rate of space occupation, for patch growth can be also accelerated by recruitment of new clones, from sexual reproduction, to the patch. However, sexual reproduction is sparse in most seagrass species (Hemminga and Duarte 2000), so that patch growth is dominated by clonal growth (Duarte and Sand-Jensen 1990a, Vidondo et al. 1997).

Branched (DLA) vs compact (Eden) growth behaviour of seagrass clones

The nature of the emergent properties developed during *Cymodocea nodosa* clonal growth is best examined through the examination of the dependence between radial patch size and the number of living shoots (Fig. 5). Small patches, containing less than 10^3 shoots, corresponding to patches <3 years old, are characterised by an increase in radial patch size with an exponent $\alpha = 0.6 \pm 0.05$ of the number of living shoots within the patch. The observed patches at these ages (Fig. 1) are highly ramified, and their growth is closely dependent on branching pattern, and comparable to those generated by a diffusion-limited aggregation (DLA) process, as further supported by the resulting fractal dimension Df ($\alpha \approx 1/D_f$) of 1.67, which is remarkably close to the $D_f = 1.7$ associated to a two dimensional DLA cluster (Witten and Sander 1981). The diffusion-limited aggregation, DLA, model (Bunde and Havlin 1996) has been used to examine the formation of dendritic patterns in a broad range of diciplines (Miller et al. 1986, Knight 1987, Roberts and Knackstedt 1993, Batty and Longley 1994, Sintes et al. 1994) and results in branched structures with radial size $R_g \approx n^{1/Df}$ where the fractal dimension, D_f, equals 1.7 (Witten and Sander 1981), as observed for the rhizomatous plant modelled.

Although the initial formulation of the DLA growth process, where new units diffuse with higher probability to join the cluster at the tips of the branches, departs from the mode of addition of new ramets to clonal plants, the net result of the DLA process is similar to the growth behaviour of *Cymodocea nodosa* – and possibly other seagrasses and clonal plants – patches, where ramets are added to the apical regions of the rhizome network. Indeed the applicability of the DLA model to structures growing from internally derived units, rather than externally diffusing ones, has already been demonstrated in, for instance, the propagation of lightning in the atmosphere (Niemayer et al. 1984).

The growth of older (>5 years old), larger patches, containing more than 10^5 living shoots, is completely different (Fig. 1). The interstices left during the early stages of clonal extension by the outgrowing rhizomes have been filled in through the branching process after 5 years, with space only becoming available within the patch through shoot mortality. At this stage, patch extension takes place mainly along the perimeter of the patch, where most rhizome apices are located (Fig. 1), This is equivalent to the so-called active zone in the Eden model. As a consequence, the patches develop into compact structures with an increasingly rough outline, and the radial patch size then grows with the number of shoots with an exponent $\alpha = 0.5 \pm 0.01$ (Fig. 5). This growth mode of older patches conforms to the main characteristics that identify an Eden growth process. The

Eden growth process (Jullien and Botet 1985) describes the growth of rough interfaces of compact structures (Stanley and Ostrowsky 1986). The Eden model, initially developed to investigate the growth of cell colonies (Eden 1961), has been applied to the study of skin cancer (Williams and Bjerkness 1972) and epidemic behaviour (Vandewalle et al. 1998) among others. In a simple representation, a cell in the perimeter of the colony divides, locating the daughter cell in an unoccupied nearest neighbourhood position of the mother cell yielding compact structures with a rough contour or surface and a radial size (R) scaled to the number of individuals (n) as $R \approx n^{1/2}$. This scaling is similar to those modeled for older than 5 yr *Cymodocea nodosa* clones. Therefore, the complex behaviour of *Cymodocea nodosa* patch growth appears to result from a mode shift from an initially diffusional-limited (DLA model) to an Eden-like growth model, and a corresponding shift from a dendritic to a compact clone structure.

The critical event accounting for the shift in patch growth mode is the requirement that patch growth must progress from an initial, random directional growth to a uniform centrifugal growth. This change requires sufficient branching events within the clone as to allow a 180° shift from the initial direction of clone propagation in some of the branches. Provided an average branching frequency of 2.3 branches apex^{-1} year^{-1}, and the fact that the plants branch at alternate sides of the rhizome, and an average branching angle of 46°, the time scale required for this 180° shift from the initial direction of clone propagation is 3.4 years (i.e. 180° /[46° (2.3 br yr^{-1}/2)] = 3.4 yr), comparable to the critical time over which a shift from the diffusion-limited to the compact growth modes occurs (Fig. 1). Hence, the branching frequency of the rhizome and branching angle are the controlling factors setting the transition from a diffusion-limited to a compact growth mode, occurring in patches 3 to 5 years old for this species.

Once the compact growth mode has been reached, at *Cymodocea nodosa* patches of >5 years of age, rhizome apices are predominantly located along the periphery of the patch, supporting a centrifugal, radial patch growth in all directions. This growth mode is conducive to the achievement of a uniform horizontal patch growth rate, similar to the rhizome extension rate of this species (Fig. 6), and to the stabilisation of the internal shoot density (Fig. 2). Whereas the horizontal extension rate is maximal for older, compact patches, the rate of increase in the total length of the rhizome network and the total number of shoots contained therein is much less than that over the initial growth phase (Fig. 3). This reduction in the rate of increase in total rhizome length and shoot number within fast growing patches derives from the onset of density-dependent in rhizome growth within patches. Although there is evidence for such density-dependent growth in clonal plants (De Kroon and

Kwant 1991, Cain et al. 1995), our understanding of such effects is still poor. However, the existence of a dependence of clonal growth on neighbouring shoot density would explain the lack of self-thinning observed in some seagrasses (Olesen and Sand-Jensen 1994) and other clonal plant populations (Hutchings 1979).

Comparison with alternative modeling approaches

Different models have been developed, over the past three decades to simulate and analyse clonal growth. The spread of plant clones has been simulated using deterministic, stochastic as well as lattice models (Oborny and Cain 1997). The first models (Bell et al. 1979, Brouns 1987) simulated the growth of plant clones on the basis of deterministic plant architectural parameters and, thus, they did not incorporate intrinsic variability (e.g. plasticity), and often, they failed to account for interactions with neighbours. These deterministic models were, therefore, primarily heuristic tools, which did not accurately represent clones growing in the field. Stochastic models, such as that used by Callaghan et al. 1990 to study the clonal spread of *Lycopodium annotinu* and examine genet demographic dynamics, contained a large number of parameters (more than 12 in Callaghan et al. 1990), which made it difficult to extract the key parameters controlling clonal growth. Lattice models, including agent-based or cell automata models (Oborny 1994), cannot incorporate an exclusion area different than the lattice size, and force the plant to grow on the lattice, which constrains the branching angle, a key parameter determinating the transition time between branched to compact growth regimes. Cain (1990) used a diffusion model to try to explain the observed spread of *Solidago altissima* clones in the field. Cain (1990) concluded that the long-term growth rate of ramet spread only showed a linear increase in clone surface with time at developed stages of the clone, and that young clones show a slower growth rate than expected, as also reported by Vidondo et al. (1997) for a seagrass species. Simpler models combining deterministic and stochastic components were produced by Marbà and Duarte (1998) to model the growth of seagrass species. Although limited computing power only allowed examination of the early stages of clonal growth, the model already captured some of the observed nonlinearities in its output (Marbà and Duarte 1998). Hence, none of the models produced so far succeeded in accounting for the nonlinearities observed in clone spread over time. The model presented here combined (1) a parsimonic, but robust, stochastic model allowing for interactions between the shoots, (2) far greater computing power than used in the past, and (3) a posteriori analytical investigation of the model behavior to successfully explain the transition between both growth domains

and identifying the main drivers of the observed behaviour.

Conclusion

The model presented allowed the explanation, using simple growth rules, of the complex growth pattern reported for *Cymodocea nodosa* patches, and identified the critical role of the rhizome branching frequency and the branching angle in determining the growth rate of the clonal network, particularly in young clones, and the timing of the mode shift experienced from an initial diffusion-limited growth of a filamentous patch to the compact growth mode of an older patch. Yet, evidence of nonlinear patch growth extends beyond the species investigated here (Cain 1990, Marbà and Duarte 1998, Kendrick et al. 1999). Indeed, the critical components of the observed nonlinear behaviour (branching frequency and angle) are basic components of the growth of all seagrass and clonal species. For instance, branching frequency and angles vary greatly (0.03–14.29 year^{-1} and 19–81 degrees, respectively, Marbà and Duarte 1998) among seagrass species, suggesting that the time scales for the domain shifts in patch growth as well as their efficiency to spread their clones, must differ widely among species. Indeed, sensitivity analysis indicates that differences in branching frequency of two orders of magnitude might result into clones with sizes ranging over 4 order of magnitude (Fig. 7a). Knowledge of the time scales of domain shifts is essential to forecast space occupation by clonal plants, since the rate of patch extension of *Cymodocea nodosa* varied >30 fold with patch size.

The diffusion-limited and compact growth modes, alternatively displayed along the life span of *Cymodocea nodosa* clones, yield space occupation patterns equivalent to the guerrilla-type and phalanx-type strategies described for clonal plants, respectively (Lovett Doust 1981). Hence, *C. nodosa* clones, and most probably the rest of seagrasses and clonal plants shift from a guerrilla-type to a phalanx-type growth at one point, dependent on their branching frequency and angle, mode during their life. Whereas guerrilla- and phalanx-growth were believed to be species-specific traits, our results suggest that they also result from differences in the growth phase of the clones.

Although a simple process, involving essentially three components (rhizome elongation rate, branching rate and branching angle), internal interactions may render the growth of clonal networks complex, leading to the development of nonlinear behaviour and the emergence of two domains pertain to early diffusion-limited expansion and subsequent compact growth, respectively. The modelling approach used here provides a new avenue to explore these processes and improve our capacity to forecast the expansion rates of rhizomatous plants, and demonstrates the value of the application of models generated within complex system theory to the understanding of ecological processes. A modelling approach is particularly important, since the time scales involved in clonal growth (decades to centuries in some seagrass species, Duarte 1995) are too long for direct observation and experimentation.

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