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# **Shoot micro-distribution patterns in the Mediterranean seagrass**  *Posidonia oceanica*

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**Abstract** *Posidonia oceanica* meadows host a huge number of shoots and their dynamics is strictly related to the spatial distribution patterns of those shoots. To investigate the structure of *P. oceanica* meadows at very small spatial scale (i.e. in the  $10^0 - 10^2$  cm range), point patterns of shoot micro-distribution were analyzed. Spatial distribution of shoots was recorded by cutting all the leaves and by digitizing shoot location from pictures of square frames  $(1 \text{ m}^2)$  that were randomly positioned in seemingly uniformly dense stands. Ten frames were sampled, all from Southern Italian meadows, and the position of 7828 shoots was recorded. Nearest neighbour distance (NNd) statistics revealed recurring patterns at the diferent spatial scales: regular patterns were recognized among shoots at smaller spatial scale  $(10^{0} - 10^{1}$  cm), while aggregated shoot distribution emerged in the  $10^{1}$ – $10^{2}$  cm range and an important stochastic component was observed at larger spatial scales. Reasons underpinning diferent spatial point patterns in *P. oceanica* meadows were discussed by relating the observed patterns to ecological processes (i.e. competition among shoots, role of "species-specifc" drivers or "site-specifc"

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features), also including relationships between shoot NNd and shoot density counts. The raw data, provided as supplementary material, are currently the frst and the only source of information available about shoot spatial micro-distribution. In this regard, although our data set cannot represent the whole spectrum of variability in *P. oceanica* meadows, it can be regarded as a frst step towards a better knowledge of small scale shoot point patterns in *P. oceanica* meadows.

### **Introduction**

While seagrass meadows often appear as uniform landscapes, their inner structure, and, therefore, their dynamics, can be very complex (Den Hartog [1971](#page-9-0)). Seagrass meadows, at any one time, consist of a nested structure of clones, possibly fragmented into diferent ramets, each supporting a variable number of shoots (Duarte et al. [2006](#page-9-1)). The shoots are borne by rhizomes growing either vertically (orthotropic rhizomes), thus preventing burial, or horizontally (plagiotropic rhizomes), enabling colonization of surrounding substrates (Caye [1980](#page-9-2)). As the plagiotropic rhizomes grow horizontally, meadows expand themselves with wide spacing between vertical shoots and only a few horizontal apices (Boudouresque and Meinesz [1982](#page-9-3); Bou-douresque et al. [2016](#page-9-4)). Thus, continuous recruitment of new clones to the meadow, shoots growth and shoots turnover support the intense dynamics of seagrass ecosystems, results from the combination of processes operating at various scales, which, if balanced, preserve the stability of the whole ecosystem (Duarte et al. [2006](#page-9-1)).

In the Mediterranean Sea, the seagrass *Posidonia oceanica* (L.) Delile forms monospecifc meadows with diferent types of coverage pattern (continuous to patchy) (Molinier and Picard [1952](#page-9-5); Boudouresque et al. [2012\)](#page-9-6) with shoot densities

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up to more than 1000 shoots  $m^{-2}$ . Density depends on depth and other factors and ranges in most cases from 150 to 300 shoots m<sup>-2</sup>(very sparse meadows) to more than 700 shoots m−2 (very dense meadows) (Giraud [1977](#page-9-7)).

Research on *P. oceanica* meadow structure can be carried out at diferent spatial scales (Van Rein et al. [2009\)](#page-10-0). At larger spatial scales, the investigations usually focus on the way meadows cover the substrate, e.g. by mapping their limits, while shoot density measurements are usually the main goal of studies at smaller spatial scales (Pergent-Martini et al. [2005](#page-10-1)). However, density measurements are based on shoots counts and the spatial distribution of shoots is not uniform. Therefore, at very small spatial scales, density estimates become highly variable, depending on point patterns of shoot position (Panayotidis et al. [1981;](#page-10-2) Bacci et al. [2015\)](#page-9-8).

While the latter depend on interactions between rhizomes, there are very few scientifc studies aimed at understanding this process in clonal growth of *P. oceanica* (Kendrick et al. [2005a](#page-9-9)), with particular reference to the growth rates of rhizomes and patterns of branching (Marba and Duarte [1998](#page-9-10); Molenaar et al. [2000\)](#page-9-11). Point patterns of shoot position are also relevant to simulations of the dynamics of plant growth related to expansion of plagiotropic rhizomes (Kendrick et al. [2005b](#page-9-12)) and to optimize strategies for transplantation aimed at reforestation activities (Renton et al. [2011](#page-10-3)). No information is available about point patterns of *P. oceanica* shoots, neither on other marine seagrasses. In terrestrial ecology in contrast, there is an extensive history of observational research involving the analysis of spatial point patterns (for a review see Velasquez et al. [2016](#page-10-4)). In fact, several studies have sought to explain the formation of plant spatial patterns by connecting observed patterns to ecological processes (e.g. Haase et al. [1996](#page-9-13); Tirado and Pugnaire [2003;](#page-10-5) Rayburn and Monaco [2011\)](#page-10-6). While plant spatial patterns have been often analyzed as the outcome of underlying ecological processes, studies focusing on their effects on population and community dynamics are less common (Tilman and Kareiva [1997;](#page-10-7) Murrell et al. [2001](#page-10-8); Stoll and Prati [2001;](#page-10-9) Dunstan and Johnson [2003;](#page-9-14) Maestre et al. [2005;](#page-9-15) Turnbull et al. [2007](#page-10-10)).

The goal of this research is to investigate shoot distribution patterns of the Mediterranean seagrass *P. oceanica* at a very small spatial scale(i.e. in the  $10^0 - 10^2$  cm range), to reveal recurring patterns at the diferent spatial scales and to gain new insights into meadow structure.

### **Methods**

### **Study area and sampling methods**

Field activities were carried out in August 2011 at three sites in the Capo Rizzuto Marine Protected Area and in September 2012 at two sites in the Riviera dei Cedri Marine Park (Central Mediterranean, Italy, Fig. [1](#page-2-0)). As the feld work demanded a large amount of underwater activity by SCUBA diving, we selected rather shallow sites (about 5 m depth). Moreover, at all sites, *P. oceanica* was settled on matte (i.e. the whole mass composed of rhizomes, sheaths, roots and the sediment that flls the interstices) and looked uniformly dense at repeated visual inspections. At each site, two 1 m  $\times$  1 m quadrats were randomly positioned a few meters apart from each other. Within each quadrat, we cut all the leaves right above the ligule (thus allowing regrowth) and took pictures to arrange a photomosaic of the whole quadrat.

#### **Image pre-processing**

Pictures from each quadrat were processed to correct distortion and stitched into a high-quality photomosaic. The exact position of the apical portion of each rhizome (i.e. at the leaf insertion) was then digitized (Fig. [2\)](#page-3-0). This choice has a practical justifcation, because the green tissue of the leaves just above the ligule can be easily recognized in the photomosaics. In addition, this choice has also a theoretical justifcation. In fact, regardless of the point of insertion of the rhizome in the substrate, the location of the apical portion plays a fundamental role in the way each shoot competes for space with its neighbours.

Finally, a sensitivity analysis was carried out to test robustness of the resulting point patterns relative to digitization errors. Each point in the pattern was subjected to a random displacement, uniformly distributed within a circle of radius 0.5 cm, and the resulting point pattern was compared to the original one. The procedure was repeated 1000 times.

### **Spatial point pattern analysis**

Nearest neighbour statistics was computed for the whole data set as well as for each quadrat. Distances (*r*) from any shoot to its nearest neighbour were also analyzed in relation to shoot density values within independent subquadrats  $(20 \text{ cm} \times 20 \text{ cm})$  by means of the Spearman's rank corre-lation coefficient (Spearman [1904](#page-10-11)) and the observed relationship was then compared the one expected for a random (Poisson) point processes. In addition, we used the inhomogeneous *J*-function (van Lieshout [2010](#page-10-12)), which is the counterpart for inhomogeneous spatial point patterns of the *J*-function for homogeneous point patterns, to defne the properties of the spatial distribution patterns of *P. oceanica* shoots in each quadrat.

The *J*-function is a distance-dependent function that is often applied to the analysis of spatial point patterns (Van Lieshout and Baddeley [2006](#page-10-13)). The rationale supporting



<span id="page-2-0"></span>**Fig. 1** Location of the study areas within the two study sites in Mediterranean Sea, Italy. **a** MPA-Capo Rizzuto (area *I* 38°55′10′′N, 17°00′05′′E; area *II* N 38°53′56′′N, 17°05′24′′E; area *III* 38°54′53′′N,

this function is to compare distances from points in the pattern to their nearest neighbour (nearest-neighbour distance *G*-function) and distances from arbitrary points to their nearest neighbor in the pattern (empty space *F*-function). This can be written as:

## $J(r) = [1 - G(r)]/[1 - F(r)]$

where  $G(r)$  is the nearest-neighbour distance function and  $F(r)$  is the empty space function. Both functions show the cumulative distribution of these distances (*r*) in a point pattern. In the inhomogeneous *J*-function, which was applied

17°02'11''E); **b** MP-Riviera dei Cedri (area *IV* 39°41'55''N, 15°48'13''E); **c** MP-Riviera dei Cedri (area *V* 39°52'24''N, 15°48'13"E); **c** MP-Riviera dei Cedri (area 15°46′53′′E)

in our work, the *G*-function and the *F*-function are obviously of the inhomogeneous type. In this regard, an inhomogeneous Poisson process was chosen because our plots were partly infuenced by frst-order heterogeneity. Hence, the intensity  $\lambda$  is not approximately constant, but varies with the location  $(x, y)$  over the entire observation quadrat. To estimate the intensity function, which defnes the expected number of shoots per unit area at each location, we used kernel estimators (Waller and Gotway [2004](#page-10-14)), which are among the best established nonparametric estimation techniques (Efromovich [1999\)](#page-9-16). An estimate of



<span id="page-3-0"></span>**Fig. 2** A sample image (*left*) and the shoot point pattern (*right*). *Black dots* mark the apical portion of each rhizome. The image (*left*) was captured from above and the elongated forms correspond to dead shed leaves

inhomogeneous *J*-functions derived from a spatial point pattern dataset can be used to support exploratory data analysis and formal inference about the pattern (Szmyt [2014](#page-10-15); Wiegand and Moloney [2014](#page-10-16); Velazquez et al. [2016](#page-10-4)). In exploratory analyses, the shape of the function provides details about the way in which events (shoots, in our case) are spaced in a point pattern. Generally, if  $J(r) = 1$ , the distance distribution follows the inhomogeneous Poisson process, while deviations from that value, i.e.  $J(r) > 1$  or  $J(r)$ <1, indicate spatial regularity or clustering, respectively (Fortin and Dale [2005;](#page-9-17) Van Lieshout and Baddeley [2006](#page-10-13)). For inferential purposes, the observed value of the inhomogeneous *J*-function was compared to the expected value of *J*-function for an inhomogeneous Poisson point process and deviations between the empirical and theoretical *J* curves suggested spatial clustering or spatial regularity. Signifcance of the deviations from the heterogeneous null model hypothesis, assuming 0.05 as the *p* level in Monte Carlo tests, was tested using simulated confdence envelopes. The latter were computed by point-wise simulation (i.e. for each value of the distance argument  $r$ ) of the inhomogeneous Poisson process, with the same intensity *λ* (mean number of shoots per unit area) from the study region. Finally, the position of the empirical function relative to the envelopes was checked (Bivandet al. [2008](#page-9-18)). The estimation of inhomogeneous *J*-functions is hampered by edge effects arising from the impossibility to observe points outside the quadrat. An edge correction is, therefore, needed to reduce this bias (Baddeley et al. [2000\)](#page-9-19). The edge correction we applied

was based on the border method (van Lieshout [2010](#page-10-12)). All the statistical analyses were performed using the package spatstat 1.24-2 (for full details about spatstat see Baddeley et al. [2015](#page-9-20)) in R Project for Statistical Computing, version 2.13.2.

### **Results**

Spatial point patterns were analyzed in ten quadrats for a total of 7828 shoots (Fig. [3](#page-4-0)), highlighting very diferent shoot density values among quadrats (min 566 shoots  $m^{-2}$ ; max 1011 shoots  $m^{-2}$ ).

Sensitivity analysis highlighted robustness of the shoot digitization process. In this regard, the lowest diference between medians of shoot Nearest neighbour distances (NNd) of the observed quadrat and the simulated quadrats was 0.003 cm (in quadrat d), while the highest diference between medians of shoot NNd of the observed quadrat and the simulated quadrats was 0.052 cm (in quadrat e). The frequency distribution of NNd of shoots is unimodal and positively skewed. The NNd median value was 1.85 cm and 99% of the values fell between 0.45 and 4.38 cm (Fig. [4](#page-4-1)). In addition, a signifcant and negative Spearman's rank correlation (rs =  $-0.51$ ,  $N=250$ ,  $p < 0.001$ ) was detected between median of shoot NNd and shoot density in the available subquadrats (size 20 cm  $\times$  20 cm, 250 subquadrats overall) (Fig. [5\)](#page-5-0). In this regard, most of the points characterized by higher shoot density values fell above the



<span id="page-4-0"></span>**Fig. 3** Shoot distribution of the Mediterranean seagrass *Posidonia oceanica* within 1 m × 1 m quadrats in meadows settled on *matte* and uniformly dense at repeated visual inspections. **a, b** Area I\_ MPA-Capo Rizzuto; **c, d** area II\_ MPA-Capo Rizzuto; **e, f** area III\_ MPA-Capo Rizzuto; **g, h** area IV\_MP-Riviera deiCedri; **i**–**l** area V\_MP-Riviera deiCedri



<span id="page-4-1"></span>**Fig. 4** Frequency distribution of nearest neighbour distances (NNd) of shoots. Very low frequency of nearest neighbour distances are shown in numbers in the  $6-7$  (cm),  $7-8$  (cm) and  $8-9$  (cm) intervals

interval of expected values for a Poisson point process, thus indicating regular patterns within those subquadrats. The shoot NNd are also shown separately by means of box plots (Fig. [6\)](#page-5-1), one for each of the spatial point pattern shown in Fig. [3.](#page-4-0) In this regard, Kolmogorov–Smirnov test (with Bonferroni correction) detected signifcant statistical diferences in shoot NNd between spatial point patterns in most cases (37 times out of 45 possible pairwise comparisons). Finally, in most spatial point patterns, the observed  $J(r)$  function was  $>1$  and fell above the 95% Monte Carlo interval for small values of  $r$  up to 2–3 cm, indicating a regular pattern. At spatial scales larger then about 3 cm, the most frequent values of the  $J(r)$  function were  $\langle 1 \rangle$  and fell below the 95% limit of the Monte Carlo interval, indicating aggregated shoot distribution. Quadrat a and quadrat g, can be regarded as exceptions to this rule, as at a spatial scale larger than about 3 cm, the observed  $J(r)$  function values fell within Monte Carlo interval, thus suggesting a random pattern (Fig. [7\)](#page-6-0). Raw data are provided as supplementary material.

### **Discussion**

Data collected in this research allowed to map the position of each single shoot in ten quadrats sampled at two Central Mediterranean sites. As each quadrat was  $1 \text{ m} \times 1 \text{ m}$ , an overall area of 10  $m<sup>2</sup>$  of *P. oceanica* meadow has been mapped at the fnest possible scale.

The lack of similar data in current literature and the amount of data collected in this study makes the presented



<span id="page-5-0"></span>**Fig. 5 a** *Scatter plot* of medians of shoot nearest neighbour distances (NNd) and shoot density in the available subquadrats (20 cm  $\times$  20 cm, 250 subquadrats overall). Expected median values for shoot NNd for a Poisson point process with 95% Monte Carlo intervals (*grey line*) (1000 simulations) are also shown in the plot. Shoot density values computed within 20 cm  $\times$  20 cm subquadrats

were extrapolated to  $1 \text{ m}^2$ . **b** Ternary plot showing, for each range of shoot density, the percentage of points of the adjacent *scatterplot* which fall above (indicating regular patterns), inside (indicating random patterns) or below (indicating aggregated patterns) the expected median values for a Poisson point process



<span id="page-5-1"></span>**Fig. 6** *Box-plot* of nearest neighbour distances (NNd) for each of the ten quadrats (*a*–*l*). Number of shoots (*N*) and median NNd value are also shown

results of potential interest to scientists involved in seagrass research. Nevertheless, due to the complexity of the processes involved in the generation of the patterns we analyzed, this study is to be regarded as a frst step towards a broader understanding of the small scales spatial structure of *P. oceanica* meadows.

Although our data may not represent the full spectrum of small scale spatial structures in *P. oceanica* meadows, they provide considerable information about the potential variability of a very common type of meadows, i.e. those settled on *matte*, in shallow waters and in good health.

A meadow contains a huge number of shoots and its dynamics depends on the spatial distribution of those shoots. The variables that infuence the shoot distribution depend on spatial scale and their number is presumably increasing in direct proportion to the spatial scale (Fig. [8\)](#page-7-0).

First, the horizontal exploratory expansion of a meadow is controlled by species traits, such as rhizome elongation, branching patterns and clonal growth (Caye [1982](#page-9-21); Marbà and Duarte [1998\)](#page-9-10). In this regard, using the nearest neighbour statistics is justifed by the role that interactions between neighbouring shoots play at very small spatial scale.

Second, dynamics of *P. oceanica* meadows depend on an extensive range of biological and physical variables such as those related to depth, currents, geomorphology and substrate type (e.g. Duarte [1991;](#page-9-22) Lorenti et al. [1995](#page-9-23); Montefalcone et al. [2016](#page-9-24)) as well as irradiance, temperature and nutrient availability (e.g. Buia et al. [1992;](#page-9-25) Alcoverro et al. [1995](#page-9-26); Zupo et al. [1997;](#page-10-17) Leoni et al. [2007](#page-9-27)), detritus accumulation and sedimentation (Boudouresque and Jeudy de Grissac [1983](#page-9-28); Romero et al. [1992;](#page-10-18) Gacia and Duarte [2001\)](#page-9-29) and also anthropogenic impacts (e.g. Pergent-Martini and Pergent [1996](#page-10-19); Di Carlo et al. [2011](#page-9-30); Romero et al. [2012](#page-10-20); Bacci et al. [2016](#page-9-31)). While these biological and physical features are generally relevant at large spatial scales, some of them can also play a role at smaller spatial scales.

Although the quadrats we analyzed have been set on matte in stands that looked uniformly dense at repeated <span id="page-6-0"></span>**Fig.** 7 Two  $J(r)$  functions are shown for each of the ten quadrats. **a**–**l** Observed (*thick line*) and expected for an inhomogeneous random (Poisson) point process (*dashed line*) with 95% Monte Carlo intervals (*thin line*). Observed patterns that fall above, below or within the Monte Carlo intervals indicate regular, aggregated or random patterns, respectively



visual inspections, in most cases, shoot distribution appeared less homogeneous within the sampling quadrats.

In particular, some roughly circular patches with no shoots (i.e. Fig. [3](#page-4-0), quadrat i) could be connected to direct anthropogenic impacts (e.g. anchors) or to natural causes. In this regard, small patches of dead matte in a healthy *P. oceanica* meadow may result merely from the death of such vulnerable shoots. These structures, which are natural,



<span id="page-7-0"></span>**Fig. 8** Point patterns of *Posidonia oceanica* shoots at diferent spatial scales. While inter-shoot relationships drive small scale dynamics, a broader set of environmental conditions play a role in shoot point patterns and in shoot density at mesoscale

have been termed autogenic dead matte patches (Boudouresque et al. [2009\)](#page-9-32). In other cases (i.e. Fig. [3,](#page-4-0) quadrat f), in analogy with the autogenic dead matte patches, our results showed the infuence of natural causes as the discontinuities in matte surface on shoot distribution at small spatial scale: for instance, reduced density or absence of shoots was observed where the matte profle was locally steeper.

The reduced homogeneity in shoot distribution that was previously mentioned is to be understood as "site-specifc" and strictly related to the quadrats inspected. Therefore, their spatial point patterns were treated as inhomogeneous, to remove any local spatial structure (i.e. when intensity *λ* is not approximately constant, but varies with location over the entire observation quadrat), thus highlighting recurring patterns, which are not "site-specifc", but likely to be a more general feature of *P. oceanica* meadows.

Our results showed three diferent spatial scales that are relevant to analyses aimed at studying shoot point patterns, which are afected by diferent factors at diferent spatial scales.

The frst of those spatial scales roughly coincides with the quadrat size  $(10^2 \text{ cm})$ , where an important stochastic component, related to small scale features of the seafoor, afects distribution of shoots.

The second and the third spatial scales were smaller (roughly between  $10^1$  and  $10^0$  cm) and emerged from recurring patterns that were highlighted by the inhomogeneous *J*-function. Patterns recognized in the investigated quadrats show that shoots tend to be regularly distributed at very small spatial scale (in the 2–3 cm range, close to the average nearest neighbour distance). At this spatial scale, competition for space among shoots is the main factor afecting shoot spatial distribution, which is aimed at optimal packing. At spatial scales larger than about 3 cm, some "species-specifc" factors seem to become determining. These factors, strictly related to *P. oceanica* morphology, impose angles, distances, etc., and afect rhizome growth as well as the way shoots are arranged on each rhizome and the way diferent rhizomes interact with each other, thus determining aggregated shoot patterns.

The shoot point patterns analyzed by NNd in independent subquadrats (20 cm  $\times$  20 cm) revealed regular patterns in most cases, but regularity in point patterns was much more frequent where shoot density grew larger. In fact, at the highest density levels, no points were found under the curve that showed the expected NNd as a function of shoot density in case of random shoot distribution.

The analysis of shoot distribution patterns can be very useful to better understand the high degree of small scale variability in shoot density that has been reported in literature. In fact, although the existence of density patchiness within *P. oceanica* meadows has long been recognized (Panayotidis et al. [1980,](#page-10-21) [1981](#page-10-2)), small scale structural variability in *P. oceanica* meadows is poorly known and few authors have addressed the problem so far (Balestri et al. [2003](#page-9-33); Gobert et al. [2003;](#page-9-34) Zupo et al. [2006;](#page-10-22) Bacci et al. [2015](#page-9-8)). This variability, however, is likely to be a general feature of *P. oceanica* meadows, as it depends on how shoots grow, compete for space with each other, and on how they adapt their propagation to small scale features of the seafoor (Bacci et al. [2015\)](#page-9-8). Our results highlight how patchiness (i.e. aggregation) in shoot distribution at small spatial scales (mainly at  $10^1 - 10^2$  cm scale) is the main responsible for the variability in shoot density estimates obtained from shoot counts. Diferently, the recurring patterns highlighted at the smallest spatial scale  $(10^{0} - 10^{1}$  cm) revealed a homogeneous spacing among shoots, making it clear that most of the uncertainty on density estimates does not originate by uneven shoot distribution at this spatial scale. Further assurances about the existence of recurring patterns at the smallest spatial scales  $(10<sup>1</sup>$  and  $10<sup>o</sup>$  cm) derive from the nearest neighbor distances among shoots in each inspected quadrat. In this regard, although the quadrats differed in shoot density (from 566 to 1010 shoots  $m^{-2}$ ), the median NNd value was always close to 2 cm. Nevertheless, the NNd among quadrats revealed small, but signifcant diferences from a formal point of view. However, neighbouring quadrats did not seem to show more similarities between them than farther quadrats and the magnitude of the diferences did not appear to be related to distance between quadrats. This might suggest that the observed level of spatial variability in the data is characteristic of the type of meadow selected for our study, i.e. in shallow water, in good health, settled on matte, regardless of sitespecific characteristics.

In the end, our fndings seem consistent with those, entirely independently from this study, obtained by Bacci et al. ([2015\)](#page-9-8). In fact, the latter paper suggested smaller quadrats (20 cm  $\times$  20 cm instead of 40 cm  $\times$  40 cm or larger) as the most efective solution for shoot density counts, playing down error in density estimates and optimizing the monitoring methodology.

In the light of the role of *P. oceanica* meadows in the Mediterranean basin and their subsequent assumed relevance under European Directives (Habitat Directive 92/43/ EEC; Water Framework Directive 2000/60/EC; Marine Strategy Framework Directive 08/56/EC) and national laws, monitoring is crucial to support environmental decision-making and management of the coastal zone. Our results as well as other sources (e.g. Pergent-Martini et al. [2005](#page-10-1)) dealing with investigations in seagrass macrostructure agree in highlighting the importance of shoot density as a very useful descriptor in *P. oceanica* studies. At the same time, however, some limitations of this descriptor are becoming increasingly evident, especially when it is not appropriately measured (e.g. Bacci et al. [2015;](#page-9-8) Schultz et al. [2015\)](#page-10-23). Future studies could contribute with additional insights into these issues, providing useful details about shoot distribution patterns in *P. oceanica* meadows and about their potential use as additional macrostructure descriptors in seagrass monitoring. With this in mind, while shoot density is commonly used to assess environmental quality, we wonder whether point patterns in shoot distribution can possibly reveal something more.

Independently of any potential diagnostic interpretation of shoot distribution patterns, small scale information about meadow structure might play a role in supporting development and validation of models for growth and expansion of *P. oceanica* rhizomes. In this regard, a few models have been implemented to represent the dynamic development of the branching structure of a *P. oceanica* rhizome developing from a single shoot over time, as it slowly spreads out across the seafoor (Kendrick et al. [2005b](#page-9-12); Renton et al. [2011](#page-10-3)). Diferently, no research has yet been carried out to model the dynamic development of plagiotropic and orthotropic rhizomes in a three-dimensional space, i.e. in a way that more closely and more generally resembles the real processes.

In the framework of *P. oceanica* transplantation activities within restoration projects, the analysis of shoot microdistribution might also prove useful as a tool for comparing transplanted areas to surrounding natural meadows. After low density transplantation, rhizome growth is plagiotropic, but as soon as shoot density becomes high enough, rhizome growth turns to orthotropic and the resulting point patterns are expected to become more and more similar to those of the natural meadow as the matte builds up.

Although spatial point pattern analysis (SPPA) has become increasingly popular in terrestrial ecological research over the last two decades (Velasquez et al. [2016](#page-10-4)), most of these techniques are almost unknown in aquatic environments. This is partly understandable, since SPPA is not a standard technique to most ecologists and collecting suitable point pattern data was not an easy task until recently, especially at large spatial scale. In today's world, not only affordable underwater cameras, but also new instruments and technologies (i.e. drones, R.O.V.) allow to easily collect high resolution images, ready to be processed, above and below the water at any spatial scale. With this in mind, we hope that our work helps to stimulate the use of SPPA in marine ecology. In this regard, detailed knowledge of the characteristics of spatial distribution patterns of animal and plant species are the key for developing a deep understanding in many branches of ecology (Velasquez et al. [2016\)](#page-10-4).

In conclusion, although our data set is far from representing the whole spectrum of small scale variability in *P. oceanica* meadows, it has helped to shed light on shoot distribution patterns of the Mediterranean seagrass *P. oceanica*. We hope that it will be of use to other seagrass scientists too, thus promoting further SPPA-based studies in seagrass ecology. As far as we know, our raw data, here provided as supplementary material, are the frst source of information available about point patterns of shoot distribution. We hope that they will help to stimulate research activities aimed at studying shoot distribution patterns in *P. oceanica* and other seagrasses at very small spatial scale.

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#### **Compliance with ethical standards**

All plant experiments were done with permission from the Marine Protected Area of Capo Rizzuto and the Marine Park of Riviera dei Cedri.

**Confict of interest** The authors declare that they have no confict of interest.

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