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Patch dynamics of the Mediterranean seagrass *Posidonia oceanica*: Implications for recolonisation process

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ABSTRACT

Patch dynamics of the Mediterranean slow-growing seagrass *Posidonia oceanica* was studied in two shallow sites (3–10 m) of the Balearic Archipelago (Spain) through repeated censuses (1–2 year^{-1}). In the sheltered site of Es Port Bay (Cabrera Island), initial patch density (October 2001) was low: 0.05 patches m^{-2}, and the patch size (number of shoots) distribution was bimodal: most of the patches had less than 6 shoots or between 20 and 50 shoots. Mean patch recruitment in Es Port Bay (0.006 ± 0.002 patches m^{-2} year^{-1}) exceeded mean patch loss (0.001 ± 0.001 patches m^{-2} year^{-1}), yielding positive net patch recruitment (0.004 ± 0.003 patches m^{-2} year^{-1}) and a slightly increased patch density 3 years later (July 2004, 0.06 patches m^{-2}). In the exposed site of S'Estanyol, the initial patch density was higher (1.38 patches m^{-2}, August 2003), and patch size frequency decreased exponentially with size. Patch recruitment (0.26 patches m^{-2} year^{-1}) and loss (0.24 patches m^{-2} year^{-1}) were high, yielding a slightly increased patch density in the area 1 year later (October 2004, 1.40 patches m^{-2}). Most recruited patches consisted of rooting vegetative fragments of 1–2 shoots. Seedling recruitment was observed in Summer 2004 at both sites. Episodic, seedling recruitment comprised 30% and 25% of total patch recruitment in Es Port Bay and S'Estanyol, respectively. Patch survival increased with patch size and no direct removal was observed among patches of 5 shoots or more. Most patches grew along the study, shifting patch distribution towards larger sizes. Within the size range studied (1–150 shoots), absolute shoot recruitment (shoots year^{-1}) increased linearly with patch size ($R^2 = 0.64$, $p < 4 \times 10^{-5}$, $N = 125$), while specific shoot recruitment was constant (about 0.25 ± 0.05 year^{-1}), although its variance was large for small patches. Given the slow growth rate and the high survival of patches with 5 or more shoots, even the low patch recruitment rates reported here could play a significant role in the colonisation process of *P. oceanica*.

1. Introduction

Seagrasses develop key coastal ecosystems (Hemminga and Duarte, 2000), which are experiencing widespread decline, parallel to human coastal development (Orth et al., 2006). In the last years, partial recovery has been observed in some seagrass meadows following reductions of local impacts (e.g. Kendrick et al., 1999; Pergent-Martini et al., 2002; Hernández-Cruz et al., 2006), but not in others (e.g. Kendrick et al., 2002). An improved understanding of the environmental (e.g. Marbà and Duarte, 1995; Ramage and Schiel, 1999; de Falco et al., 2000; Frederiksen et al., 2004; Di Carlo et al., 2005, 2007) and life-history constraints (e.g. Duarte and Sand-Jensen, 1990b; Olesen et al., 2004; Sintes et al., 2006) controlling seagrass colonisation are of major importance to predict and facilitate meadow recovery.

Seagrasses are clonal plants, and their spatial spread relies on apical elongation and branching of their rhizomes (Duarte, 1995). New seagrass patches are formed from successfully established seeds (e.g. Duarte and Sand-Jensen, 1990a,b; Balestri et al., 1998; Olesen et al., 2004) or drifting vegetative fragments (Boudouresque et al., 1990; Campbell, 2003; Hall et al., 2006), which subsequently spread through clonal growth. Patch growth has been studied (e.g. Duarte and Sand-Jensen, 1990a; Kendall et al., 2004) and modelled (Marbà and Duarte, 1998; Sintes et al., 2005, 2006; Kendrick et al., 2005a,b) for some seagrasses. Efforts indicate that patch growth rate and growth mode change with patch size (Sintes et al., 2005, 2006), as a direct consequence of allometrically scaled growth rules (Duarte, 1991a,b; Marbà and Duarte, 1998) and clone size benefits (Olesen and Sand-Jensen, 1994; Kendrick et al., 2005a).

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Patch initiation is the primary step of the colonisation process, and continuous patch recruitment may accelerate it (Kendrick et al., 1999; Kendall et al., 2004). Despite an increasing number of studies on seagrass patch dynamics (e.g. Duarte and Sand-Jensen, 1990a; Campbell, 2003; Di Carlo et al., 2005), the role of patch recruitment in spatial colonisation is still poorly assessed (Kendrick et al., 2005a), and the relative role of sexual versus vegetative propagules in seagrass spatial colonisation is known for few seagrass species (e.g. Olesen et al., 2004).

Posidonia oceanica, the endemic and dominant seagrass in the Mediterranean (Den Hartog, 1970), is the most slow growing seagrass species in the world in terms of rhizome elongation rate (Marbà and Duarte, 1998), with very sparse sexual reproduction (e.g. Diaz-Almela et al., 2006, 2007). It is experiencing widespread decline (Marbà et al., 2005). *P. oceanica* meadows may persist over millennia (Boudouresque et al., 1980; Mateo et al., 1997), but its extremely slow horizontal elongation rate (1–10 cm year^{-1}, Marbà and Duarte, 1998) renders spatial colonisation of this species a process extending over centuries (Meinesz and Lefevre, 1984; Duarte, 1995; Sintes et al., 2006). Although there is evidence of patch recruitment (e.g. Balestri et al., 1998), its relative role in the colonisation process is poorly understood, because the exceedingly slow dynamics of this species complicates direct measures of patch recruitment and growth, necessary to feed models of colonisation dynamics.

Here we examine the inter-annual patch dynamics (recruitment, survival and growth) of the seagrass *P. oceanica*, through direct censuses in two shallow sites off the Balearic Islands (Spain). Our aims were to determine the relative importance of patch recruitment rate in *P. oceanica* spatial colonisation and to quantify the rate of vegetative and sexual recruitment in *P. oceanica.*

2. Materials and methods

The population dynamics of *P. oceanica* patches were studied in two shallow sites off the Balearic Islands: one site was located in Es Port Bay (Cabrera Archipelago National Park, 39°9.03′N; 2°56.05′E, Fig. 1). This is a sheltered bay, with a long water residence time (Orfila et al., 2005). The area was 2.5–6.5 m depth, and was situated between a small harbour and a dense, small meadow, with muddy sediment, and the thickness of the soft substrate ranged from 30 cm to over 60 cm, measured with a rigid plastic meter. The water transparency is high. The other site was located in S'Estanyol Bay, on the Southeast coast of Mallorca (39°21.42′N; 2°54.90′E, Fig. 1). The area is shallow (3–4 m) and exposed to southern winds, but there is no published information on its hydrodynamics. The area consists of rock plates with interspersed small troughs (around 200 m^2 each) with coarse sand and gravel (depth of the soft substrate <1–10 cm), partially covered by turf of small macroalgae. The bulk of the seagrass patches is concentrated in the troughs, whereas the rocks are shallower and more exposed.

In Es Port Bay, patch dynamics was studied from October 2001 until September 2004. A rectangular area of 915 m^2 was delimited with four metal sticks. During each visit, scuba divers divided the area into four quadrants and surveyed it. Every rooted plant of *P. oceanica* (vegetative shoot, seedling or patch, consisting in a cluster of connected shoots) inside the perimeter was localised with angular coordinates (distance to the closest corner stick, degrees North) and was tagged attaching a cable tie with a numbered tag around the rhizome of 1–4 shoots at the patch periphery. The patch was additionally marked by sticking a metal pin attached to a small buoy next to the plant, labelled with the patch number. A map of the patches within the area was elaborated with the patch coordinates obtained as in Vidondo et al. (1997), in order to facilitate subsequent censuses. The area was visited twice per year, at intervals of 4–9 months. During each visit, a new census of the patches present in the area was done. The presence/absence of the marked patches was noted and all newly rooted patches within the area were positioned and labelled.

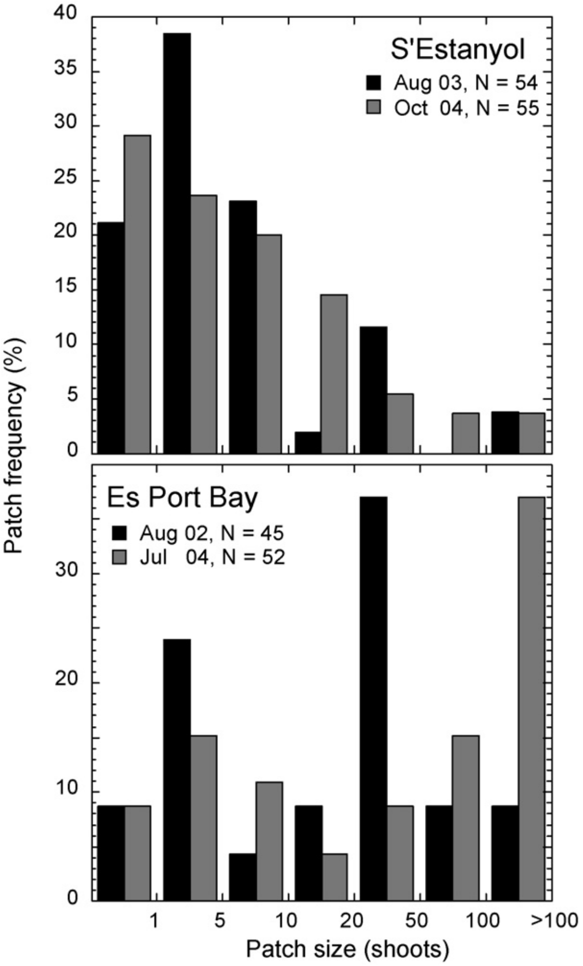

Fig. 1. Patch size distribution (percentage of patches within each size class, size as number of shoots) in S'Estanyol and Es Port Bay in the first (grey bars) and last (black bars) censuses.

In S'Estanyol, patch dynamics were studied only during 1 year, from July 2003 to October 2004 using the same procedures as in Es Port Bay. Due to the high patch density, the area surveyed, localised within a trough, was substantially smaller (39.3 m^2), and consisted of two opposed quarters of an imaginary circle of 10 m in diameter.

At both sites we measured the patch size through counts of the number of shoots forming them if they were smaller than 50 shoots. The larger patches were classified into patches with 50–100 shoots and patches with more than 100 shoots. During each visit, the shoot recruitment of the patches smaller than 50 shoots in the previous census was quantified by counting the number of shoots. In the following visits, the shoots in some of the patches that had grown larger than 50 shoots were counted in order to quantify the shoot recruitment rate within larger patches. Absolute shoot recruitment rate was calculated as the number of new shoots appearing in the patch within the period between two censuses (in years). Assuming an exponential population growth model, the specific net shoot recruitment was calculated as in Eq. (1), as shown in Sheil et al. (1995).

$$g = \frac{\ln(n_t/n_{t-1})}{\Delta t} \qquad \text{Specific net shoot recruitment (year}^{-1}\text{)} \qquad (1)$$

where n_{t-1} and n_t were the initial and final patch shoot numbers. Annual shoot recruitment rates were compared between sites, performing a *t*-test for unpaired samples with equal variances (the *F* test or inequality of variances was not significant). The relationships between absolute/specific patch shoot recruitment and initial patch size were explored graphically and through regression analysis (type II, least squares distances) with the "fit model" procedure of JMP 5.0.1 for MacOs X.

We calculated absolute (M) and specific (m) patch removal rates in the period Δt (in years) between two censuses ($t-1$ and t) in the study areas (S in m^2), from the difference between the total number of patches marked in the first census (N_{t-1}) and the total number of surviving patches found in the second census ($N_{t\text{surv}}$), following the Eqs. (2) and (3).

$$M = \frac{N_{t-1} - N_{t\text{surv}}}{\Delta t \cdot S} \qquad (2)$$

Absolute patch removal rate (patches m^{-2} year^{-1})

$$m = \frac{\ln(N_{t\text{surv}}/N_{t-1})}{\Delta t} \qquad \text{Specific patch removal rate (year}^{-1}\text{)} \qquad (3)$$

Absolute rates correspond to a geometric population growth model, and specific rates to an exponential population growth model. We calculated absolute and specific patch recruitment rates from the number of new patches appearing in the subsequent censuses ($N_{t\text{new}}$), as in the Eqs. (4) and (5).

$$R = \frac{N_{t\text{new}}}{\Delta t \cdot S} \qquad (4)$$

Absolute recruitment rate (patches m^{-2} year^{-1})

$$r = \frac{\ln(N_{t\text{new}}/N_{t\text{surv}})}{\Delta t} \qquad (5)$$

Specific patch recruitment rate (year^{-1})

This fraction slightly overestimates the specific patch recruitment. If, alternatively, we had divided the number of recruited patches by the initial number of patches marked, we would instead have slightly underestimated the specific patch recruitment. When there are few survivors, a more accurate estimator can be obtained dividing the number of recruits by the average between the initial number of patches in the first census and the number of survivors in the second census. However, when the percentage of survivors is high, like in this case, the output difference between the three methods is minimal.

Vegetative and sexual patch recruitment were calculated in the same way, but counting only the new patches consisting on vegetative new fragments or seedlings (respectively), which were easy to distinguish in their initial state.

At every survey, patches were assigned to one of the following size categories: 1 shoot, $1 < \text{patch} \leq 5$ shoots, $5 < \text{patch} \leq 10$ shoots, $10 < \text{patch} \leq 20$ shoots, $20 < \text{patch} \leq 50$ shoots, $50 < \text{patch} \leq 100$ shoots, and $\text{patch} > 100$ shoots.

With the exception of the first category (1 shoot = 1 ramet, i.e. not clonal), the size of each category was defined as doubling the size of the previous one.

During each visit, the number of surviving patches that belonged to each size class in the previous census was counted (independently of whether they remained in the same size class or changed to another size class), and this was used to estimate the patch probability to survive, p_x for each size class, as $1 - m$, where m is the specific patch removal rate, calculated as in Eq. (2) only within patches of this size class. In Es Port Bay, where 5 censuses were conducted, we estimated p_x for each period between two censuses and computed the mean and standard errors of survival probability of each size class. We also calculated the probability of fragments with one shoot to initiate clonal growth, calculating the fraction of patches with only one shoot that produced at least one new shoot between two censuses (fraction of branching patches per year). We calculated the patch branching probability for patches with two shoots or more in the same way. The annual fraction of patches growing from size class <5 shoots to ≥ 5 shoots, the annual patch fraction that lost shoots, passing from class ≥ 5 shoots to <5 shoots, and the annual fraction of patches with less than 5 shoots to be reduced to only 1 shoot, were also calculated in that way.

3. Results

In October 2001 we found 44 patches of *P. oceanica* growing in the studied area at Es Port Bay (Cabrera), yielding an initial density of 0.05 patches m^{-2} (Table 1). In S'Estanyol (Mallorca), patch density was substantially higher, with 1.38 patches m^{-2} in the census area (Table 1). The size distribution of patches in Es Port Bay was bimodal, most patches were composed of 21–50 shoots, or had less than 5 shoots (Fig. 2). In S'Estanyol, most patches were small, containing less than 5 shoots (Fig. 2).

Table 1
Patch demographic parameters at Es Port Bay and S'Estanyol

	N m^{-2}	%N_0	M	R	R_s	λ	m	r	r_s	μ	Pg$_1$	Pg$_{x>1}$	Pg$_{x\geq5}$	Pr$_{<5}$	Pr$_1$
Es Port Bay											$n = 13$	$n = 82$	$n = 38$	$n = 47$	$n = 38$
October 2001	0.048	100	–	–	–	–	–	–	–	–					
January 2002	0.051	100	0	0.011	0	0.011	0	0.229	0	0.229					
August 2002	0.049	96	0.0038	0.002	0	−0.002	0.114	0.039	0	−0.075	0	0.81	0.46	0.58	0.31
March 2003	0.052	96	0	0.006	0	0.006	0	0.120	0	0.120	0.47	1.27	0.16	0	0
November 2003	0.051	93	0.0016	0	0	−0.002	0.030	0	0	−0.030	0	0.81	0.20	0.12	0.14
July 2004	0.057	91	0.0017	0.008	0.007	0.007	0	0.155	0.125	0.155	0	1.14	0.66	0	0
Mean	0.052	–	0.0014	0.006	0.002	0.004	0.029	0.109	0.025	0.080	0.12	1.01	0.37	0.17	0.11
S.E.	0.001	–	0.0008	0.002	0.002	0.003	0.025	0.046	0.028	0.064	0.13	0.14	0.14	0.16	0.09
S'Estanyol Bay															
August 2003	1.38	100	–	–	–	–	–	–	–	–	$n = 12$	$n = 35$	$n = 17$	$n = 25$	$n = 17$
October 2004	1.40	78	0.237	0.259	0.065	0.022	0.193	0.208	0.057	0.016	0.21	0.55	0.25	0.07	0.00

Patch density (N m^{-2}), percentage of survivors of the patches initially marked (%N_0). M: absolute patch loss rate, R: recruitment rate (vegetative plus seedlings), R_s: absolute seedling recruitment rate, λ: absolute net patch recruitment (patches m^{-2} year^{-1}). m: specific patch loss, r: specific total recruitment, r_s: specific seedling recruitment, μ: specific net patch recruitment (year^{-1}). Pg$_1$: annual fraction of patches initiating clonal growth (i.e. branching of patches with only 1 shoot), Pg$_{x>1}$: annual branching fraction of patches with 2 or more shoots, Pg$_{x\geq5}$: annual fraction of patches to grow to the size class with 5 shoots or more; Pr$_{<5}$: annual fraction of patches with 5 shoots or more to pass to the lower size classes ($1 = x < 5$), Pr$_1$: annual fraction of patches in the class size $2 < x < 5$ to decrease to the smaller size class $x = 1$.

Patch density in Es Port Bay increased by 23% along the 3 years of the study, reaching 54 patches in the area, or 0.06 patches m^{-2}, in July 2004 (Table 1). Patch recruitment rates in Es Port Bay (0.006 ± 0.002 patches m^{-2} $year^{-1}$) generally exceeded patch removal (0.001 ± 0.001 patches m^{-2} $year^{-1}$) rates, yielding a positive net population growth rate of 0.004 ± 0.003 patches m^{-2} $year^{-1}$ (Table 1).

In S'Estanyol Bay balance between patch removal (0.24 patches m^{-2} $year^{-1}$) and recruitment (0.26 patches m^{-2} $year^{-1}$) was also positive the sampled year (Table 1).

There were strong differences in patch recruitment and survival between both sites: in S'Estanyol, absolute patch recruitment rates were 24 times higher than the maximal recruitment rate registered at Es Port Bay, while absolute patch removal rates were 60 times higher than the highest patch removal rate recorded in Es Port Bay. As a result, the mean net patch recruitment rate in the sheltered site of Es Port Bay was 5 times higher than net recruitment rate in the more exposed site of S'Estanyol (special two sample *t*-test when one sample has a single observation: $p < 0.05$, d.f. = 4).

Patch recruitment at both sites occurred mainly through drifted vegetative cuttings of 1 or 2 shoots, naturally detached and re-rooted (Table 1). Seedling recruitment was recorded in summer and autumn 2004 in Es Port Bay (4 rooted seedlings) and S'Estanyol (3 rooted seedlings), respectively. In Es Port Bay, the mean seedling recruitment rate during the study was of 0.002 ± 0.002 seedlings m^{-2} $year^{-1}$, but it was an irregular and rare event (Table 1). Sexual recruitment represented on average 30% of total recruitment rate. In S'Estanyol sexual recruitment in the annual period was of 0.065 shoots m^{-2} $year^{-1}$ (Table 1), representing 25% of total recruitment that year. Assuming no sexual recruitment at S'Estanyol during the previous 2 years, sexual recruitment in S'Estanyol would have a down-weighted mean of 0.032 shoots m^{-2} $year^{-1}$. Nevertheless, the actual contribution of seedlings to total recruitment at a longer time-scale is probably lower in both sites, because no established seedlings were detected at any of the sites during the first census. Among small patches of 1–3 shoots no seed remains were distinguished, and in many of them, the morphology of adult vertical shoots that had reverted to horizontal growth could still be observed. This suggests that no sexual recruitment took place in the years immediately before the study, also because the seedling recruitment registered at both sites in 2004 seems to be part of a large scale, synchronous event (cf. Diaz-Almela et al., 2006, 2007). In S'Estanyol patch survival was lower than in the sheltered site of Es Port Bay: only 80% of the patches initially marked in S'Estanyol were found 1 year later, while in Es Port Bay 91% of the patches initially marked were still there, after almost 4 years. Patch survival increased with patch size (in terms of number of shoots conforming it, Fig. 2). Survival probability of small patches (<5 shoots) was higher in Es Port Bay than in S'Estanyol (Fig. 2). In both sites, survival of patches containing more than 5 shoots was of 100%. Nevertheless, in Es Port Bay, one patch initially consisting on 11 shoots decreased in size during the study, having only 1 shoot left by November 2003, it had disappeared by the next census (July 2004, Fig. 3).

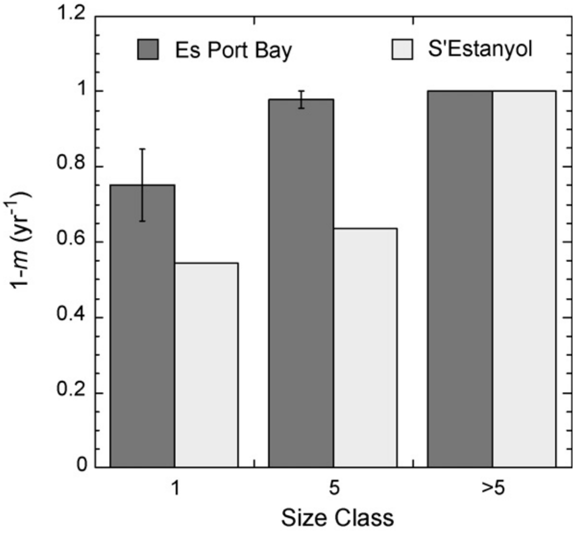

Fig. 2. Patch permanence probability ($year^{-1}$) depending on patch size in Es Port Bay (deep grey bars) and S'Estanyol (clear bars). The error bars represent standard error between censuses in Es Port Bay.

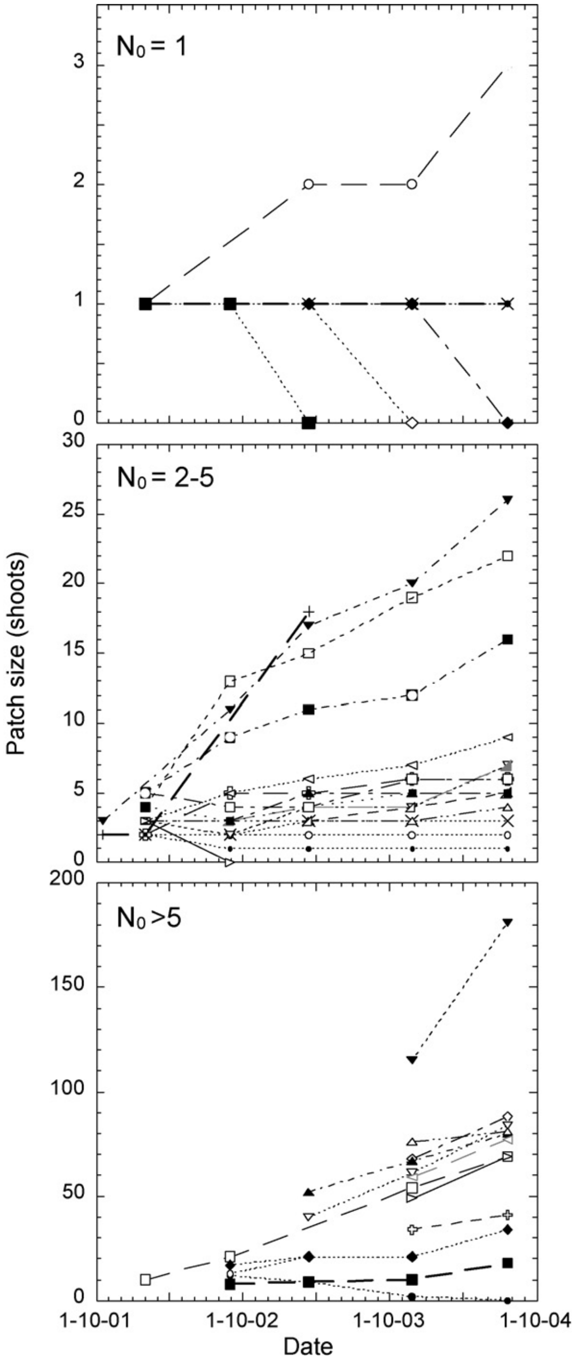

Fig. 3. Evolution of individual patch sizes (in terms of number of shoots) during the study. Symbols indicate different individual patches.

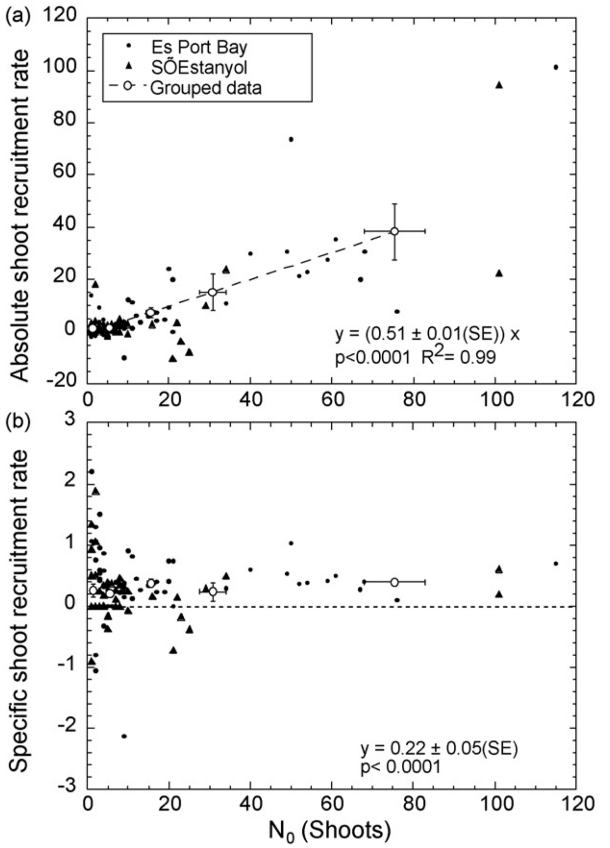

Fig. 4. The relationship between the absolute (shoots year^{-1}) and relative (year^{-1}) net shoot recruitment rate and the initial patch size (as the number of shoots). The dashed line in (a) represents the fitted regression equation ($R^2 = 0.64$, $p < 4 \times 10^{-5}$, $n = 125$). Black triangles correspond to patches from S'Estanyol, black circles correspond to patches from Es Port Bay. White circles correspond to averages of values grouped in size bins and the bars represent the standard errors of the bin averages.

Most patches survived and grew with time (Fig. 3), producing the global increase in patch size distribution at both sites (Fig. 1). Absolute shoot recruitment did not differ among sites ($p > 0.5$, t-test, $t = 0.68$, d.f. = 125, $N_{\mathrm{Es\ Port}} = 40$, $N_{\mathrm{S'Estanyol}} = 87$), and increased linearly with patch size at both sites (S'Estanyol Bay: $R^2 = 0.56$, F-test: $p < 0.001$; Es Port Bay: $R^2 = 0.68$, F-test: $p < 0.001$) and globally ($R^2 = 0.64$, F-test: $p < 10^{-28}$, $N = 127$, Fig. 4a) within the size range studied (1–150 shoots). Despite the lower number of data on large patches, the scatter of absolute shoot recruitment was apparently larger for large patches (Fig. 4a). Specific shoot recruitment rate did not depend on patch size, and was on average 0.22 ± 0.05 (S.E.) year^{-1}, although it was highly variable for patches with less than 30 shoots (Fig. 4b). The annual fraction of patches consisting on a unique ramet that branched was nearly 9 times lower than the annual fraction of patches with two shoots or more that branched: all patches with more than one shoot branched at least once in a year (Table 1). Annually, 37% ± 14% of patches with less than 5 shoots developed to a patch size of 5 shoots or more (a size class from which no direct patch loss was observed). Annually, 17% ± 16% of patches with 5 shoots or more lost shoots, entering the lower size class, and 11% ± 9% of patches with 2–4 shoots were reduced to a fragment with only one shoot (Table 1).

4. Discussion

During this study, a spontaneous colonisation took place at both shallow sites, with a slight increase in patch density and mean patch size, as well as some patch coalescence events. Net patch recruitment was 8% of the gross rates of patch establishment in the exposed site of S'Estanyol, while in the sheltered site of Es Port Bay, net patch recruitment represented 67% of gross patch establishment rates. The rapid patch turnover in S'Estanyol, strongly limiting the fraction of small patches that survived and grew to large size classes, determined the observed exponential decrease in abundance with patch size. The same skewed distribution of patch size has been described for expanding patches of other seagrass species (e.g. Duarte and Sand-Jensen, 1990a; Vidondo et al., 1997). In shallow sites, the balance between patch removal and settlement appears highly controlled by hydrodynamics (Ramage and Schiel, 1999; Campbell, 2003; Di Carlos et al., 2005), substrate characteristics and shelter (Piazzi et al., 1998; de Falco et al., 2000; Di Carlo et al., 2005), which determine a depth limit above which seagrass propagules fail to establish (Piazzi et al., 1998; Campbell, 2003). The depth and substrate differences between the rocky platforms and the trough at S'Estanyol (1–2 m) probably account for the concentration of patches in the troughs. Nevertheless, survival rate there was similar to that reported in exposed rubble-mound crests at 5 m (Di Carlo et al., 2005). In Es Port Bay, the bimodal patch size distribution suggests that most patch recruitment is strongly episodic, as previously suggested for this site (Marbà et al., 2002).

Seedling recruitment in Es Port Bay and S'Estanyol was observed only at the end of the study, 9–12 months after an outstanding flowering event in the region (Diaz-Almela et al., 2006, 2007). This coincides with observations of other authors, indicating that *P. oceanica* seedling recruitment is episodic (Buia and Peirano, 1988; Gambi et al., 1996; Balestri et al., 1998). However, given the low patch recruitment rates observed at both sites, seedling recruitment constituted a significant fraction of total patch recruitment rates (30% and 25% of total recruitment in Es Port Bay and S'Estanyol, respectively). This is low when compared with other large seagrasses like Enhalus acoroides (100%, Olesen et al., 2004) or *Zostera marina* (96%, Greve et al., 2005), for which seedling recruitment plays a very important role in meadow development and persistence. This coincides with reports for other species of the genus *Posidonia*, from Campbell (2003), indicating a high contribution of vegetative fragments to patch formation. In the tropical large seagrass *Thalassia hemprichii*, seedling recruitment is rare, but sometimes it can become very high (e.g. 85% ± 14%, Olesen et al., 2004). This may be a response to episodic meadow perturbations and could also operate in the long-lived *P. oceanica*.

Most of the *P. oceanica* patch recruits consisted on drifted and re-rooted vegetative cuttings of 1 or 2 shoots. Fragmentation is a successful strategy leading to vegetative propagation in many macroalgae (Walters and Smith, 1994; Smith and Walters, 1999) and also in some seagrasses (Vermaat and Verhagen, 1996; Campbell, 2003; Hall et al., 2006). In the case of *P. oceanica*, forming persistent meadows (Mateo et al., 1997) that contain billions of shoots (ramets) of infrequent flowering (Diaz-Almela et al., 2006, 2007), such thick, lignified shoots detached during storms may play an important role in plant dispersal. This mechanism has been invoked to explain the finding of identical genotypes across tens of kilometers (Ruggiero et al., 2002; Arnaud-Haond et al., unpublished data).

The increased patch survival and growth with patch size (expressed in number of shoots) reported here for *P. oceanica* is in agreement with reports for other seagrass species, as *Z. marina* (Olesen and Sand-Jensen, 1994), *Cymodocea nodosa* (Vidondo et al., 1997) and *Z. novazelandica* (Ramage and Schiel, 1999). The size-dependence of patch growth and survival has been attributed to mutual shoot sheltering (Vermaat et al., 1987), enhanced encroachment and resource foraging and sharing (Olesen and Sand-Jensen, 1994), as well as a reduction of perimeter to area ratio with increased patch size, which would increase the resources available for peripheral patch growth (Kendrick et al., 2005a). Large clones are apparently more resistant to perturbations (Diaz-Almela et al., 2007). If only, the complete removal of patches through fragmentation or shoot mortality should take longer for large patches, than for small patches with few shoots.

The negative shoot recruitment rates observed among small *P. oceanica* patches with less than 20 shoots, and the progressive stabilisation of specific shoot recruitment rate with patch size suggest that resources and/or erosion may strongly limit growth and survival of small *P. oceanica* patches. The annual fraction of fragments with only one shoot that initiated clonal growth (i.e. produced a new shoot) was very low, as compared to the annual fraction of patches with more than one shoot that branched. This has also been described for the seagrass *C. nodosa* in Alfacs Bay (Spain), where clonal growth initiation from seedlings was limited by P availability (Duarte and Sand-Jensen, 1996). Seedlings of *P. australis* take 2.7 ± 0.3 years on average to produce a second shoot (Meehan and West, 2004), and the branching rate of *P. oceanica* seedlings is of 0.14 ± 0.03 year^{-1} (Balestri et al., 1998), which is 6 times lower than apex branching rate in developed meadows (Díaz-Almela, unpublished data). Transplanted cuttings of *P. oceanica* with two shoots or more show higher survival, growth and branching rates than cuttings with only one shoot (Molenaar et al., 1993; Piazzi et al., 1998).

Past research on other seagrass species (Duarte and Sand-Jensen, 1990a; Vidondo et al., 1997; Meehan and West, 2004) and growth models indicate that growth rate initially increases with patch size and will stabilize later, as the clone would move into a compact growth phase (Sintes et al., 2005, 2006). In this study we only found a linear increase of absolute growth rate with patch size, although, the scatter of absolute growth appears to increase in large patches. This linear relationship is in agreement with model outputs predicting that the modal growth change to compact growth for *P. oceanica* clones would take place in patches of 70–120 years, containing 10^3–10^4 shoots (Sintes et al., 2006). This size greatly exceeds the range measured in this study (<200 shoots).

Patch recruitment rates of *P. oceanica* were very low, so that the time estimated to double patch density ranged between 9 years at Es Port Bay and 45 years at S'Estanyol. Nevertheless, the patch recruitment and removal rates have been measured at an early stage of colonisation, during limited periods (1–4 years), for a species that takes centuries to develop a meadow (Meinesz and Lefevre, 1984; Marbà et al., 2002; Sintes et al., 2006). Patch growth affects local hydrodynamics as patches expand and coalesce (Folkard, 2005) and may change the conditions for other patches to set up and grow. Large patches may produce shelter in their surroundings, increasing the survival of adjacent small patches: Moreover, large patches may also produce a higher number of vegetative propagules, which would increase patch recruitment rates in the vicinity. The aggregate distribution of patches in Es Port Bay and S'Estanyol, with a large number of small patches growing around the largest ones (patch maps not shown), is in agreement with the idea that patch size affects the likelihood of neighbouring patch establishment. Thus, patch recruitment and turnover rates are likely to change as the colonisation process advances. This source of complexity would add up to changes in patch growth, producing decadal changes in colonisation rate.

Given the slow clonal growth of *P. oceanica*, even the thin and episodic rain of vegetative fragments and seeds observed in this study could significantly increase the colonisation speed, as compared with a unique colonisation event (Kendrick et al., 1999, 2005a,b), although meadow formation would still remain a process in the secular scale. On the other hand, the recruitment of propagules, especially of seedlings, may also increase the genetic diversity of the resulting meadow stand (Orsini et al., 2001), which could have a positive effect in the colonisation process (Procaccini and Piazzi, 2001) and on meadow resistance (Hughes and Stachowicz, 2004; Reusch et al., 2005).

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