

Influence of biotic and abiotic factors of seagrass *Posidonia oceanica* recruitment: Identifying suitable microsites

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ABSTRACT

The period between seed germination and successful seedling establishment is considered the most vulnerable phase for plant development. To better predict recruitment patterns within plant communities, it is essential to identify the abiotic constraints and biotic interactions that allow for the colonization of substrates by plant species. We evaluated which combination of factors are associated with successful survival and development of seedlings of the seagrass *Posidonia oceanica* in order to identify the most important microsite features acting together on recruitment success. Our results show that *P. oceanica* seedlings are rather specific in their environmental requirements during their first 18 months of life, when their development and survival are favored in microsites of consolidated substratum (solid rock, and to a lesser extent *P. oceanica* mat) covered by macroalgae (mainly crustose algae) and located in sheltered locations (with energy flux values not exceeding $7 \times 10^5 \text{ kg s}^{-2} \text{ m s}^{-1}$). After this phase, their probability of surviving becomes more independent from external conditions.

1. Introduction

The identification of factors influencing recruitment rates is a main objective of plant population biology (Crawley, 1990). To establish a new individual, a seed must be placed on a suitable microsite, germinate, and the developing plant must overcome the threats to plant survival at that site (Eriksson and Ehrlén, 1992). Thus, identifying the processes affecting the early phases of the life cycle of a species, from those limiting seed dispersal to those affecting seed germination and seedling establishment, is a prerequisite for understanding the factors controlling recruitment in plant communities (Seddon, 2004; Irving et al., 2010). Within this multi-stage process, the period between seed germination and successful seedling establishment is considered the most vulnerable phase for plant development (Harper, 1977), and represents a bottleneck in the plant life-cycle, compromising species abundance and distribution (Gomez-Aparicio, 2008). Recruitment patterns result from processes operating at multiple scales that determine the survival and growth of new individuals, being crucial to identify the environmental conditions that characterize a site as “safe” (sensu Jarèr et al. 1961; Jarèr et al., 1961). These small-scale locations suitable for seedling establishment are known as “microsites” (Eriksson and Ehrlén, 1992), and the abiotic constraints and biotic interactions within them determine the colonization success of the species (Gotelli et al., 2010;

Soliveres et al., 2011).

Engineering organisms (e.g. seagrasses, mangroves, kelps) carry out important ecosystem functions, such as modulating sedimentary processes, attenuating wave action and creating and regulating the habitat for other organisms (Gutiérrez et al. 2012; Gutiérrez et al., 2012). In this study we focus on seagrasses, which develop key coastal ecosystems (Hemminga and Duarte, 2000) and have been suffering worldwide declines during the last century due to human activities (Boudouresque et al., 2009; Waycott et al., 2009). Seagrass meadow expansion occurs mainly through clonal growth (Marbà and Duarte, 1998), although sexual reproduction is essential for the consolidation of existing meadows and for the colonization of new ones (Olesen et al., 2004). Furthermore, seedlings provide genetic variation, necessary for adaptation (Kendrick et al., 2012, 2016) that contributes to the recovery of degraded meadows and they also allow for long distance dispersal. However, as mentioned before, the period between seed germination and seedling successful establishment represents a demographic “bottleneck” limiting recruitment within populations (James et al., 2011; Statton et al., 2017). Consequently, a better understanding of the biotic and abiotic filters regulating seagrass recruitment represents a main goal to predict meadow formation and recovery.

Here we focus our attention on the dominant seagrass of the Mediterranean Sea, *Posidonia oceanica*. This species has a very slow growth

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rate (Marbà and Duarte, 1998) and sparse sexual reproduction, which varies unpredictably in both frequency and intensity (e.g. Buia and Mazzella, 1991; Balestri, 2004; Diaz-Almela et al., 2006, 2007). Indeed, *in situ* observations of seedlings are few (Buia and Piraino, 1989; Piazzzi et al., 1999; Gambi and Guidetti, 1998; Alagna et al., 2013), since one-year survival represents a major bottleneck in their life cycle (Balestri et al., 1998; Piazzzi et al., 1999). Due to the strong decline suffered by *P. oceanica* meadows in the last decades (Boudouresque et al., 2009), and given the increased rates of environmental change predicted for the coming years (IPPC, 2014), it is of special interest to evaluate the main factors controlling seedling recruitment of this species. Here, we evaluate the association of microsite features with successful seedling settlement and development, in order to identify the most important variables acting together on recruitment success. In addition to intrinsic traits of seedlings, such as their seed reserves (Balestri et al., 2009) or their morphology (Pereda-Briones et al., 2018a) in determining seedling settlement and survivorship, the type and number of variables comprising the dimensions of an environmental niche vary from one species to another and according to the abiotic and biotic contexts (Krebs, 2001; Gray et al., 2015).

Seeds are transported by wave energy and currents until settlement occurs. Later, physical dislodgement of seedlings by wave and current forces is a primary factor impeding successful recruitment ((Alagna et al. 2015), Statton et al., 2017; Alagna et al. (2015); Marion and Orth 2012; Rivers et al., 2011; Infantes et al., 2011; Balestri et al., 1998), hence the characterization of the hydrodynamic conditions is crucial to evaluate recruitment success. Small-scale topography is important in determining dispersion and establishment patterns (Orth et al., 1994, 2006; Inglis 2000; Balestri and Lardicci 2008, Alagna et al. (2013, 2019)2019), Pereda-Briones et al. (2018a) and substratum type can strongly influence seedling survival (Piazzzi et al., 1999; Olesen et al., 2004; Alagna et al. (2015, 2019)2019); Pereda-Briones et al., (2018a). Indeed, *P. oceanica* seedlings are firmly established when they occur in consolidated substrates (Balestri et al., 1998; Piazzzi et al., 1999; Alagna et al., 2013; Baladamenti et al., 2015), as these provide strong anchoring when plants experience hydrodynamic shear. In addition, biological factors also influence the success of seedling recruitment. For instance, the presence and composition of the macroalgal community associated with the settlement area can also affect anchoring success, nutrient uptake, vegetative development and herbivory pressure, among others

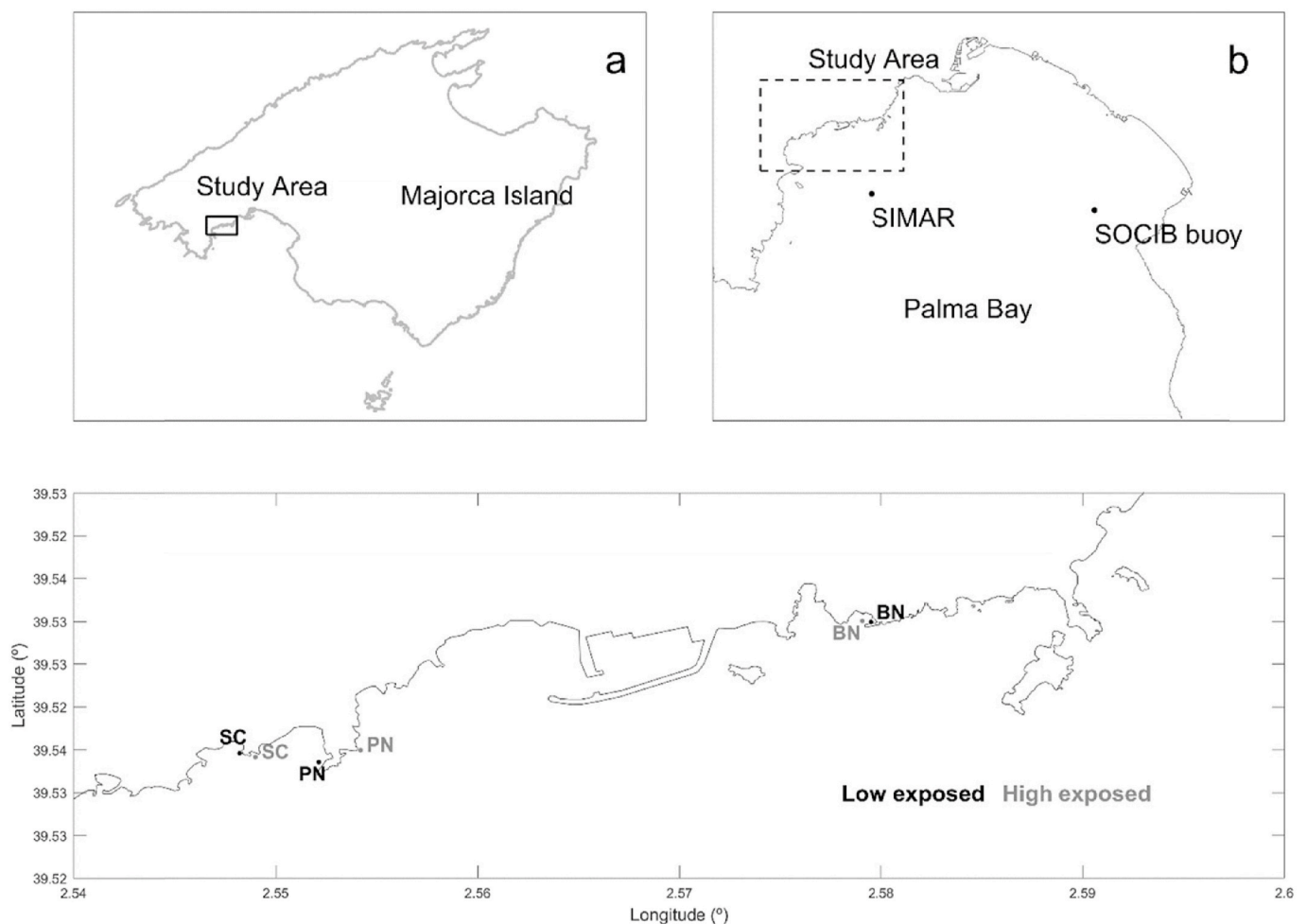


Fig. 1. Location of study area in Mallorca Island (a), location of SIMAR reanalysis point and SOCIB oceanographic buoy in Palma bay (b), location of the experimental sites: Son Caliu (SC), Punta Negra (PN) and Bendinat (BE) (c). The high exposed zones are marked in grey. The three sites are located in shallow embayments, between 0.5 and 6 m deep, and are southward orientated. The sea floor in these embayments consists of rocky substrate interspersed with mat of dead *P. oceanica* (sensu Boudouresque et al., 1980), and some sand and coarse gravel throughout. Rocky substrates (meaning solid rock) and *P. oceanica* dead mat were mostly covered by macroalgal assemblages, although some bare rock was also present, while sand and coarse gravel were almost devoid of vegetation, with occasional exceptions of patches covered with macroalgae or seagrass. At each of the three sites we marked 56 seedlings haphazardly distributed in two zones which were separated from each other by about 50 m and were differentiated by their degree of wave exposure (see Results section 3). Seedlings were estimated to have germinated and attached during late spring or early summer 2014, since their vegetative development (see next section 2.2 "sampling procedures") was similar to that measured for one-year-old seedlings (Gambi and Guidetti, 1998; Balestri et al., 2009).

(Blanchette et al., 1999; Alagna et al., 2013). The aim of the present study was to identify microsites suitable for survival of *P. oceanica* seedlings and evaluate the importance of different factors affecting early seedling development and survival. We examined the following hypotheses: 1) hydrodynamic conditions limit successful recruitment, 2) substratum type determines seedling survival, and 3) the association with certain macroalgae favours seedling development and survival. To this end, we marked groups of naturally-settled seedlings at different microsites around Palma Bay (Balearic Islands, Western Mediterranean) and followed their development and survival nearly two years while simultaneously characterizing the environmental and biological factors associated with the safe recruitment microsites.

2. Materials and methods

2.1. Study area

Seedlings of *P. oceanica* were detected in May 2015 at three sites along Palma Bay: Son Caliu (Long. 2.553°E – 39.525°N), Punta Negra (2.548°E – 39.525°N) and Bendinat (Long. 2.579°E – 39.532°N), south-west of Mallorca, in the Balearic Islands archipelago (Western Mediterranean) (Fig. 1).

2.2. Sampling procedures

Each individual seedling was tagged with a number and its location was additionally marked with a peg labelled with the seedling number next to the plant. At the time of marking, seedling depth was registered, and all seedlings had 5 to 6 leaves amounting to a total leaf surface of 36.64 ± 0.3 cm (mean \pm SE, N = 168) and were still bearing the seed at the base of the rhizome, which had a volume of $0.59 \text{ cm}^3 \pm 0.016$ (mean \pm SE, N = 168).

To evaluate the importance of the biotic and abiotic factors controlling *P. oceanica* seedling recruitment, we examined a set of features at each microsite while measuring the seedling population dynamics. Sampling was carried out *in situ* by SCUBA diving every four months from May 2015 until January 2017. During each survey we measured seedling morphometry (i.e. number of leaves, length of all leaves, the width of the second youngest leaf), number of bites on leaves, we estimated seed volume (derived from length and width measurements of the seed, assuming a rectangular shape), and calculated the increment in total leaf area (Δ TLA) from the previous sampling. Survival was expressed as the percentage of seedlings present with respect to the initial number present in each zone at the three sites. We also estimated the dominance of the different macroalgae species at each microsite by photographic analysis, using a 20×20 cm frame centered on each seedling. In order to quantify the main species covering the microsite we used the software “Coral Point with Excel extensions” (Kohler and Gill, 2005; Kohler and Gill, 2006) to distribute 30 random points over each 20×20 cm site image and identified the species below them. In addition, to estimate the percentage cover of macroalgae in the area directly in contact with seedling roots, we randomly overlapped 10 points over a 5×5 cm plot cut out from the original 20×20 cm image of each microsite. Subsequently, macroalgae species were grouped into functional groups, following the classification proposed by Steneck and Dethier (1994), except for *Caulerpa cylindracea*, *Caulerpa prolifera* and *Dasycladus vermicularis*, which did not fit any of these groups, and were therefore grouped as “others”. Additionally, on the first sampling date, we recorded depth, substratum type and bottom roughness of each seedling microsite. Microsite roughness was estimated by laying a metal chain (size link of 0.5 cm) over the two diagonals of the 20×20 cm quadrats centered on each seedling, and measuring the length required by the chain to follow the substratum surface along the diagonals (Luckhurst and Luckhurst, 1978). Once this length was measured, it was normalized to the same distance on a flat surface (by subtracting this distance, which would be representative of a roughness value of zero).

2.3. Hydrodynamic conditions

The swell generated by the wind in deep waters travels in groups of waves until it reaches the coast. Consequently, the physical parameters that define the waves are mainly modified by the effect of refraction, diffraction, white-capping, bottom friction and breaking, among other less important effects (Camus et al., 2013; Roland and Arduin, 2014). Significant wave height (H_s), peak period (T_p), and mean direction (θ) were obtained from the climate database of Puertos del Estado (Martínez-Asensio et al., 2013; SIMAR node – 2.583°E – 39.50°N) from January 2015 until July 2018 as a reference of deep water wave conditions. This hindcast point is located about 3.6 km from the study area. The validation of this near-shore database was done through the comparison of its oceanographic parameter values with respect to those registered by a SOCIB oceanographic buoy (Tintoré et al., 2013) see Supplementary material, Text A1; Fig. A1), and confirmed its reliability with respect to the real wave conditions in the study area. Maritime climate from deep to shallow water was propagated by using a numerical model (SWAN-Simulating Waves Nearshore (Booij and Holthuijsen, 1987), in order to obtain the historical wave series at our study sites (for further details of the propagation methodology see Supplementary material, Text A2, Fig. A2).

In order to analyse the hydrodynamic forces to which seedlings were exposed to, it is necessary to consider the H_s (m) and its associated T_p (s), since the energy transfer from surface to bottom largely depends on both parameters jointly (Holthuijsen, 2007). Therefore, we identified the extreme events of every zone of each site from the Wave Energy Flux (F). This parameter accurately represents the energy that arrives to the coast due to the incident waves (Galparsoro et al., 2012), taking into account the significant wave height (H_s) and its associated period (T_p) for each sea state. First, the total wave energy per surface unit (E) was calculated, where ρ is the seawater density (1.025 g/cm^3), g is the gravity constant, and H_s the significant wave height.

$$E = \frac{1}{8} \rho * g * H_s^2$$

Second, we calculated the celerity of the waves group, where k is the wave number ($k = 2\pi/L$), L is wave length, and h is the depth.

$$C_g = \frac{1}{2} \left(1 + \left(\frac{2 * k * h}{\sinh(k * h)} \right) \right)$$

Third, we multiplied $E * C_g$ in order to obtain the Wave Energy Flux (F) parameter:

$$F = E * C_g$$

Then, the time series was divided into six periods, each of 4 months, from January 2015 until January 2017, and those mean energy flows which overcame the 95% percentile in every period were selected as they represent the amount of energy related to extreme events (Galanis et al., 2011) that potentially would affect seedling persistence. To take into account not only storm intensity, but also its persistence, all F values at each period were integrated (see Supplementary material, Fig. A4). Finally, we evaluated the wave exposure degree (in terms of wave flux energy) of each zone in the three study sites and related the variation in seedling abundance over time at each microsite with the wave energy flux characteristic of each period (Fig. 2b).

2.4. Data analysis

To analyse the influence of the environmental factors (wave energy flux, bottom roughness and depth) on *P. oceanica* seedling survivorship, a Generalized Linear Model (GLM) was performed. A binomial family of errors with a “logit” link function was selected to meet the assumptions of linearity and normality of errors, which were checked by a visual inspection of residuals. Similarly, another GLM was performed to evaluate the importance of the same environmental factors on seedling total

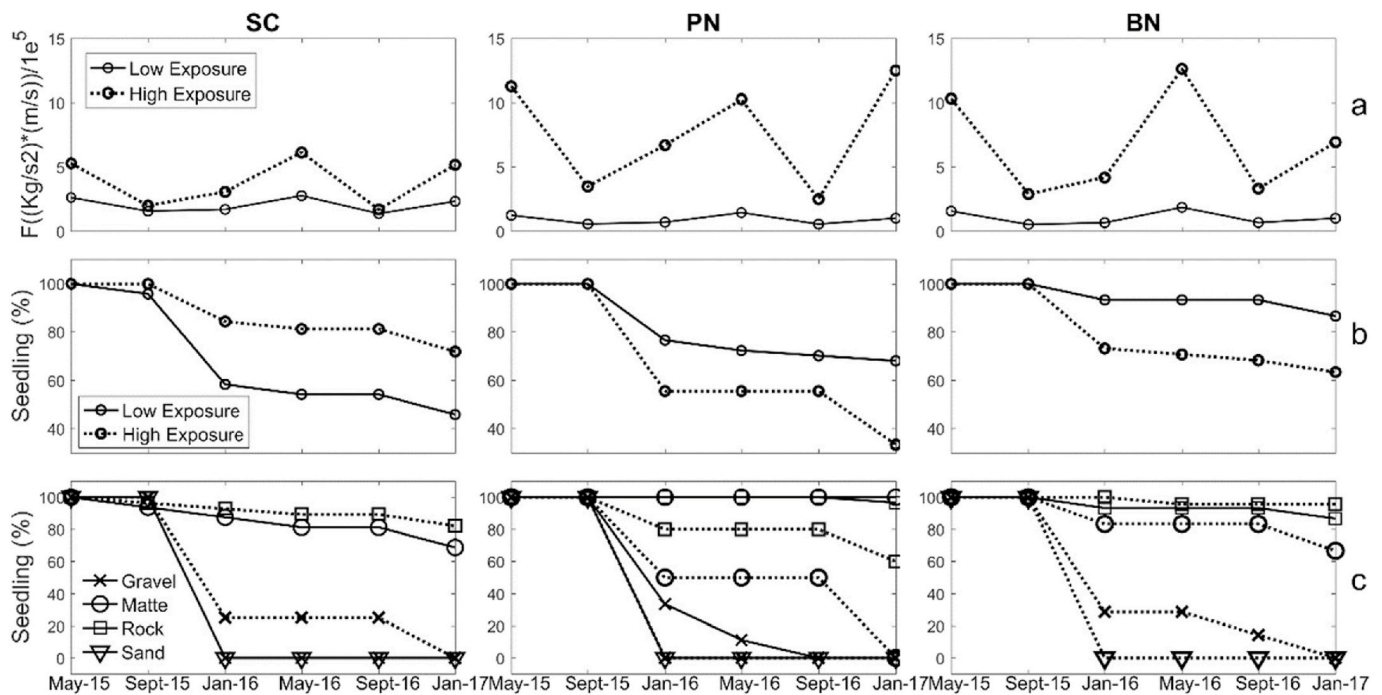


Fig. 2. Wave Energy Flux (F) (a) and percentage of seedling survival (b) across time at the low exposure (black line) and high exposure (dashed line) zones for each site: Son Caliu (SC), Punta Negra (PN) and Bendinat (BN). Percentage of seedling survival along the different substrates (c): gravel (crosses), matte (circles), rocks (squares) and sand (triangles).

leaf area (TLA). In this case we selected a Gaussian family of errors with an “identity” link function. Furthermore, to ensure that the flux energy values (F) were significantly different between the high and the low exposed zones at every site, pairwise *t*-test were performed at each site. In addition, to confirm the different wave exposure regimes between the two zones at each site, we performed a pairwise *t*-test using F values.

In order to examine differences in survivorship over time as a function of substratum type, a homogeneity of slopes model was used. Survivorship was the dependent variable, substratum the categorical predictor [with 7 levels: rocks, matte, gravel and sand (all covered with macroalgae), and rocks, gravel and sand (all devoid of vegetation)], and time was the continuous predictor. A post hoc Tukey’s test was performed to detect differences in survivorship between levels of the categorical predictor. We were not able to statistically analyse differences in seedling survivorship or performance amongst macroalgae functional groups due to lack of sufficient statistical power.

In addition, we assessed if the variation of seed volume among seedlings influenced seedling survivorship and foliar development (TLA) by conducting One-way ANOVAs (fixed factor seed volume). Since seed volume measurements did not vary through time, we used the initial values for the current analysis. Seed volume was categorized into nine levels of 0.1 cm^3 increments (from 0.4 cm^3 to 1.2 cm^3). Finally, we tested if the seed volume of seedlings differed between substrata with another One-way ANOVA (fixed factor substrata).

We also categorized the different microsites where seedlings were found taking into account those biotic and abiotic factors that we considered the most important according to our results: degree of exposure (i.e. exposed vs. protected, see Results), depth (i.e. 0–1.5 m; 1.5–3 m; 3–4.5 m; 4.5–5.5 m), substratum type (i.e. sand, gravel, matte and rocks) and the dominant macroalgal species present (see more details in Figure A5, Supplementary material).

3. Results

The reconstruction of the maritime climate at the three study sites by the SWAN propagation model did not identify strong storm surges at our

study sites ($H_s q95 = 0.49 \text{ m} \pm 0.14$). Nonetheless, at the three sites, we confirmed different wave exposure regimes between the two zones [pairwise *t*-test of Wave Energy Flux (F): Son Caliu ($t = -3.42$; $df = 5$; P-value = 0.018), Punta Negra ($t = -4.32$; $df = 5$; P-value = 0.007) and Bendinat ($t = -3.99$; $df = 5$; P-value = 0.010); Fig. 2a]. Accordingly, hereafter, zone will represent the degree of exposure, with a low-exposure and a high-exposure zone at each site. Seedlings that had established in the high exposure zone experienced higher mortality rates than those established in the less exposed (Table 1, Fig. 2b), except for at Son Caliu, where there was no difference in mortality between zones (Tukey’s test).

Taking into account the main biotic and abiotic factors (i.e. degree of exposure, depth, substratum type and dominant macroalgal species) recorded for each of the 168 tagged seedlings, we characterized 64 microsite types (see Supplementary material Fig. A5 Supplementary material Fig. A5). These microsite types represent the combination of the biotic and abiotic factors associated with successful seedling establishment, since all seedlings initially found were between 9 and 11 months old. However, we observed that these microsites differed in time in terms of ongoing survival of the established seedlings. After almost two years, certain microsites had higher survivorship and plant development, while others underwent high seedling mortality (Fig. A5 Fig. A5).

Regarding substratum type, the vast majority of seedlings were

Table 1

Results of the Generalized Linear Model (GLM) analysing the influence of environmental factors (i.e. energy flux, roughness and depth) on *Posidonia oceanica* seedling survivorship. Significant effects are highlighted in bold.

Survivorship ~ depth + energy flux + roughness)			
Family	binomial (logit)		
AIC	101.22		
Coefficients:		Estimate	P-value
	Depth	1.167	0.01
	Energy flux	-0.369	0.001
	Roughness	0,754	0.08

established on consolidated substrates, i.e. rocks (60%) or dead matte (16%) rather than sand or gravel (Fig. 2c; Fig. A5Fig. A5). Due to the unequal distribution of settled seedlings between consolidated and unconsolidated substrates from the beginning of the monitoring phase, we have not included this variable in the GLM analysis since it would not be able to detect significant differences. Therefore, we performed a homogeneity of slopes model on survival rates, taking into account all microsites together. We found that the slopes were significantly different between substrates across the time period analysed (significant interaction Substratum x Time; Table 2). Rocks and matte covered with macroalgae were the most successful substrates for seedling survivorship (92% and 67% respectively), followed by bare rock (50%), coarse gravel covered with macroalgae (2%), and lastly by bare coarse gravel and sand, either covered by macroalgae or bare, where no seedling survived at the end of the experimental period (Tukey's test). Rocks and matte substrate were also those where development was higher (see Supplementary material, Fig. A5, A6 and A7). In contrast, all seedlings settled on sand were lost during the first autumn-early winter; and only 25% of the seedlings remained in the coarse gravel habitat at that time (i.e. January 2016). Bottom roughness was strongly related with substratum type, having each substratum a specific roughness interval, increasing from sand (0.69 ± 0.04), matte (1.63 ± 0.04), coarse gravel (2.16 ± 0.09) to rocks (3.18 ± 0.11).

We detected a negative relationship between seedling survival and bare substrates (Table 2, see also Supplementary material, Fig. A5, A6 and A7), being seedling survivorship always below 34%, and seedling TLA $\Delta < 0.5 \text{ cm}^2$ on these substrates (Table 3). On the other hand, we detected a positive relationship with survivorship and TLA when microsites were dominated by macroalgae. Certain species were associated with higher survivorship and plant development, whereas others were less correlated to seedling success.

When grouping macroalgae species in functional groups, seedlings survived best in the presence of crustose algae (96%, Table 3), with *Litophyllum incrustans* and *Peyssonnelia rubra* as the dominant species. Articulated calcareous algae were the functional group associated with the highest abundance of seedlings, with *Jania adhaerens* being the dominant species and being associated with high TLA increments (Table 3, Fig. A5Fig. A5). *Ellisolandia elongata* was associated with low TLA increment, but with almost 94% seedling survivorship. No seedlings survived in *Acetabularia acetabulum* whereas seedlings associated with *Amphiroa rigida*, even though it was only dominant in 10% of the microsites, exhibited 100% survivorship. Corticated foliose algae was the second most abundant functional group observed near seedlings. *Padina pavonica* was the dominant species, having a particularly high TLA increment associated with it. *Dictyota dichotoma* was the second species in terms of abundance, but only half of the seedlings settled over it survived. Seedlings associated with the other species of this group, *Flabellia petiolata* and *Dictyopteris polypodioides*, although scarcer, exhibited 75% survivorship. Lastly, the species grouped as "others" were mostly dominant at the base of the seedling radicular system (5×5 microsites) mainly represented by *Caulerpa cylindracea*, which was associated with 100% survivorship. In contrast, seedlings growing next to *Caulerpa prolifera* underwent total seedling mortality, whereas

Table 2

Homogeneity of slopes model. Survivorship was the dependent variable, substratum the categorical predictor [with 7 levels: rocks, matte, gravel and sand (all covered with macroalgae), and rocks, gravel and sand (all devoid of vegetation)], and time was the continuous predictor. Significant effects are highlighted in bold.

Variable	Source	df	MS	F	p
Survivorship (%)	Substratum	6	1394.48	2.95	0.023
	Time	1	29670.58	62.90	<0.01
	Substratum*Time	6	1476.69	3.13	0.017
	Error	28	471.71		

Dasycladus vermicularis was associated with more than 75% survivorship and with a high TLA increment (Table 3, Fig. A5Fig. A5).

At the beginning of the sampling period (May 2014), seedlings were 9–11 months old and were still bearing their seed attached to the base of the rhizome. However, around the age of 24 months old (i.e. in September 2016), all survivors were missing their seed. Seed measurements revealed that seedling survival was positively related to seed volume ($F_{(8,100)} = 1.95$; P-value < 0.05 ; One-Way ANOVA), and above a certain volume (0.7 cm^3), all seedlings survived (Tukey). Furthermore, bigger seeds were found on harder substrates (rocks and matte; $F_{(3,100)} = 38.6$; P-value < 0.01 ; One-Way ANOVA, Tukey). On the other hand, seedlings with bigger seeds (higher seed volume) did not exhibit higher TLA ($F_{(8,100)} = 0.72$; P-value > 0.05). Seedling TLA increased with energy flux (GLM, Table 4), with seedlings established at the more exposed sites being bigger than those in the less exposed ones.

4. Discussion

In this study we have been able to identify certain abiotic and biotic factors that provide the most suitable microsites for successful recruitment of *P. oceanica* seedlings. These microsites are locations which are sheltered from waves, generally between 1.5 and 4.5 m depth (and even less than 1.5 m in very sheltered areas), over consolidated substrates, and dominated by macroalgal assemblages, particularly crustose algae.

Seedling establishment is clearly biased towards sheltered locations, with survivorship decreasing significantly with higher energy flux. Preference for calmer areas has also been previously reported for *P. oceanica* seedlings (Balestri et al., 1998; Infantes et al., 2011) and for other seagrass species. Physical removal by hydrodynamic forces, especially in winter storms, is the primary factor hampering successful recruitment of *Amphibolis antarctica* and *Posidonia australis* (Rivers et al., 2011; Statton et al., 2017), and is also the major cause of transplant failure in restoration efforts for many species (van Katwijk and Hermus, 2000; Irving et al., 2010). The forces that seedlings need to overcome is caused by accelerations-generated at the bottom due to the hydrodynamics conditions forced by wind waves (Holthuijsen, 2007). At the three studied sites, we identified two different zones in terms of degree of exposure to waves. In Punta Negra and Bendinat, maximum F values at the exposed area during winter months were between 10×10^5 and $13 \times 10^5 \text{ kg s}^{-2} \text{ m s}^{-1}$, decreasing to around $7 \times 10^5 \text{ kg s}^{-2} \text{ m s}^{-1}$ during the summer months, when storms are less frequent and of lesser magnitude. At Son Caliu, maximum F values were much lower, not exceeding $7 \times 10^5 \text{ kg s}^{-2} \text{ m s}^{-1}$ at the exposed area during the winter months. This lower wave energy flux (due to the fact that the most energetic waves come from the SSW, see Supplementary material, Fig. A3Fig. A3) indicates that Son Caliu is the more protected site. The minor differences in degree of exposure between the two zones in Son Caliu, (and the fact that the more exposed site is largely dominated by rocky substrate) likely contribute to the lack of difference in survival between the two zones at this site in comparison to the other two sites. Importantly, at the three sites, the number of seedlings scarcely changed during summer of 2015, i.e. when F values do not exceed $3 \times 10^5 \text{ kg s}^{-2} \text{ m s}^{-1}$. The greatest decrease in the number of seedlings occurred between September 2015 and January 2016, (with 30–50% of seedlings lost in the exposed area of Punta Negra and Bendinat, and almost 50% in the less exposed area of Son Caliu), when these areas experienced F values of at least $7 \times 10^5 \text{ kg s}^{-2} \text{ m s}^{-1}$. Conversely, from January 2016, practically all seedlings survived until January 2017 (with moderate decreases of between 5 and 20% for all the sites; Fig. 2a and b). Indeed, by analysing the raw data, total seedling survivorship from 9–11 months–18 months was around 65%, while from 18 until 30 months it was around 90%. This suggests that seedlings are more vulnerable to strong hydrodynamic conditions during their first year and a half of life. After reaching about 18 months of age, the surviving seedlings are more resistant, despite experiencing higher magnitude extreme events ($\sim 10^5 \text{ kg s}^{-2} \text{ m s}^{-1}$). In addition, most successful establishment of seedlings

Table 3

Abundance of *Posidonia oceanica* seedlings settled in different algal functional groups (and each macroalgal species), seagrass, bare rock, bare coarse gravel and bare sand in 5 × 5 and 20 × 20 plots, in relation to seedling survivorship and foliar development [increment in total leaf area (Δ TLA)].

FUNCTIONAL GROUP	5 × 5			20 × 20		
	Dominance (%)	Survivorship (%)	Δ TLA (cm ²)	Dominance (%)	Survivorship (%)	Δ TLA (cm ²)
Corticated foliose	14.88	52	2.78 ± 0.76	24.4	73	1.88 ± 0.82
<i>Padina pavonica</i>	56	50	4.08 ± 1.0	65.85	74.07	5.02 ± 1.2
<i>Dictyota dichotoma</i>	24	50	0.89 ± 0.62	19.51	50	1.25 ± 0.56
<i>Flabellia petiolata</i>	16	75	1.66 ± 0.42	4.87	100	1.5 ± 0.46
<i>Dictiopteris</i>	4	0	0	9.75	100	1.85 ± 0.4
Corticated	25.59	83.72	0.66 ± 0.24	8.33	64.28	3.76 ± 1.32
<i>Caulerpa cylindracea</i>	65.7	100	0.41 ± 0.25	0	0	0
<i>Caulerpa prolifera</i>	9.3	0	0	14.28	0	0
<i>Dasycladus vermicularis</i>	25	83.33	3.76 ± 1.32	85.72	75	4.58 ± 1.22
Articulated calcareous	29.16	65.3	2.62 ± 0.54	30.35	74.5	5.56 ± 1.90
<i>Jania adhaerens</i>	59.14	57.14	3.39	58.82	76.66	4.87 ± 1.3
<i>Ellisolandia elongata</i>	20.39	88.88	1.56 ± 0.4	31.37	93.75	1.73 ± 0.51
<i>Amphiroa rigida</i>	12.25	100	1.16 ± 0.20	0	0	0
<i>Acetabularia acetabulum</i>	8.22	0	0	9.8	0	0
Crustose	15.47	96.15	3.3 ± 0.92	16.07	96.29	3.65 ± 0.84
<i>Peysionellia rubra</i>	59	92.3	2.72 ± 0.96	59.25	93.75	2.61 ± 0.95
<i>Lithophyllum incrustans</i>	41	100	1.46 ± 0.62	40.75	100	2.59 ± 0.74
Seagrass	2.38	0	0	3.57	16.66	1.63 ± 0.84
<i>Cymodocea nodosa</i>	100	0	0	100	16.66	1.63 ± 0.84
Bare rock	3.57	33.33	0.3 ± 0.17	4.76	50	0.48 ± 0.34
Bare coarse gravel	5.35	0	0	7.14	0	0
Bare sand	3.57	0	0	5.35	0	0

Table 4

Results of the Generalized Linear Model (GLM) analysing the influence of environmental factors (i.e. energy flux, roughness, depth and substratum type) on *Posidonia oceanica* seedlings' total leaf area (TLA). Significant effects are highlighted in bold.

Δ TLA ~ depth + energy flux + roughness + substratum)			
Family	Gaussian (identity)		
AIC	658.57		
Coefficients:		Estimate	P-value
	Depth	-0.734	0.214
	Energy flux	0.509	0.01
	Roughness	-0.925	0.187

took place on consolidated substrates, whereas unconsolidated substrates appear to hamper seedling retention and survival. Indeed, seedlings between 14 and 18 months old experienced increased mortality on unconsolidated substrates, such as sand and gravel, while their populations were more stable over consolidated ones.

Another aspect which suggests that consolidated substrates contribute to higher seedling survival is that seedlings with bigger seeds were found on them (rocks and matte), and our results show that seed volume is positively correlated with seedling survival. This correlation was also observed by Balestri et al. (2009), who suggested that during the first year of life, seeds supply N and P to the plant, guaranteeing rapid growth of leaves and roots. Bigger seeds, which contain more reserves, likely provide seedlings with a higher capacity to face environmental stressors than the smaller ones. In addition, smaller seeds experienced lower drag (Pereda-Briones et al., 2018b), being higher flow velocities necessary to move them over the bottom. Perhaps, this contributed to the higher amount of smaller seeds over sand and coarse gravel substrates, because although they may be poorer contributors to survivorship than larger seedling, smaller seeds could better establish due to their lower drag.

While we did not quantify the cover of algal functional groups in the field (thus precluding us from performing statistical tests), the success of seedlings does appear to be associated with macroalgal cover, which indirectly favour seedlings by ameliorating environmental conditions. Environmental facilitation by co-habiting plants is a common phenomenon in other systems (e.g. Mediterranean forests; Gómez-Aparicio et al. 2008; Gómez-Aparicio et al., 2008, salt marshes; Hacker and Bertness,

1999), and has also been suggested for *P. oceanica* (Alagna et al., 2013). In their study, Alagna et al. (2013) observed higher seedling persistence on rock substratum covered by *Cystoseira spp.*, which was attributed to the macroalgae decreasing water flow and providing anchoring substrate for seedling roots. However, not all functional groups appear to influence seedling recruitment and development in the same way. Crustose algae, with *L. incrustans* and *P. rubra* as the dominant species, appear to be the most favourable functional group for seedling survival. Crustose algae are characterized by a stony thallus, and probably this solid structure has allowed adequate anchorage of the seedling's radicular system to the hard substrates. Indeed, *P. oceanica* seedlings can regulate root traits during their early development in relation to substrate typology (Balestri et al., 2015), and the presence of sticky hairs covering *P. oceanica* seedling roots (Baladamenti et al., 2015) allows them to successfully anchor and persist over hard substrates, improving their resistance against physical disturbances and ensuring nutrient uptake. Articulated calcareous algae, with *J. adhaerens* as the most representative species, was the predominant functional group in terms of seedling abundance. *Jania adhaerens* is fixed to the substrate by small discs, and it is relatively common in well illuminated environments that are slightly exposed to waves (Litter and Litter, 2000; Litter and Litter, 2000). Perhaps the higher abundance of seedlings over *J. adhaerens* is due to the predominant presence of this algae in the study area. *E. elongata* was the second most important species of articulated calcareous and it is considered a "stress-tolerant species" (Arévalo et al., 2007). Its calcified structure gives it resistance to abrasion and predation, and due to having an algal body composed of both prostrate filaments and protruding upright filaments, it is able to recover rapidly after disturbances (Littler and Kauker, 1984). Perhaps, under a wide range of stress factors, the presence of *E. elongata* provides a stability that allows *P. oceanica* seedlings to persist longer.

The corticated foliose functional group was also highly abundant at *P. oceanica* seedling microsites, and it was dominated by *P. pavonica*. Seedlings growing on microsites dominated by *P. pavonica* had the largest increment in TLA. This alga is a common and characteristic species in well-illuminated communities of the infralittoral (Rodríguez-Prieto et al., 2013), and perhaps the association of seedlings with this alga is due to its high abundance. Lastly, *C. cylindracea* was mostly dominant at the base of the seedling radicular system (5 × 5 microsites), and may play an important role regarding initial attachment of the roots.

The presence of *C. cylindracea* may facilitate seedling retention and further survival on rocky and matte substrates. In fact, this invasive species promotes *P. oceanica* seedling root development, facilitating the anchorage to the matte substrate (Pereda-Briones et al., 2018b). Additionally, it could be that *Caulerpa prolifera* depletes oxygen in the underneath sediment, negatively affecting seedling survival, since we have observed total seedling mortality when this macroalgae was dominant.

Lastly, it is important to highlight that once seedlings have overcome the second winter, at an age of approximately 18 months old, they have a high probability of persistence in the population. Their risk of mortality decreases as they become older, independently of the environmental conditions. Overall, we suggest that the recruitment success of *P. oceanica* seedling is limited largely by the availability of suitable safe microsites during ca. its first year and a half of life. This success is favored by microsites those characterized by rocky substrates and, to a lesser extent matte, covered by macroalgae, and located in sheltered locations.

CRedit authorship contribution statement

L. Pereda-Briones: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **J. Terrados:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Supervision. **M. Agulles:** Software, Validation, Formal analysis, Visualization. **F. Tomas:** Conceptualization, Methodology, Formal analysis, Resources, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2020.105076>.

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