ORIGINAL PAPER



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

Tiziano Bacci¹ · Francesco Sante Rende¹ · Michele Scardi²

Received: 18 December 2016 / Accepted: 28 February 2017 / Published online: 20 March 2017 © Springer-Verlag Berlin Heidelberg 2017

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 m²) 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 different spatial scales: regular patterns were recognized among shoots at smaller spatial scale $(10^0 - 10^1 \text{ cm})$, 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 different 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-specific" drivers or "site-specific"

Responsible Editor: P. Kraufvelin.

Reviewed by M. Montefalcone and an undisclosed expert.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-017-3121-1) contains supplementary material, which is available to authorized users.

features), also including relationships between shoot NNd and shoot density counts. The raw data, provided as supplementary material, are currently the first 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 first 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). Seagrass meadows, at any one time, consist of a nested structure of clones, possibly fragmented into different ramets, each supporting a variable number of shoots (Duarte et al. 2006). 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). 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; Boudouresque et al. 2016). 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).

In the Mediterranean Sea, the seagrass *Posidonia oceanica* (L.) Delile forms monospecific meadows with different types of coverage pattern (continuous to patchy) (Molinier and Picard 1952; Boudouresque et al. 2012) with shoot densities

Tiziano Bacci tiziano.bacci@isprambiente.it

¹ ISPRA–Institute for Environmental Protection and Research, Rome, Italy

² Department of Biology, University of Rome "Tor Vergata", Rome, Italy

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^{-2} (very sparse meadows) to more than 700 shoots m^{-2} (very dense meadows) (Giraud 1977).

Research on *P. oceanica* meadow structure can be carried out at different spatial scales (Van Rein et al. 2009). 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). 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; Bacci et al. 2015).

While the latter depend on interactions between rhizomes, there are very few scientific studies aimed at understanding this process in clonal growth of P. oceanica (Kendrick et al. 2005a), with particular reference to the growth rates of rhizomes and patterns of branching (Marba and Duarte 1998; Molenaar et al. 2000). 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) and to optimize strategies for transplantation aimed at reforestation activities (Renton et al. 2011). 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). 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; Tirado and Pugnaire 2003; Rayburn and Monaco 2011). 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; Murrell et al. 2001; Stoll and Prati 2001; Dunstan and Johnson 2003; Maestre et al. 2005; Turnbull et al. 2007).

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 different 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). As the field 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 fills 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). This choice has a practical justification, 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 justification. 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 cm × 20 cm) by means of the Spearman's rank correlation coefficient (Spearman 1904) 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), which is the counterpart for inhomogeneous spatial point patterns of the *J*-function for homogeneous point patterns, to define 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). The rationale supporting



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°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 influenced by first-order heterogeneity. Hence, the intensity λ is not approximately constant, but varies with the location (x, y) over the entire observation quadrat. To estimate the intensity function, which defines the expected number of shoots per unit area at each location, we used kernel estimators (Waller and Gotway 2004), which are among the best established nonparametric estimation techniques (Efromovich 1999). An estimate of

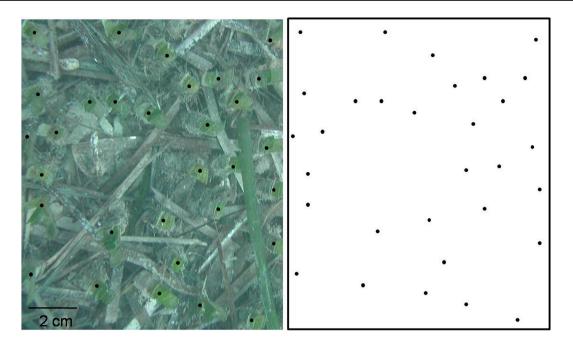


Fig. 2 A sample image (*left*) and the shoot point pattern (*right*). *Black dots* mark the apical portion of each rhizome. The image (*left*) was captured from above and the elongated forms correspond to dead shed leaves

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; Wiegand and Moloney 2014; Velazquez et al. 2016). 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; Van Lieshout and Baddeley 2006). 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. Significance of the deviations from the heterogeneous null model hypothesis, assuming 0.05 as the *p* level in Monte Carlo tests, was tested using simulated confidence 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). 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). The edge correction we applied

was based on the border method (van Lieshout 2010). All the statistical analyses were performed using the package spatstat 1.24-2 (for full details about spatstat see Baddeley et al. 2015) 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), highlighting very different 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 difference 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 difference 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). In addition, a significant 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 × 20 cm, 250 subquadrats overall) (Fig. 5). In this regard, most of the points characterized by higher shoot density values fell above the

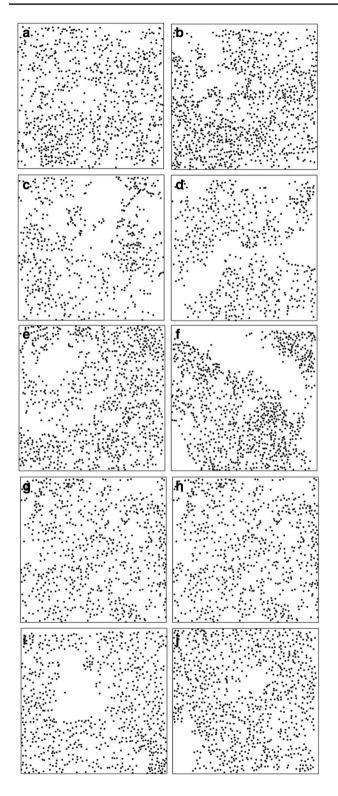


Fig. 3 Shoot distribution of the Mediterranean seagrass *Posidonia* oceanica within $1 \text{ m} \times 1$ m quadrats in meadows settled on *matte* and uniformly dense at repeated visual inspections. **a**, **b** Area I_ MPA-Capo Rizzuto; **c**, **d** area II_ MPA-Capo Rizzuto; **e**, **f** area III_ MPA-Capo Rizzuto; **g**, **h** area IV_MP-Riviera deiCedri; **i**-l area V_MP-Riviera deiCedri

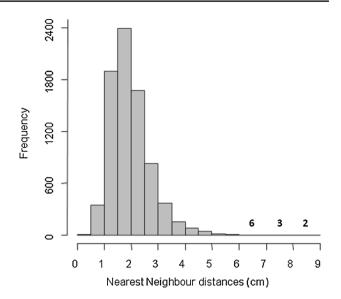


Fig. 4 Frequency distribution of nearest neighbour distances (NNd) of shoots. Very low frequency of nearest neighbour distances are shown in numbers in the 6-7 (cm), 7-8 (cm) and 8-9 (cm) intervals

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), one for each of the spatial point pattern shown in Fig. 3. In this regard, Kolmogorov-Smirnov test (with Bonferroni correction) detected significant statistical differences 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 <1 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). 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^2 of *P. oceanica* meadow has been mapped at the finest possible scale.

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

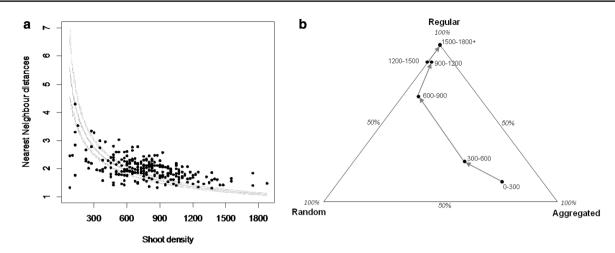


Fig. 5 a Scatter plot of medians of shoot nearest neighbour distances (NNd) and shoot density in the available subquadrats (20 cm \times 20 cm, 250 subquadrats overall). Expected median values for shoot NNd for a Poisson point process with 95% Monte Carlo intervals (*grey line*) (1000 simulations) are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

were extrapolated to 1 m². **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

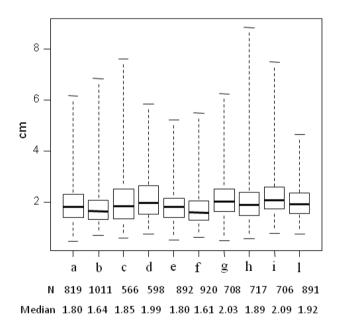


Fig. 6 *Box-plot* of nearest neighbour distances (NNd) for each of the ten quadrats (a-l). Number of shoots (*N*) and median NNd value are also shown

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 first 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,

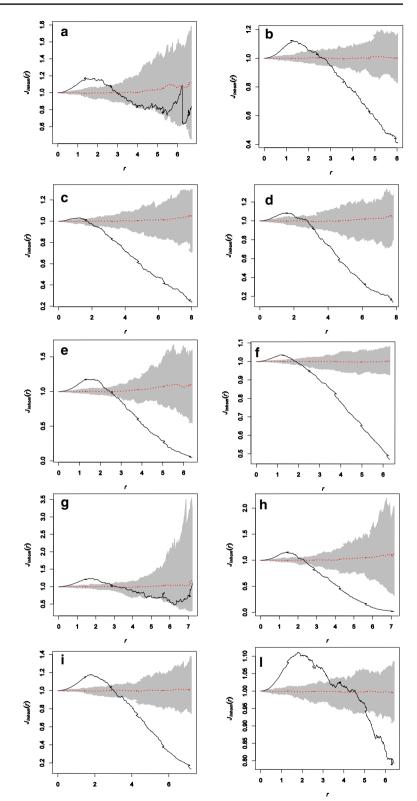
they provide considerable information about the potential variability of a very common type of meadows, i.e. those settled on *matte*, in shallow waters and in good health.

A meadow contains a huge number of shoots and its dynamics depends on the spatial distribution of those shoots. The variables that influence the shoot distribution depend on spatial scale and their number is presumably increasing in direct proportion to the spatial scale (Fig. 8).

First, the horizontal exploratory expansion of a meadow is controlled by species traits, such as rhizome elongation, branching patterns and clonal growth (Caye 1982; Marbà and Duarte 1998). In this regard, using the nearest neighbour statistics is justified 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; Lorenti et al. 1995; Montefalcone et al. 2016) as well as irradiance, temperature and nutrient availability (e.g. Buia et al. 1992; Alcoverro et al. 1995; Zupo et al. 1997; Leoni et al. 2007), detritus accumulation and sedimentation (Boudouresque and Jeudy de Grissac 1983; Romero et al. 1992; Gacia and Duarte 2001) and also anthropogenic impacts (e.g. Pergent-Martini and Pergent 1996; Di Carlo et al. 2011; Romero et al. 2012; Bacci et al. 2016). 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 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, 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,

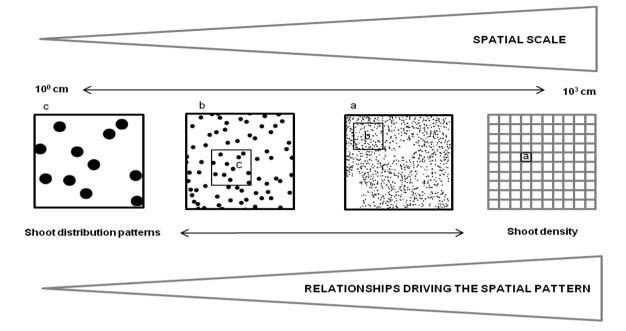


Fig. 8 Point patterns of *Posidonia oceanica* shoots at different spatial scales. While inter-shoot relationships drive small scale dynamics, a broader set of environmental conditions play a role in shoot point patterns and in shoot density at mesoscale

have been termed autogenic dead matte patches (Boudouresque et al. 2009). In other cases (i.e. Fig. 3, quadrat f), in analogy with the autogenic dead matte patches, our results showed the influence 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 profile was locally steeper.

The reduced homogeneity in shoot distribution that was previously mentioned is to be understood as "site-specific" 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-specific", but likely to be a more general feature of *P. oceanica* meadows.

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

The first of those spatial scales roughly coincides with the quadrat size (10^2 cm) , where an important stochastic component, related to small scale features of the seafloor, affects 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 affecting shoot spatial distribution, which is aimed at optimal packing. At spatial scales larger than about 3 cm, some "species-specific" factors seem to become determining. These factors, strictly related to *P. oceanica* morphology, impose angles, distances, etc., and affect rhizome growth as well as the way shoots are arranged on each rhizome and the way different 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, 1981), small scale structural variability in *P. oceanica* meadows is poorly known and few authors have addressed the problem so far (Balestri et al. 2003; Gobert et al. 2003; Zupo et al. 2006; Bacci et al. 2015). 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 seafloor (Bacci et al. 2015). 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. Differently, 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 (10^1 and 10° 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 significant differences 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 differences 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 findings seem consistent with those, entirely independently from this study, obtained by Bacci et al. (2015). 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 effective 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) 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; Schultz et al. 2015). 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 seafloor (Kendrick et al. 2005b; Renton et al. 2011). Differently, 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), 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).

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 first 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.

Acknowledgements All our thanks to the "R Development Core Team" and to the authors of various Statistical Packages utilized and downloaded from the CRAN (Comprehensive R Archive Network). The authors wish to thank the personnel of the MPA of Capo Rizzuto and Marine Park of Riviera dei Cedri for rendering this investigation possible, Claudio Bacci for assistance in the development of the sampling methodology, Domenico Rocca and Ezio Zito for their collaboration in scuba diving data collection and two anonymous reviewers and the associate editor for their comments, which improved the quality of the manuscript.

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.

Conflict of interest The authors declare that they have no conflict of interest.

References

- Alcoverro T, Duarte CM, Romero J (1995) Annual growth dynamics of *Posidonia oceanica*: contribution of large-scale versus local factors to seasonality. Mar Ecol Prog Ser 120:203–210
- Bacci T, Rende SF, Rocca D, Scalise S, Cappa P, Scardi M (2015) Optimizing *Posidonia oceanica* (L.) Delile shoot density: lessons learned from a shallow meadow. Ecol Indic 58:199–206
- Bacci T, Penna M, Rende SF, Trabucco B, Gennaro P, Bertasi F, Marusso V, Grossi L, Cicero AM (2016) Effects of Costa Concordia shipwreck on epiphytic assemblages and biotic features of *Posidonia oceanica* canopy. Mar Pollut Bull 109:110–116
- Baddeley A, Kerscher M, Schladitz K, Scott BT (2000) Estimating the J function without edge correction. Stat Neerl 54:315–328
- Baddeley A, Rubak E, Turner R (2015) Spatial point patterns: methodology and applications with R. Chapman and Hall, London
- Balestri E, Cinelli F, Lardicci C (2003) Spatial variation in *Posidonia oceanica* structural, morphological and dynamic features in a northwestern Mediterranean coastal area: a multi-scale analysis. Mar Ecol Prog Ser 250:51–60
- Bivand RS, Pebesma EJ, Gómez-Rubio V (2008) Applied spatial data analysis with R. Springer, The Netherlands
- Boudouresque CF, Jeudy de Grissac A (1983) L'herbier à *Posidonia* oceanica en Méditerranée: les interactions entre la plante et le sédiment. J Rech Océanogr 8:99–122
- Boudouresque CF and Meinesz A (1982) D'ecouverte de l'herbier de Posidonies. Cah Parc nation Port-Cros 4:1–79
- Boudouresque CF, Bernard G, Pergent G, Shili A, Verlaque M (2009) Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. Bot Mar 52:395–418
- Boudouresque CF, Bernard G, Bonhomme P, Charbonnel E, Diviacco G, Meinesz A, Pergent G, Pergent-Martini C, Ruitton S, Tunesi L (2012) Protection and conservation of *Posidoniao ceanica* meadows. RAMOGE and RAC/SPA publ, Tunis, p 1–202
- Boudouresque CF, Pergent G, Pergent-Martini C, Ruitton S, Thibaut T, Verlaque V (2016) The necromass of the *Posidonia oceanica* seagrass meadow: fate, role, ecosystem services and vulnerability. Hydrobiologia 781:25–42

- Buia MC, Zupo V, Mazzella L (1992) Primary production and growth dynamics in *Posidonia oceanica*. PSZNI Mar Ecol 13:1–16
- Caye G (1980) Analyse du polymorphisme caulinaire chez Posidonia oceanica (L.) Del. Bull Soc Bot Fr 127:257–262
- Caye G (1982) Etude de la croissance de la posidonie, *Posidonia oce-anica* (L.) Delile, formation des feuilles et croissance des tiges au cours d'une année. Tethys 10:229–235
- Den Hartog C (1971) The dynamic aspect in the ecology of seagrass communities. Thalass Jugosl 7:101–112
- Di Carlo G, Benedetti-Cecchi L, Badalamenti F (2011) Response of *Posidonia oceanica* growth to dredging effects of different magnitude. Mar Ecol Prog Ser 423:39–45
- Duarte CM (1991) Seagrass depth limits. Aquat Bot 40:363-377
- Duarte CM, Fourqurean JW, Krause-Jensen D, Olesen B (2006) Dynamics of seagrass stability and change. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrass: biology, ecology and conservation. Springer, Dordrecht, pp 271–294
- Dunstan PK, Johnson CR (2003) Competition coefficients in a marine epibenthic assemblage depend on spatial structure. Oikos 100:79–88
- Efromovich S (1999) Nonparametric curve estimation: methods, theory and application. Springer, New York
- Fortin MJ, Dale MRT (2005) Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge
- Gacia E, Duarte CM (2001) Sediment retention by a Mediterranean *Posidonia oceanica* meadow: the balance between deposition and resuspension. Estuar Coast Shelf Sci 52:505–514
- Giraud G (1977) Essai de classement des herbiers de *Posidonia oceanica* (Linné) Delile. Bot Mar 20:487–491
- Gobert S, Kyramarios M, Lepoint G, Pergent-Martini C, Bouquegneau JM (2003) Variations à differentes échelles spatiales de l'herbier à *Posidonia oceanica* (L.) Delile; effet sur les paramètres physico-chimiques du sédiment. Oceanol Acta 26:199–207
- Haase P, Pugnaire FI, Clark SC, Incoll LD (1996) Spatial patterns in a two tiered semi-arid shrubland in southeastern Spain. J Veg Sci 7:527–534
- Kendrick GA, Marbà N, Duarte CM (2005a) Modelling formation of complex topography by the seagrass *Posidonia oceanica*. Estuar Coast Shelf Sci 65:717–725
- Kendrick GA, Duarte CM, Marbà N (2005b) Clonality in seagrasses, emergent properties and seagrass landscapes. Mar Ecol Prog Ser 290:291–296
- Leoni V, Pasqualini V, Pergent-Martini C, Vela A, Pergent G (2007) Physiological responses of *Posidonia oceanica* to experimental nutrient enrichment of the canopy water. J Exp Mar Biol Ecol 349:73–83
- Lorenti M, Mazzella L, Buia MC (1995) Light limitation of *Posidonia* oceanica (L.) Delile growth at different depths. Rapp Comm Int Mer Médit 34:34
- Maestre FT, Escudero A, Martinez I, Guerrero C, Rubio A (2005) Does spatial pattern matter to ecosystem functioning? Insights from biological soil crusts. Funct Ecol 19:566–573
- Marbà N, Duarte CM (1998) Rhizome elongation and seagrass clonal growth. Mar Ecol Prog Ser 174:269–280
- Molenaar H, Barthélémy D, Reffye P, Meinesz A, Mialet I (2000) Modelling and growth patterns of *Posidonia oceanica*. Aquat Bot 66:85–99
- Molinier R, Picard J (1952) Recherches sur les herbiers de phanérogames marines du littoral méditerranéen français. Ann Inst Oceanogr 27:157–234
- Montefalcone M, Vacchi M, Carbone C, Cabella R, Schiaffino CF, Elter FM, Morri C, Bianchi CN, Ferrari M (2016) Seagrass on the rocks:*Posidonia oceanica* settled on shallow-water hard substrata with stands wave stress beyond predictions. Estuar Coast Shelf Sci 180:114–122

- Murrell DJ, Purves DW, Law R (2001) Uniting pattern and process in plant ecology. Trends Ecol Evol 16:529–553
- Panayotidis P, Boudouresque CF, Marcot-Coqueugniot J (1980) Végétation marine de l'île de Port-Cros (Parc national). XX. Répartition spatiale des faisceaux des *Posidonia oceanica* (Linnaeus) Delile. Trav Sci Parc nation Port-Cros 6:223–237
- Panayotidis P, Boudouresque CF, Marcot-Coqueugniot J (1981) Microstructure de l'herbier à *Posidonia oceanica* (Linnaeus) Delile. Bot Mar 24:115–124
- Pergent-Martini C, Pergent C (1996) Spatio-temporal dynamics of *Posidonia oceanica* beds near a seawage outfall (Mediterranean-France). Dredged and undredged sites in the Owen anchorage region of Southwestern Australia. In: Kuo J, Phillips RC, Walker DI, Kirkman H (eds) Proceedings of an international workshop on seagrass biology, Western Australia Museum, Perth, pp 299–306
- Pergent-Martini C, Leoni V, Pasqualini V, Ardizzone GD, Balestri E, Bedini R, Belluscio A, Belsher T, Borg J, Boudouresque CF, Boumaza S, Bouquegneau JM, Buia MC, Calvo S, Cebrian J, Charbonnel E, Cinelli F, Cossu A, Di Maida G, Dural B, Francour P, Gobert S, Lepoint G, Meinesz A, Molenaar H, Mansour HM, Panayotidis P, Peirano A, Pergent G, Piazzi L, Pirrotta M, Relini G, Romero J, Sanchez-Lizaso JL, Semroud R, Shembri A, Shili A, Tomasello A, Velimirov B (2005) Descriptors of *Posidonia oceanica* meadows: use and application. Ecol Indic 5:213–230
- Rayburn AP, Monaco TA (2011) Using a chronosequence to link plant spatial patterns and ecological processes in grazed Great Basin plant communities. Rangel Ecol Manag 64:276–282
- Renton M, Airey M, Cambridge ML, Kendrick GA (2011) Modelling seagrass growth and development to evaluate transplanting strategies for restoration. Ann Bot 108:1213–1223
- Romero J, Pergent G, Pergent-Martini C, Mateo MA, Regnier C (1992) The detritic compartment in a *Posidonia oceanica* meadow: litter features, decomposition rates and mineral stocks. PSZNI Mar Ecol 13:73–83
- Romero J, Pérez M, Alcoverro T (2012) L'alguer de Posidonia oceanica de les illes Medes: més de trenta anys d'estudi. El fonsmarí de les illes Medes i el Mongrí. Quatredè cades de recerca per a la conservació. En: Hereu B, Quintana X (édit) Recerca i territori, vol. 4, Càtedra d'ecosistemes litorals mediterranis publ, L'Estartit, p 79–100

- Schultz ST, Kruschel C, Bakran-Petricioli T, Petricioli D (2015) Error, power, and blind sentinels: The statistics of seagrass monitoring. PLoS One 10:e0138378
- Spearman C (1904) The proof and measurement of association between two things. Am J Psychol 15:72–101
- Stoll P, Prati D (2001) Intraspecific aggregation alters competitive interactions in experimental plant communities. Ecol 82:319–327
- Szmyt J (2014) Spatial statistics in ecological analysis: from indices to functions. Silva Fenn 48:1–31.
- Tilman D, Kareiva P (1997) The role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton
- Tirado R, Pugnaire FI (2003) Shrub spatial aggregation and consequences for reproductive success. Oecologia 136:296–301
- Turnbull LA, Coomes DA, Purves DW, Rees M (2007) How spatial structure alters population and community dynamics in a natural plant community. J Ecol 95:79–89
- Van Lieshout MNM (2010) A J-function for inhomogeneous point processes. Stat Neerl 65:183–201
- Van Lieshout MNM, Baddeley A (2006) A J-function for marked point patterns. Ann I Stat Math 58:235–259
- van Rein HB, Brown C, Quinn R, Breen J (2009) A review of sublittoral monitoring methods in temperate waters: a focus on scale. Underw Technol 28:99–113
- Velazquez E, Martinez I, Getzin S, Moloney KA, Wiegandl T (2016) An evaluation of the state of spatial point pattern analysis in ecology. Ecography 39:1042–1055
- Waller L A, Gotway C A (2004) Applied spatial statistics for public health data. Wiley, Hoboken
- Wiegand T and Moloney KA (2014) Handbook of spatial point-pattern analysis in ecology. CRC Press, Boca Raton
- Zupo V, Buia MC, Mazzella L (1997) A production simulation model for *Posidonia oceanica* based on temperature. Estuar Coast Shelf Sci 44:483–492
- Zupo V, Mazzella L, Buia MC, Gambi MC, Lorenti M, Scipione MB, Cancemi G (2006) A small-scale analysis of the spatial structure of a *Posidonia oceanica* meadow off the Island of Ischia (Gulf of Naples, Italy): relationship with the seafloor morphology. Aquat Bot 84:101–109