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Spatial patterns and temporal variability of seagrass connectivity in the Mediterranean Sea

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Abstract

Aim: The endemic seagrass *Posidonia oceanica* is a key component of the coastal seascapes of the Mediterranean Sea, where it provides crucial ecosystem services and promotes the assembly of diverse ecological communities. Although protection policies exist, *P. oceanica* meadows have been steadily declining in the recent past because of human activities and climate change. Here, we quantitatively analyse basin-wide patterns of seagrass connectivity over a 30-year-long period and identify connectivity hotspots that may serve as priority targets for conservation actions.

Location: Mediterranean Sea.

Time period: 1987–2016.

Major taxa studied: The seagrass *P. oceanica*.

Methods: A biophysical Lagrangian approach is used to simulate dispersal of seagrass fruits operated by marine currents. Connectivity metrics (self-retention, in-degree and outdegree) are evaluated on top of Lagrangian simulations to identify the most ecologically connected areas. Time series of local connectivity scores are analysed to study temporal variability and possibly detect trends at different spatial scales.

Results: Spatio-temporal variability is an important component of seagrass connectivity in the Mediterranean. Connectivity hotspots are unevenly distributed in all of its four main sub-basins, and along both European and African coastlines. Although statistically significant local trends in connectivity are generally quite infrequent across the whole basin, they appear to be relatively more prevalent in connectivity hotspots. The interannual variability of average connectivity scores seems to be at least partially linked to meteorological fluctuations.

Main conclusions: The present study represents a step forward in the application of a quantitative, scalable and replicable methodological framework for the prioritization

of seagrass conservation actions in the Mediterranean large marine ecosystem, a challenging environment characterized by complex socio-economic boundary conditions and high sensitivity to the localized effects of global climate change.

1 | INTRODUCTION

Posidonia oceanica (L.) Delile is a seagrass species endemic to the Mediterranean Sea; it inhabits the coasts of the entire Mediterranean basin in a 1–45 m depth range, except for large estuaries and regions where extreme thermal and salinity conditions are not favourable for its persistence (Gobert et al., 2006; Telesca et al., 2015). *P. oceanica* plays a pivotal ecological role as a habitat-forming species. Its vast underwater meadows shape the submarine seascape in coastal areas (Montefalcone, Albertelli, Bianchi, Mariani, & Morri, 2006). They also create favourable conditions for the assembly of diverse and complex communities that include also many commercially important fish species (Pergent et al., 2016). For these reasons, *P. oceanica* can be considered an ecosystem engineer, that is a species providing crucial ecosystem services, such as water oxygenation, carbon sequestration, nutrient cycling, water purification and protection from coastline erosion, and offering shelter or nursery to other species (Campagne, Salles, Boissery, & Deter, 2015; Vassallo et al., 2013). Despite remaining the most widespread seagrass in the Mediterranean Sea, *P. oceanica* populations have been sharply declining in recent decades due to multiple stressors, including the localized effects of climate change and human activities, with an estimated 13%–50% decrease in areal extent over the past 60 years (de los Santos et al., 2019; Marbà, Díaz-Almela, & Duarte, 2014; Telesca et al., 2015). In this respect, *P. oceanica* shares the same fate as the majority of seagrass species in coastal waters across the globe (Orth et al., 2006; Waycott et al., 2009). Owing to its importance in the context of the Mediterranean Sea coastal ecosystems, associated with the current trends of species distribution decline, *P. oceanica* has been identified as a key target for conservation by European institutions since the 1990s (Boudouresque et al., 2012).

Posidonia oceanica can reproduce sexually, producing seed-carrying, positively buoyant fruits that may be carried by marine currents and thus represent the main dispersal agents for this species (McMahon et al., 2014). Data on the dispersal distances of *P. oceanica* fruits are scarce. As an example, Arnaud-Haond et al. (2007) showed that the dispersal of *P. oceanica* fruits can be restricted to the scale of a few metres in some meadows, in spite of the apparent potential for larger-scale seed dispersal. In the same study, the authors showed the existence of genetic structure within individual seagrass meadows and genetic differentiation among populations on scales ranging from tens of kilometres up to the great divergence between populations inhabiting the eastern and western basins of

the Mediterranean Sea. However, evidence also exists suggesting that dispersal distances for *P. oceanica* may be significantly greater and more variable than previously considered. For instance, Serra et al. (2010) reported dispersal distances up to 50 km. Realized connectivity in *P. oceanica* is likely mainly limited by the episodic nature of flowering, sexual reproduction and the overall low production rate of fruits in most locations (e.g. Balestri & Cinelli, 2003; Balestri, Vallerini, & Lardicci, 2017; Procaccini, Orsini, Ruggiero, & Scardi, 2001). This implies that local management alone may not be enough for *P. oceanica* and that spatial planning should not dismiss connectivity out of hand. In fact, sexual reproduction and fruit dispersal, even at a low rate, can play a critical role in the colonization of new sites, recovery after disturbance and establishment of new genotypes in existing seagrass populations. Because of the widespread distribution of this foundation species along Mediterranean coasts and the reported large-scale trajectories of loss, conservation strategies should be planned at a whole-basin scale, with priority being given to sites that play a key role in structuring population connectivity, thus supporting effective conservation and restoration strategies. This coordinated effort would also be coherent with habitat-based policies that constitute the cornerstone of Europe's nature conservation policy (e.g. "Habitats Directive," 92/43/EEC).

Designing prioritization strategies at the scale of the whole Mediterranean Sea is necessary to channel resources where interventions are most urgently needed and/or likely to be effective. However, this requires a comprehensive framework able to capture the complexity of both patterns and processes, and duly accounting for the challenges imposed by such a large spatial extent. This problem is further exacerbated by the trans-boundary nature of the Mediterranean Sea, the complex social, cultural and political conditions of the countries surrounding it and its high sensitivity to global climate change (Lejeusne, Chevaldonné, Pergent-Martini, Boudouresque, & Perez, 2010; Micheli et al., 2013). Indeed, a regional approach for the protection and enhancement of the status of the marine environment in the Mediterranean Sea requires a close cooperation among states and international organizations, which is one of the founding principles of the Barcelona Convention ("Convention for the Protection of the Marine Environment and the Coastal Region of the Mediterranean"). Also, the Marine Strategy Framework Directive (MFSD, 2008/56/EC) has established detailed criteria and methodological standards according to which each member state has to take the necessary measures to achieve or maintain "Good Environmental Status"

in the marine environment. In general, identifying areas for protection in large marine ecosystems requires techniques involving multiple scales of analysis. The spatial structuring imposed by the interplay between local environmental conditions and basin-wide circulation patterns, in particular, calls for the design of marine protected areas ensuring and promoting seascape connectivity (Planes, Jones, & Thorrold, 2009). In fact, if a protected area is not sufficiently connected to others, it may not effectively receive/send propagules (such as larvae or seeds), thus possibly thwarting natural recovery (McCook et al., 2009). In other words, spatial planning of marine protection should be conceived as the design of a coherent network of protected areas ecologically connected at various spatial scales, in order to fulfil ecological aims more effectively than single individual sites could do (Boero, 2015; WCPA/IUCN, 2007). Assessing the functional connectivity of species that are target of protection efforts, such as *P. oceanica*, is thus of paramount importance to large-scale conservation planning (Jahnke et al., 2017; Kendrick et al., 2017).

In this work, connectivity patterns of *P. oceanica* are evaluated at the scale of the whole Mediterranean Sea over a 30-year-long time span. We propose a definition of species-specific functional connectivity (suitability-weighted connectivity—for brevity, *s*-connectivity) accounting for both local suitability conditions and dispersal patterns driven by marine currents. This definition aims to account not only for the amount of propagules potentially exchanged between marine sites but also for the environmental conditions that may influence local suitability for the species under study. To that end, a Lagrangian approach is used to build a biophysical model for the dispersal of *P. oceanica*. Following the methodological framework proposed by Melià et al. (2016), *s*-connectivity is then evaluated on top of the results of Lagrangian simulations to single out the strongest and most time-persistent ecological connections for *P. oceanica* across the Mediterranean Sea, specifically in terms of the possible functional roles that a local population can play in the context of a larger metapopulation, namely retainer, sink and source. The multi-decadal temporal span of the simulation exercise also allows the study of temporal variability in *P. oceanica* connectivity and the identification of trends, as well as the investigation of the possible relationships between connectivity and meteorological fluctuations. The ultimate goal of the analysis is to improve spatial prioritization
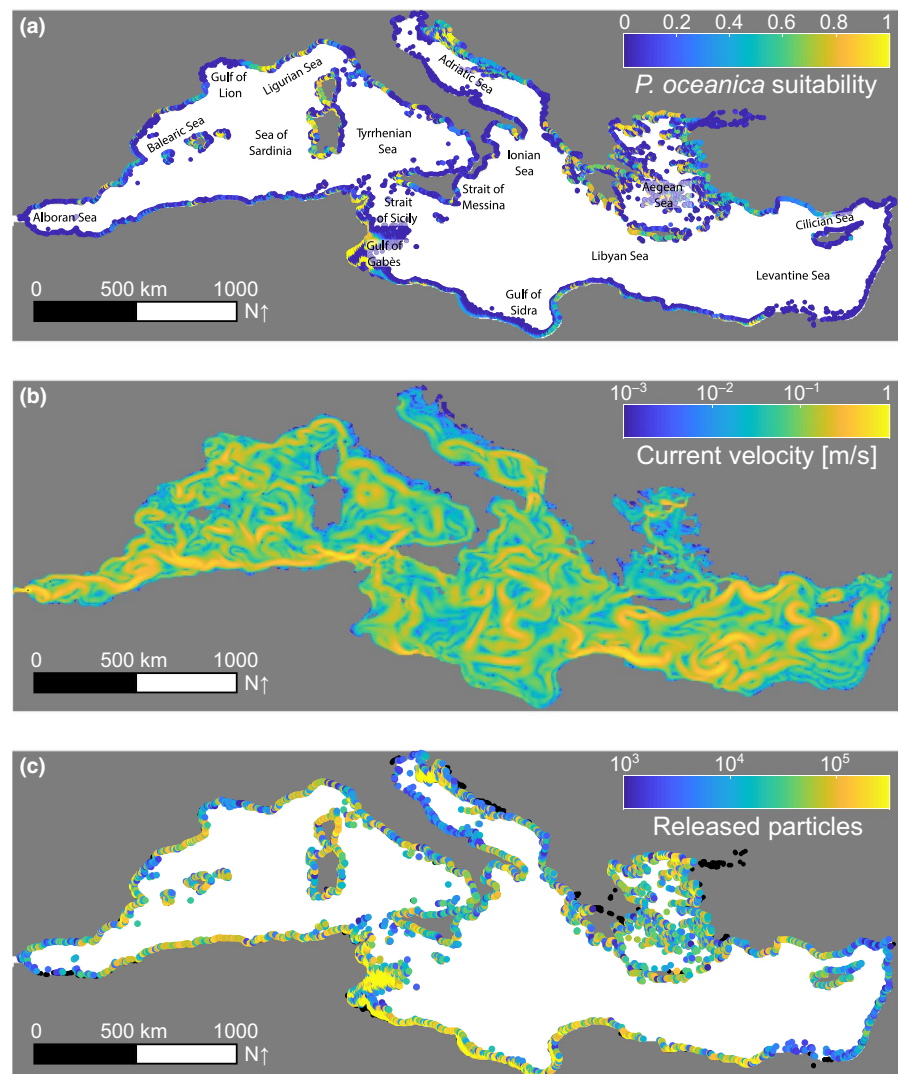

FIGURE 1 The biophysics of *Posidonia oceanica* connectivity in the Mediterranean Sea. (a) Species-specific suitability map (Giannoulaki et al., 2013). Colour-coded scores represent estimated probabilities of *P. oceanica* presence. (b) Example of circulation field. Colours represent the speed of surface currents for 1 January 2014, obtained through bilinear interpolation of data from a physical reanalysis of Mediterranean circulation (Lecci et al., 2017; Simoncelli et al., 2014). (c) Marine sectors for the analysis of *P. oceanica* connectivity (centroids, coloured dots). Colours represent the number of simulated Lagrangian trajectories starting from each sector in each year of the simulation time span (1987–2016). This variability reflects the small-scale spatial heterogeneity in the distribution of suitable sites. Black dots are suitable sites that fall outside the spatial domain of the physical reanalysis and that are thus not used in the numerical simulations

practice in conservation planning for an iconic foundation species at a Mediterranean-wide spatial scale.

2 | METHODS

2.1 | Biophysical simulations of dispersal

Basin-wide potential connectivity for *P. oceanica* in the Mediterranean Sea is estimated through Lagrangian simulations (Van Sebille et al., 2018), with dispersing agents representing *P. oceanica* fruits. Lagrangian particles are released at marine sites that are suitable for *P. oceanica* meadows, are transported by currents and may eventually settle at some suitable sites.

Release sites are determined based on a species-specific suitability map produced by the MediSeH project (Giannoulaki et al., 2013), in which binary observations of *P. oceanica* presence–absence (Telesca et al., 2015) and a set of 36 mapped predictor variables (encompassing bathymetry and geographical features, physico-chemical characteristics, nutrient and pollutant concentrations, as well as human impact indicators) were used to train a random forest algorithm (Breiman, 2001) estimating the probability of *P. oceanica* occurrence throughout the whole Mediterranean Sea basin. The predictive variables that played the most relevant roles in the final species distribution model by Giannoulaki et al. were nitrate and silicate concentrations, average depth, sea surface temperature and salinity, with distance from river mouths, phosphate concentration, pH, bottom salinity and photosynthetic active radiation also featuring prominently. The estimated occurrence probability of *P. oceanica* meadows (a proxy for suitability) at site *A*, s_A, was projected as a high-resolution (1/240°, around 0.5 km) raster map extending over the whole Mediterranean basin (Figure 1a).

Circulation fields (daily averages, Figure 1b) are obtained from a state-of-the-art, Mediterranean-wide physical reanalysis (Lecci, Fratianni, Drudi, & Grandi, 2017; Simoncelli et al., 2014) produced by the Istituto Nazionale di Geofisica e Vulcanologia (Italy). Because circulation fields have lower spatial resolution (1/16°, around 7 km) than the suitability map, some differences in the representation of the coastlines and other details of the physical domain are clearly to be expected. For instance, the currently available physical reanalysis does not cover yet areas like the Sea of Marmara in Turkey, or many of the Greek gulfs, including the Gulf of Corinth and the Euboean Gulf.

Lagrangian simulations are performed over the time interval 1987–2016 (n^y = 30 years). In each year, timing of release is set to match the fruit-release season of *P. oceanica* (typically, January throughout April, for a total of n^d = 120 days; see Melià et al., 2016; Jahnke et al., 2017). For each day in this season, a fixed number of particles (n^p = 15) are released from each pixel of the suitability map that has strictly positive suitability and that lies, at least in part, inside the domain of the physical reanalysis. While the release of 15 particles per site and day might seem quite a low figure, the size of the spatial domain of our Lagrangian exercise (the whole Mediterranean basin) is such that matters of computational feasibility become

relevant. A total of $n^r \approx 5.69 \times 10^5$ release sites are in fact identified following the selection criteria outlined above. All in all, an excess of $n^t = n^y\, n^d\, n^p\, n^r \approx 30$ billion Lagrangian particles is tracked over the whole numerical assessment. The initial position of particles within each release site is randomly assigned to uniformly span the area of the pixel and a depth interval of 0–1 m (*P. oceanica* fruits are free-floating and positively buoyant; Serra et al., 2010).

The longitudinal and latitudinal components of the position of each particle are updated by assuming passive transport driven by marine circulation fields, while particle depth is not updated. Numerical integration is performed with a Runge–Kutta fourth-order scheme with adaptive step size (Dormand & Prince, 1980). At each time step, three-dimensional trilinear interpolation of the longitudinal and latitudinal components of the velocity field is performed. Note that the spatial grain of the circulation model (1/16°) is much coarser than the suitability map used to identify release sites (1/240°). As such, the effects of releasing a large number of particles from each pixel of the latter, higher-resolution grid would likely be dampened by the necessity of interpolating current velocities from the former, lower-resolution grid. The position of each particle is tracked for a period of time corresponding to the duration of the dispersing stage of *P. oceanica*, after which fruits dehisce and release their seeds.

Duration estimates for the floating phase of the fruits of this seagrass species vary from one/two weeks (e.g. Aliani, Gasparini, Micheli, Molcard, & Peirano, 2006; Buia & Mazzella, 1991) up to 4 weeks (Serra et al., 2010). Here, we use a value of 28 days, which is towards the maximum reported length of the dispersal window and allows an assessment of potential connectivity (an upper bound for realized connectivity). This value has consistently been used in all previous modelling studies addressing *P. oceanica* dispersal dynamics (Jahnke et al., 2017; Melià et al., 2016; Serra et al., 2010).

In our modelling framework, a dispersal event is considered successful only if a particle reaches a suitable site at the end of its dispersing phase. Although this approach differs from what has been proposed in the literature to describe connectivity in other seagrass species (see Appendix S1 for details), it has consistently been used in previous works addressing *P. oceanica* fruit dispersal via Lagrangian simulations (see again Jahnke et al., 2017; Melià et al., 2016; Serra et al., 2010).

2.2 | *Posidonia oceanica*-specific connectivity

The strength of *P. oceanica* connectivity is assumed to be proportional to the number of successful dispersal events $n_{AB}(y)$ that link (directionally) any two suitable sites (say, site *A* to site *B*) in year *y*. This quantity is clearly influenced by species-specific traits such as timing of fruit release and duration of the dispersing phase, but is mostly concerned with the hydrodynamics of passive propagule dispersal by marine currents. To account for small-scale heterogeneities in the quality and spatial distribution of suitable sites across the Mediterranean Sea, we define an ecologically motivated measure of connectivity in which successful dispersal events are weighted

according to the suitability scores of both release (source) and settling (sink) sites. Suitability-weighted connectivity (s-connectivity, from here on out) between two sites A and B in year y is thus defined as $C_{AB}{}^s(y) = s_A\, n_{AB}(y)\, s_B$. In this way, not only species-specific dispersal patterns but also local suitability conditions are effectively taken into consideration and integrated in a comprehensive measure of functional connectivity. For this reason, s-connectivity can represent an informative tool to evaluate the ecological value of marine sites, at least from the perspective of the potential connectivity of the species being studied.

For the sake of spatial robustness, instead of analysing individual sites at the fine scale of the *P. oceanica* suitability map (1/240°), we focus on the marine sectors defined by the coarser resolution of the physical reanalysis of the circulation fields (1/16°). Specifically, a suitable marine sector is defined as a cell of the circulation model that includes at least one suitable site. Each suitable sector may thus include from one to $(240/16)^2 = 225$ suitable sites. By construction, then, despite the release of a uniform number of particles at the fine spatial scale of the suitability map, the number n_i of Lagrangian trajectories starting at each marine sector i varies over space, reflecting the uneven spatial distribution of suitable sites in the seascape. In fact, upwards of three thousand particles are released daily from fully suitable sectors, for an excess of 400 thousand particles/sector/year. By contrast, marine sectors for which n_i is below a given threshold (set here to 1,000 particles per year) are excluded from further analysis to improve robustness. A set of $n^m \approx 8,000$ suitable marine sectors is identified in this way, spanning the Mediterranean shorelines (Figure 1c). The pairwise s-connectivity score between any two sectors (say i and j) in a given year (say y) is defined as.

$$C_{ij}^s(y) = \Sigma_{A \in i} \Sigma_{B \in j} C_{AB}^s(y) = \Sigma_{A \in i} \Sigma_{B \in j} s_A n_{AB}(y) s_B.$$

These scores can be suitably organized in a time-varying s-connectivity matrix $\mathbf{C}^s(y) = [C_{ij}{}^s(y)]$, which in turn can be characterized as a directed weighted graph, with nodes and edges being, respectively, marine sectors and time-varying s-connectivity scores.

2.3 | Connectivity metrics

In the theory of complex networks, two simple yet powerful metrics of connectivity are the indegree and the outdegree of network nodes, defined for weighted graphs as the sum of the incoming and outgoing links' weights, respectively (Newman, 2010). Thus, in the context of *P. oceanica* dispersal, indegree and outdegree measure the tendency of the sites within a marine sector to function as potential sinks or sources for *P. oceanica* fruits, that is to be successful at receiving/sending propagules from/to suitable sites lying in other sectors. In ecological applications, another important metric based on connectivity scores is self-retention (e.g. Melià et al., 2016). For the problem at hand, self-retention quantifies how many *P. oceanica* fruits both are released and settle within a given marine sector (say i), with the release and

settling sites being possibly different, but both lying in sector i. Technically, the diagonal elements $C_{ii}{}^s(y)$ of the s-connectivity matrix thus represent the local self-retention (SR) of each marine sector ($SR_i(y) = C_{ii}{}^s(y)$), while indegree (ID) and outdegree (OD) can be easily evaluated as the column or the row sums of the s-connectivity matrix, that is $ID_i(y) = \Sigma_{j \neq i} C_{ji}^s(y)$ and $OD_i(y) = \Sigma_{j \neq i} C_{ij}^s(y)$, with the condition $j \neq i$ being imposed to avoid multiple counting of self-retention. Because of the time-varying nature of the s-connectivity matrix (as determined by the temporal variability of circulation fields), self-retention, indegree and outdegree are all time-varying quantities too.

2.4 | Identification of *s*-connectivity hotspots

The metrics described above can be used to identify the hotspots of s-connectivity for *P. oceanica* across the Mediterranean Sea. To do so, we follow the methodological framework proposed by Melià et al. (2016) to assign each marine sector a synthetic s-connectivity score recapitulating its capacity to simultaneously act as retainer, sink and source.

First off, the across-year mean (an indicator of sheer intensity) and coefficient of variation (standard deviation-to-mean ratio, an indicator of temporal variability) are evaluated for each s-connectivity metric and marine sector. In this way, six different indicators are produced for each suitable marine sector i: $SR_i{}^{Ave}$ and $SR_i{}^{CV}$ for self-retention, $ID_i{}^{Ave}$ and $ID_i{}^{CV}$ for indegree and $OD_i{}^{Ave}$ and $OD_i{}^{CV}$ for outdegree, with the superscripts Ave and CV indicating average and coefficient of variation, respectively.

Then, for each metric, two separate rankings of marine sectors are produced, respectively, according to either decreasing intensity or increasing variability. To avoid spurious results, sectors with an average intensity score of zero (which indicates that the local values of the s-connectivity metric are null over the whole simulation time span) are listed as last in the variability ranking. For a given metric, two percentile scores can thus be assigned to each sector: the first defined as the percentage of sectors that have intensity equal to or lower than the one being considered and the second as the percentage of sectors that have equal or higher variability. Therefore, the sector endowed with highest across-year mean will receive an intensity score of 100 and the one with the lowest a score of zero; conversely, the sector with lowest coefficient of variation will receive a variability score of 100 and the one with the highest a score of zero. This procedure leads to the definition of six percentile scores for each sector (say i): $pSR_i{}^{Ave}$ and $pSR_i{}^{CV}$ for self-retention, $pID_i{}^{Ave}$ and $pID_i{}^{CV}$ for indegree and $pOD_i{}^{Ave}$ and $pOD_i{}^{CV}$ for outdegree.

Afterwards, for each sector i, we introduce summary percentile scores for self-retention, indegree and outdegree. They are defined conservatively as the minimum between the two relevant percentile scores pertaining to the intensity and variability of each metric, that is $pSR_i = \min(pSR_i{}^{Ave}, pSR_i{}^{CV})$, $pID_i = \min(pID_i{}^{Ave}, pID_i{}^{CV})$ and $pOD_i = \min(pOD_i{}^{Ave}, pOD_i{}^{CV})$. A synthetic percentile s-connectivity score pCS_i is then assigned to each of the n^m marine

FIGURE 2 Examples of time-varying *Posidonia oceanica* dispersal kernels. In each panel, colours code the relative frequency of successful dispersal events linking the selected marine sector (corresponding to the labelling of the black circles in the top inset) with other suitable sectors lying at a given distance during a specific dispersal season. The nine sample sectors (a–i) have been selected so as to span over different spatio-temporal scales of dispersal, that is encompassing sectors characterized by relatively short/long dispersal distance (across-year average of mean dispersal distance approximately half/double the across-sector mean value) and low/high temporal variability (across-year coefficient of variation of mean dispersal distance approximately half/double the across-sector mean value). The values of the across-year average (Ave) and coefficient of variation (CV) of mean dispersal distance for the nine sample sectors are reported on top of the panels

sectors by taking the minimum (again, conservatively) among the three summary scores for self-retention, indegree and outdegree, that is $pCS_i = \min(pSR_i, pID_i, pOD_i)$. This final percentile value can thus be interpreted as an overall *s*-connectivity score, and sectors where pCS is highest can be considered hotspots of *s*-connectivity for *P. oceanica* in the Mediterranean Sea and possible priority candidates for species protection. We stress again that the aggregation procedure used to evaluate pCS reflects a conservative strategy by which hotspots are marine sectors identified based on their ability to outperform others in the *s*-connectivity metric/indicator in which they are weakest.

Finally, the top-*k s*-connectivity hotspots (with *k* being the number of target hotspots) are identified as the *k* sectors whose synthetic percentile *s*-connectivity score exceeds the $(n^m - k)$th order statistic of the score distribution.

The final results of the hotspot identification procedure do evidently depend upon the spatial scale of analysis, which in the problem at hand is defined by the size of marine sectors. Sensitivity analysis can be used to check whether the procedure is robust to variations in spatial scales, namely to changing the way local (self-retention) versus in/outbound (in/outdegree) connections are defined (details in Appendix S1). Other approaches to investigate connectivity within a network of seagrass populations, thus also possibly identifying connectivity hotspots, have been explored in the literature, namely based on tools proposed in the context of complex network theory (Grech et al., 2018). A discussion of such approaches is also available in Appendix S1.

2.5 | Evaluation of *s*-connectivity temporal variability

To evaluate temporal variability in *s*-connectivity and to assess whether there may exist temporal trends, linear regression is performed on the local (sector-specific), 30-year-long time series of the three metrics introduced above, that is self-retention, indegree and outdegree. A linear trend is detected (via ordinary least square techniques; Draper & Smith, 1998) if the 95% confidence interval for the slope of the regression line does not contain zero. While a time span of 30 years may not be considered long with respect to the generation time of *P. oceanica* meadows, it is the longest currently allowed for the evaluation of current-driven connectivity in the Mediterranean, as it corresponds to the length of the state-of-the-art reanalysis of the physical parameters (including circulation fields) of the sea. Within this temporal window, relatively conservative methods to detect trends or correlations

have been applied, as only linear patterns have been included in the analysis, while more general tests (e.g. Mann–Kendall and derivatives for trend detection) have not been considered.

Temporal trends in spatially averaged *s*-connectivity are also investigated both at the scale of the whole Mediterranean Sea and for restricted sets of sectors identified as *P. oceanica* connectivity hotspots. Additionally, correlation patterns are sought between average self-retention, indegree and outdegree values and lagged time series of standard measures of meteorological variability for the Mediterranean basin, namely the Mediterranean Oscillation Index (MOI; Conte, Giuffrida, & Tedesco, 1989), in its two variants (MOI1, Algiers–Cairo, and MOI2, Gibraltar–Tel Aviv), and the Western Mediterranean Oscillation Index (WeMOI; Martin-Vide & Lopez-Bustins, 2006). All details are available in Appendix S1.
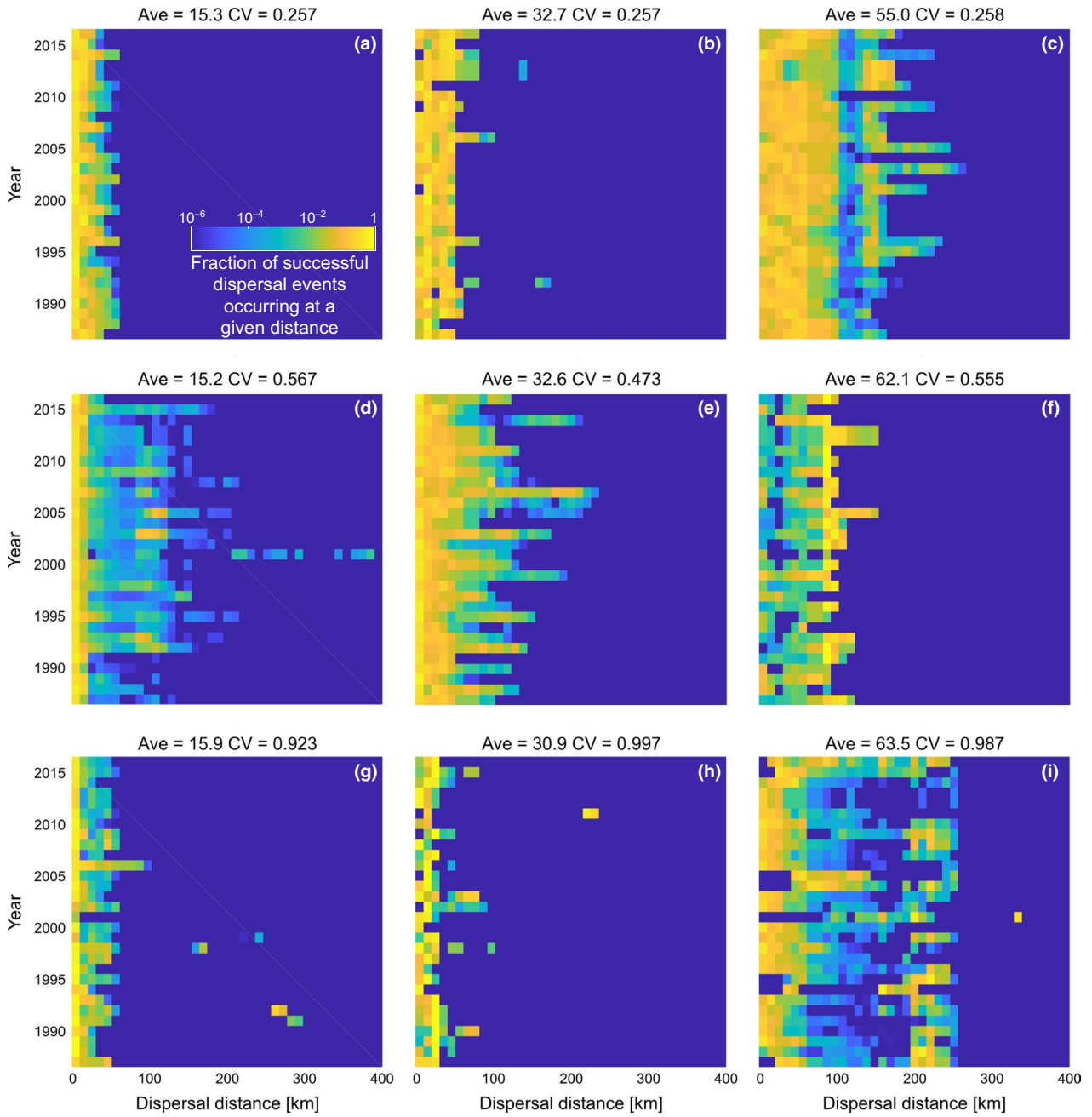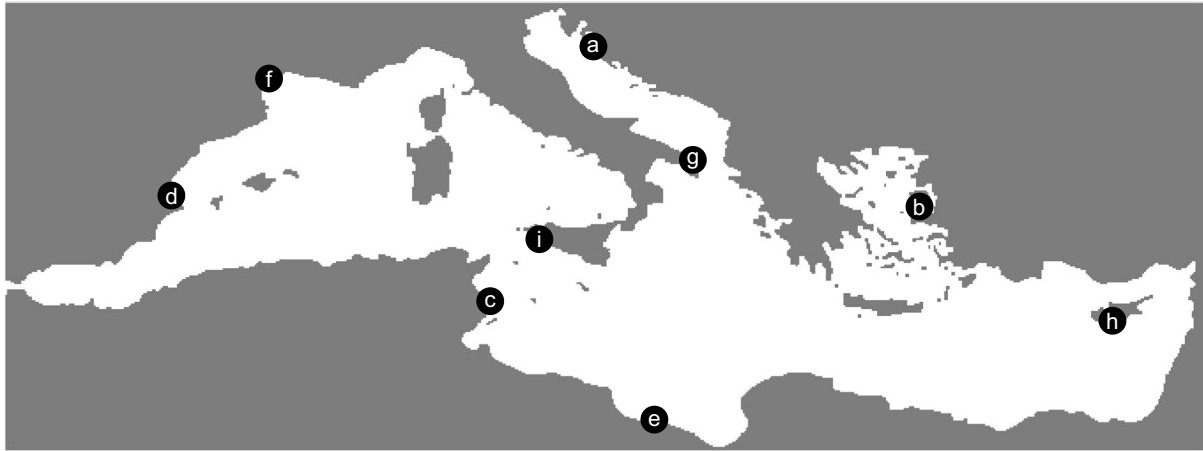
3 | RESULTS

3.1 | Spatio-temporal patterns of *Posidonia oceanica* *s*-connectivity

Posidonia oceanica dispersal patterns (Figure 2) and average dispersal distances (Figure 3) vary conspicuously among different regions of the Mediterranean Sea and fluctuate widely over time in the period 1987–2016. As a result, the *s*-connectivity scores $C^s_{ij}(y)$ turn out to be quite heterogeneous as well, as shown in Movie M1, available as supporting information. Despite the apparent spatio-temporal variability of *s*-connectivity patterns, some general features emerge: (a) along-coast transport represents a prevailing and persistent means of dispersal for *P. oceanica*; (b) crossing of relatively short sea stretches is quite common, yet fairly erratic; (c) large islands and archipelagos may serve as stepping stones to cross wider sea stretches over different reproduction seasons; (d) some sea stretches are rarely (if at all) successfully crossed by dispersing *P. oceanica* fruits; (e) the region centred on the Strait of Sicily (see Figure 1a for geographical designations), that is the area comprised between the southern coasts of Sardinia and Sicily, to the north, and the coasts of Tunisia and Western Libya, to the south, is characterized by remarkable intercontinental *s*-connectivity; and (f) the Aegean Sea forms a relatively disconnected subsystem.

3.2 | Connectivity metrics and *s*-connectivity hotspots for *Posidonia oceanica*

Across-year *s*-connectivity indicators (mean values and coefficients of variation of self-retention, indegree and outdegree for each marine sector; see Figures S1 and S2 in Appendix S2) represent the basis to
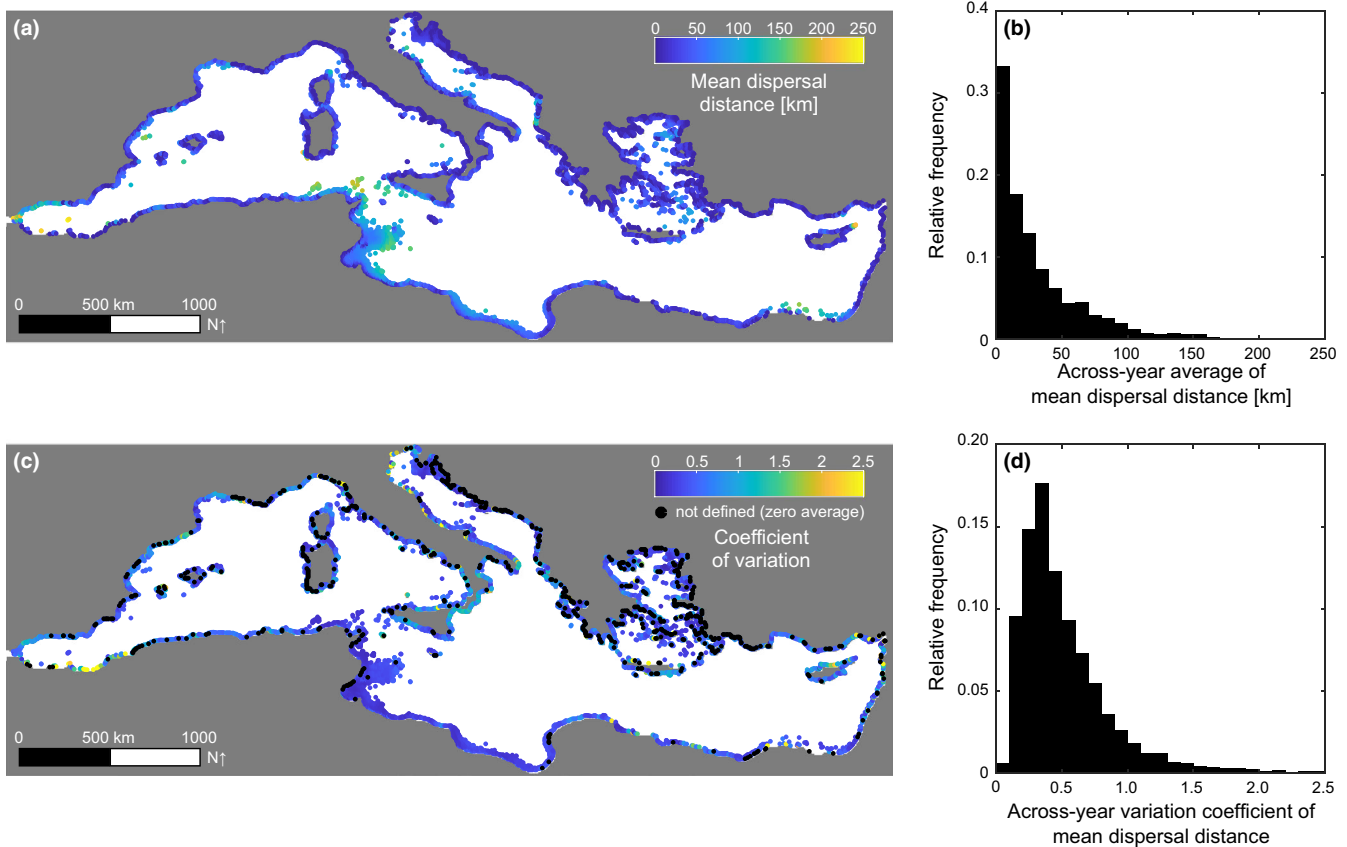
Ave = 15.3 CV = 0.257 (a); Ave = 32.7 CV = 0.257 (b); Ave = 55.0 CV = 0.258 (c); Ave = 15.2 CV = 0.567 (d); Ave = 32.6 CV = 0.473 (e); Ave = 62.1 CV = 0.555 (f); Ave = 15.9 CV = 0.923 (g); Ave = 30.9 CV = 0.997 (h); Ave = 63.5 CV = 0.987 (i)

Fraction of successful dispersal events occurring at a given distance. 10^{-6} 10^{-4} 10^{-2} 1

Dispersal distance [km]

FIGURE 3 Across-year evaluation of mean dispersal distances for *Posidonia oceanica* fruits in the Mediterranean Sea. (a) Time-averaged mean dispersal distance (colour-coded) for the period 1987–2016. (b) Frequency distribution of the time-averaged mean dispersal distance in the suitable marine sectors. The mean dispersal distance evaluated over all suitable sectors is ~31 km. (c) Coefficient of variation of mean dispersal distance evaluated over time (colour-coded, non-dimensional). (d) Frequency distribution of the across-year variation coefficient of mean dispersal distance. The mean coefficient of variation evaluated over all suitable sectors is ~0.54. Sectors characterized by zero mean dispersal distance (pure retainers, shown as black dots in panel c), for which the coefficient of variation of mean dispersal distance over time cannot be computed, have been omitted from the histogram. Note that unsuccessful dispersal events (fruits that are transported by marine currents to unsuitable sites at the end of their dispersing phase) are not included in the evaluation of mean dispersal distances

build the percentile scores for self-retention, indegree and outdegree intensity and variability (Figure S3 in Appendix S2), which are then aggregated to form the summary percentile scores for each of the three *s*-connectivity metrics (Figure S4 in Appendix S2) and, finally, the synthetic percentile *s*-connectivity score, pCS (Figure 4a). The ordered sample distributions of the summary scores for self-retention, indegree and outdegree and of pCS are shown in Figure S5 in Appendix S2. Contrasting local suitability (Figure 1a) to pCS reveals that many sectors (e.g. in the Ligurian Sea) are classified as highly suitable, but do not stand out in terms of *s*-connectivity, evidently because of suboptimal current-driven dispersal; conversely, many others (e.g. along the coasts of Tunisia and Libya, between the Gulf of Gabès and the Gulf of Sidra) are characterized by average suitability, but score high in terms of pCS, evidently because of excellent oceanographic connectivity making up for suboptimal environmental conditions. These observations are generalized in Figure S6 (Appendix S2), which shows that the correlations between pCS and local suitability, and between pCS and the various *s*-connectivity metrics, are typically quite noisy.

The top-100 and top-500 hotspots of *s*-connectivity are displayed in Figure 4b. The top-100 *P. oceanica s*-connectivity hotspots, in particular, appear to be localized along the Spanish coastline in the Balearic Sea, on the western coast of Sardinia, in the Northern Tyrrhenian Sea, along the coasts of Tunisia and Libya, in the North-Eastern Adriatic Sea (mostly in Croatia), in the Ionian Sea, in the Aegean Sea and along the Egyptian coastline. The identification of *P. oceanica s*-connectivity hotspots seems to be quite robust with respect to the spatial scale of analysis, as shown in Figure S7 in Appendix S2. In fact, modifying the definition of local versus in/outbound connections by introducing a buffer zone around each suitable marine sector does not fundamentally change the selection of *s*-connectivity hotspots. Interestingly, some regions endowed with a high hotspot density (specifically, the Gulf of Gabès and the North-Eastern Adriatic Sea) are also selected as central for *s*-connectivity by some relevant metrics of node importance proposed in the context of complex network theory (Figure S8 in Appendix S2).

FIGURE 4 Hotspots of *s*-connectivity for *Posidonia oceanica* in the Mediterranean Sea. (a) Synthetic percentile *s*-connectivity score, evaluated for each suitable marine sector as the minimum among its percentile scores for intensity and variability of self-retention, indegree and outdegree (Figure S4 in Appendix S2). (b) Top-*k* *s*-connectivity hotspots, with *k* = 100 or *k* = 500. The top-500 sectors do obviously include the top-100 as well
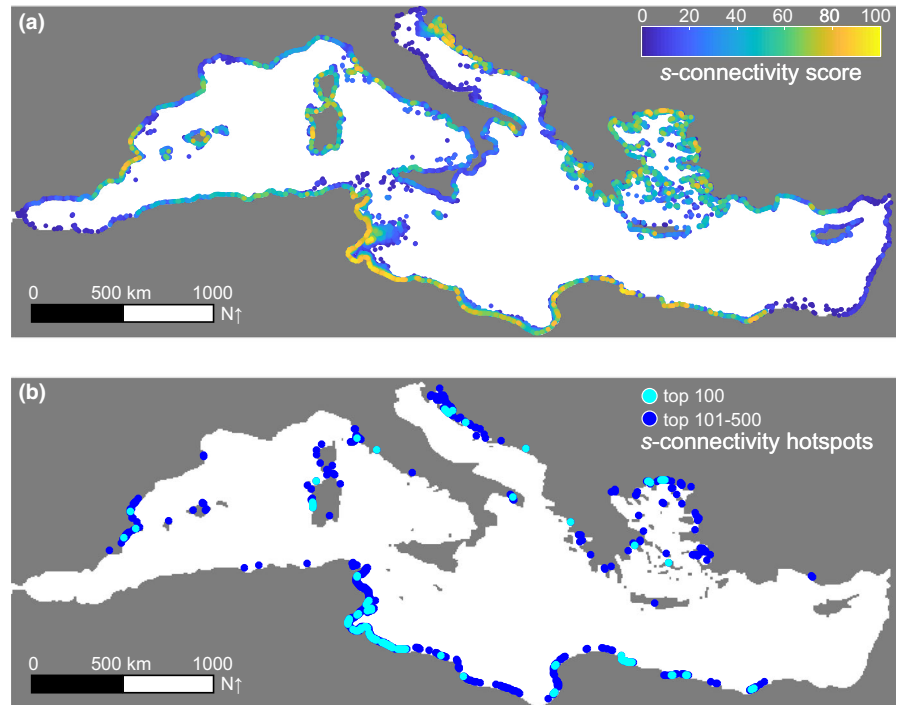
3.3 | Temporal trends in *s*-connectivity at the local scale

Temporal trends in local *s*-connectivity metrics are shown in Figure 5. As far as self-retention is concerned, the marine sectors where this metric has significantly ($p < .05$) increased over time seem to be clustered in space (e.g. in the Adriatic, Ionian and Aegean Seas). Conversely, sectors characterized by decreased self-retention appear to be quite evenly distributed along the shores of the Mediterranean Sea, along both the European and the African sides. As for indegree, declining scores tend to cluster along the French coastline, in Sardinia (west and east coasts), along the coast of Tunisia, in the Southern Tyrrhenian Sea, in the Strait of Messina region and the east coast of Sicily, in the North-Eastern Adriatic Sea and in the Aegean and Levantine Seas. Increasing indegree scores are instead recorded in Corsica and Sardinia (north–south coasts), along the northern and southern coasts of Sicily, on the shores of Libya and Egypt, and in the Ionian and Aegean Seas. Concerning outdegree, negative trends are detected in clusters along the coasts of Spain and France, in Corsica and Sardinia, in Tunisia and Libya, along both the Tyrrhenian and the Adriatic coast of Italy, in the North-Eastern Adriatic Sea and in the Ionian, Aegean and Levantine Seas. By contrast, positive trends in outdegree appear to be quite scattered, with clustered occurrences in the Strait of Messina region, in the Northern Adriatic Sea, along the coast of Libya and in the Aegean Sea.

The occurrences of statistically significant ($p < .05$) negative linear trends outnumber the occurrences of positive ones for both self-retention and indegree (Table 1). Interestingly, the *s*-connectivity hotspots identified in Figure 4 are characterized by relatively fewer occurrences of increased self-retention and more instances of decreased self-retention compared to the whole Mediterranean

Sea. By contrast, positive indegree trends are more prevalent among *s*-connectivity hotspots than in the whole Mediterranean Sea, while negative indegree trends are less prevalent among hotspots than in the whole basin. Outdegree trends appear to be less variable when evaluated over the whole Mediterranean Sea or restricted to *s*-connectivity hotspots, yet statistically significant trends (either positive or negative) in outdegree time series are more frequently observed in *s*-connectivity hotspots.

3.4 | Basin-scale *s*-connectivity trends and the role of meteorological fluctuations

At the whole-basin scale, the values of self-retention and in/outdegree averaged across all suitable marine sectors in the Mediterranean Sea seem to have been fairly erratic during the period 1987–2016 (Figure S9 in Appendix S2). Statistically significant trends can be identified ($p > .05$) in *s*-connectivity hotspots: indegree connectivity shows a positive trend in both the top-500 and the top-100 sectors, while outdegree connectivity shows a negative and statistically significant trend in the top-500 sectors.

Significant correlations ($p < .05$) between average *s*-connectivity patterns and meteorological variability indicators (Figure S10 in Appendix S2) are found for several combinations of lag and time-window length, both at the scale of the whole Mediterranean and in *s*-connectivity hotspots (Figures S11–S13 in Appendix S2).

4 | DISCUSSION

In this work, we have performed a basin-wide, multi-decadal connectivity assessment for *P. oceanica*, an iconic primary producer species
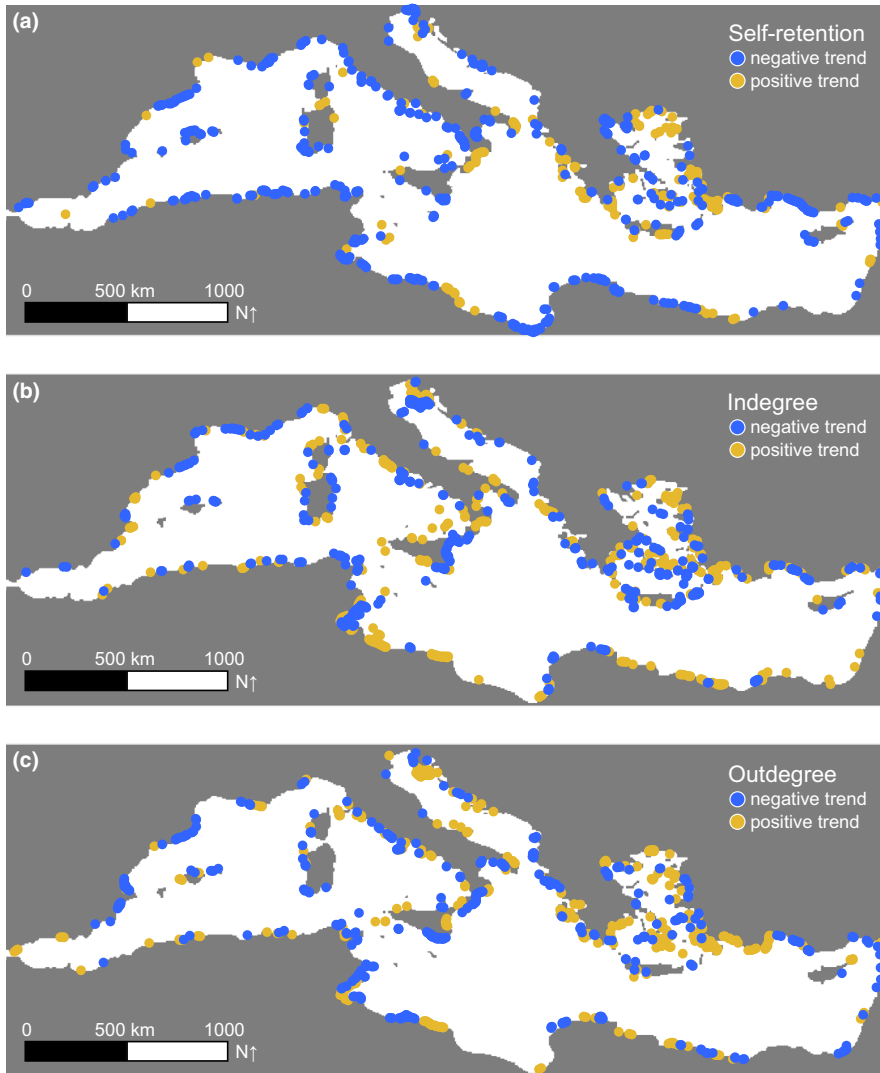
FIGURE 5 Directions of change in temporal trends of local *s*-connectivity metrics. (a) Self-retention. (b) Indegree. (c) Outdegree. Shown are the marine sectors for which a statistically significant (*p* < .05) linear negative (yellow) or positive (blue) trend is detected over the period 1987–2016

TABLE 1 Temporal trends in local time series of *s*-connectivity metrics

	All sectors		Top 500		Top 100	
	(+)	(−)	(+)	(−)	(+)	(−)
Self-retention	2.2	6.1	1.6	8.4	0	15
Indegree	4.6	5.4	10.8	5.0	20	0
Outdegree	4.8	4.8	6.2	7.0	6	6

Note: Per cent occurrence of statistically significant (*p* < .05) positive (+) or negative (−) linear trends over the period 1987–2016.

endemic to the Mediterranean Sea that plays a pivotal role as both habitat former and ecosystem service provider. Accurate assessment of connectivity among populations is crucial to determine possible drivers of population resilience (Jahnke et al., 2017; Kendrick et al., 2017). Here, connectivity patterns have been evaluated over a 30-year-long time span by using an ecologically motivated and species-specific measure, *s*-connectivity, that accounts not only for the amount of propagules potentially exchanged between marine sectors (estimated through computationally intensive biophysical Lagrangian simulations), as customary, but also for environmental

conditions possibly influencing local suitability for the species under study.

Our definition of *s*-connectivity should provide a reasonable trade-off between the results that would be obtained by looking at either local suitability or current-driven connectivity alone. This is in fact where our contribution diverges, the most from previous studies on seagrass connectivity (e.g. Grech et al., 2018; Grech et al., 2016; Jahnke et al., 2017; Jahnke et al., 2018). For instance, in the work by Jahnke et al. (2017), habitat suitability was used to identify the initial positions of dispersing *P. oceanica* fruits, but all metrics of potential connectivity were based on current-driven dispersal alone. In that case, and in a related contribution (Jahnke et al., 2018) focusing on a different species (the eelgrass *Zostera marina*), potential connectivity was contrasted to realized connectivity, as quantified by genetic analyses. Management implications were discussed in terms of the identification of either sites characterized by high levels of potential and realized connectivity as targets for conservation (Jahnke et al., 2017) or barriers to dispersal creating genetically diverse population clusters (Jahnke et al., 2018). Grech et al. (2016), instead, studied current-driven dispersal to/from sites of seagrass presence in the central Great Barrier

Reef, Australia, to evaluate the potential of seagrass dispersal in the area. Based on the results of Lagrangian simulations, different metrics of network connectivity (node-degree distribution, self-retention and outdegree) and node centrality (betweenness and PageRank) were used to identify seagrass meadows acting as retainers, sources or stepping stones for dispersal, and that could serve as priority candidates for conservation (Grech et al., 2018). We believe that our attempt to integrate habitat suitability (also a proxy for the actual distribution of the species being studied) directly into the evaluation of connectivity metrics might be especially promising when the size of the study area (the whole Mediterranean Sea basin, in our case) makes it impractical (or simply not possible) to compare potential connectivity patterns, obtained by biophysical modelling of current-driven dispersal, against realized connectivity patterns, estimated, for example, through genetic analyses. Our network-based approach could also serve as an effective starting point for the detection of communities within the time-varying graphs describing the dispersal patterns of *P. oceanica* (Newman, 2010), which in turn could assist in the definition of separated management units, that is clusters of local seagrass meadows that should be managed separately to ensure their long-term persistence (Grech et al., 2018; Jahnke et al., 2018).

The results of our assessment suggest that spatio-temporal variability is an important component of *P. oceanica s*-connectivity (Figures 2 and 3, Movie M1). Clearly, such variability makes the identification of connections that are both sufficiently strong and time-persistent to be ecologically relevant a completely non-trivial task. This difficulty has been overcome by applying a recently proposed methodological framework that allows to determine connectivity hotspots based on their potential to simultaneously function as effective retainers, sinks and/or sources for the dispersing agents of the target species (Melià et al., 2016). This approach accounts for the different functional roles of dispersal, is based on easily interpreted connectivity metrics, relies on a simple and conservative aggregation scheme and allows to effectively take into consideration both spatial and temporal variability in dispersal, thus representing a balanced framework to quantitatively discuss spatial conservation strategies at a basin scale. According to this identification procedure, hotspots of *s*-connectivity for *P. oceanica* (Figure 4) appear to be unevenly distributed in all of the four principal sub-basins of the Mediterranean Sea, mainly along the Spanish coastline in the Balearic Sea, on the western coast of Sardinia, in the Northern Tyrrhenian Sea (western Mediterranean region), along the coasts of Tunisia and Libya and in the Ionian Sea (Central Mediterranean region), in the North-Eastern Adriatic Sea (Adriatic region) and in the Aegean Sea and along the Egyptian coastline (Eastern Mediterranean region). The localization of *P. oceanica s*-connectivity hotspots, which could serve as candidates for protection, undoubtedly is one of the most important outcomes of the present work with regard to the potential impact on the prioritization of conservation efforts. In this respect, it is interesting to note that the highest ranked sectors (e.g. top-100 hotspots) are consistently surrounded by sectors also endowed with high *s*-connectivity (e.g. top-500 hotspots), which is suggestive of the fact that *s*-connectivity analysis is robust enough to be relevant for policymaking.

By contrast, it is crucial to remark that the results of our hotspot identification procedure do not necessarily provide a complete picture of *P. oceanica* connectivity in the Mediterranean Sea. As a matter of fact, although a wide spectrum of functions related to the roles that a local population can play in the context of a larger metapopulation has been considered, in terms of both sheer intensity and temporal variability, other factors might as well be at play. For instance, indegree and outdegree *s*-connectivity have been evaluated irrespective of the distances between donor and recipient marine sectors. However, the average distance at which successful dispersal events are predicted to occur by Lagrangian simulations may vary remarkably over space–time, reflecting the fact that marine sectors in different parts of the basin can be endowed with completely different spatio-temporal dispersal kernels (Figures 2 and 3). This variability in dispersal is obviously to be expected in a domain as large and complex as the Mediterranean Sea. Note that it may even represent a lower estimate of the actual heterogeneity, because the relatively coarse resolution of the oceanographic reanalysis is expected to dampen small-scale (subgrid) variations. Information about dispersal distances might be used to orient conservation priorities. In fact, a prevalence of short-range dispersal may signal the presence of hydrodynamical barriers, while the potential for long-distance dispersal may identify marine sectors that favour effective gene flow between different local populations. For instance, no marine sectors along the southern coast of Sicily are identified among the top-500 *P. oceanica* hotspots, yet sizeable portions of that coastline are characterized by remarkably long (albeit quite intermittent) outgoing dispersal, with potential implications for both cross-continental dispersal (say, between Italy and Tunisia) and propagule exchange between *P. oceanica* populations inhabiting the western/eastern basins of the Mediterranean Sea. Long-distance connectivity could also be realized over multiple generations via stepping-stone dispersal. However, the study of this type of intergenerational dynamics will require the development of an integrative modelling approach in which the basin-wide metapopulation dynamics of *P. oceanica* can effectively be explored by coupling the dispersal means provided by marine currents with local-scale demographic processes, such as shoot survival, vegetative growth and sexual reproduction.

All these considerations highlight the importance of cross-validating measures of *potential* connectivity, albeit corrected for local suitability conditions like in the present study, with measures of *realized* connectivity, as obtained through analysis of effective gene flow. In the case of *P. oceanica*, in fact, the former is often found to be possibly quite overestimated with respect to the latter (Jahnke et al., 2017; Serra et al., 2010), which in turn is thought to be relatively low overall (e.g. Arnaud-Haond et al., 2014; Procaccini et al., 2001). Comparing the findings presented in published studies of genetic connectivity for *P. oceanica* in the Mediterranean Sea with our assessment of basin-wide potential connectivity

may not be a trivial task. Some of those studies were in fact conducted over relatively small spatial domains, spanning from single meadow (e.g. Migliaccio, Martino, Silvestre, & Procaccini, 2005) to regional scales (e.g. Jahnke et al., 2017; Procaccini et al., 2001). Mediterranean-wide analyses of *P. oceanica* genetic connectivity exist (Arnaud-Haond et al., 2007; Rozenfeld et al., 2008; Serra et al., 2010), but in all those cases the number of sampled meadows was understandably limited to a few dozen at most. In general, whenever genetic connectivity was evaluated at a whole-basin scale, the Strait of Sicily was identified as a contact zone between the genetically partitioned seagrass populations inhabiting the western and eastern basins of the Mediterranean Sea. This region (the coast of Tunisia, in particular) is also highlighted as one of the richest in s-connectivity hotspots by our modelling approach (Figure 4), as well as one endowed with relatively long potential dispersal distances (see again Figure 3).

The multi-decadal temporal span of this study has allowed to ascertain the existence of recent trends in *P. oceanica* s-connectivity across the Mediterranean Sea (Figure 5). Statistically significant temporal trends in self-retention, indegree and outdegree seem to be quite infrequent among all suitable sectors (they have been detected in less than 6% of marine sectors), but relatively more frequent in s-connectivity hotspots (with frequencies ranging up to 20%; Table 1). Here, contrasting directions of change are actually found: for instance, decreasing self-retention and increasing in/outdegree are all more frequently observed in the top-100 s-connectivity hotspots than in non-hotspot sectors, possibly a sign that somewhat small changes in circulation patterns around key strategic sites may have important consequences for *P. oceanica* dispersal dynamics at large spatial scales. Also, while basin-averaged connectivity values do not show any statistically significant trends, in/outdegree in, for example, the top-500 s-connectivity hotspots do (Figure S9 in Appendix S2). All these findings suggest that the role played by s-connectivity hotspots in structuring *P. oceanica* dispersal dynamics might be changing over time, with implications for the future of its large-scale spatio-temporal dynamics. Furthermore, the observation that meteorological fluctuations may also influence s-connectivity patterns (Figures S11–S13 in Appendix S2), together with the prediction that the Mediterranean basin will be one of the regions, most affected by global climate change (Lejeusne et al., 2010), suggests that decisions regarding marine protection and maritime spatial planning in general should also aim to enforce resilience against climate change impacts (McLeod, Salm, Green, & Almany, 2009). In this respect, reliable oceanographic projections forced with future climate scenarios (Coleman et al., 2017) would represent an invaluable instrument to anticipate changes to future connectivity patterns within the Mediterranean Sea.

Like all modelling studies, ours is not devoid of limitations. One such source of possible inaccuracies in our analysis is perhaps the use of a static suitability map to both initialize Lagrangian simulations and evaluate s-connectivity scores. As a matter of fact, *P. oceanica* meadows have declined rapidly in several areas of the Mediterranean basin, possibly also as a result of decreased habitat

suitability in response to the localized effects of climate change, water quality degradation, coastal modification and other sources of human pressure (Chefaoui, Duarte, & Serrão, 2018; de los Santos et al., 2019; Marbà et al., 2014; Telesca et al., 2015). In this respect, airborne and satellite imagery could provide a dependable, deployable and cost-effective tool to produce updated distribution maps for *P. oceanica*, as testified by the growing number of related applications (Borfecchia et al., 2013; Fornes et al., 2006; Matta et al., 2014; Pasqualini et al., 2005; Traganos et al., 2018). Although most of these studies refer to relatively small areas within the Mediterranean Sea, the most recent one (Traganos et al., 2018) proposes a workflow for regional-scale mapping of seagrasses powered by remote sensing, machine learning and cloud-based technologies that could be potentially scaled up to even larger (possibly global) spatial scales. Indeed, Earth observations (both remote and in situ), species distribution modelling (Elith & Leathwick, 2009; see Chefaoui, Duarte, & Serrão, 2017; Chefaoui et al., 2018 for recent applications of niche modelling to *P. oceanica*) and ecological modelling should be considered complementary pillars for the elaboration of future large-scale conservation programmes (Pasetto et al., 2018).

We finally remark that conservation planning may require to look beyond purely ecological considerations. From a socio-economic point of view, the complex boundary conditions imposed by the heavily human-impacted coastal ecosystems of the Mediterranean Sea, further challenged by the "Blue Growth" framework, imply that not all the locations that are potential candidates for protection are equally suitable to devote portions of their seascape to conservation programmes. In fact, the Mediterranean Sea is an area of interest for a series of activities, ranging from maritime traffic to industrial fishing or tourism, for human populations of different nationalities and cultures—all of which makes the problem of setting priorities for regional conservation planning a highly non-trivial task (Micheli et al., 2013). This *caveat* notwithstanding, we believe that the present study may represent a step forward in the application of a quantitative, scalable and replicable methodological framework for the prioritization of conservation actions, with the overarching goal of saving more with less.

DATA AVAILABILITY STATEMENT

The suitability map for *P. oceanica* is available at http://www.emodnet-seabedhabitats.eu. The physical reanalysis of circulation field is available online at http://marine.copernicus.eu/. MOI1 and MOI2 data are available online at https://crudata.uea.ac.uk/cru/data/moi/,

while WeMOI data are available online at http://www.ub.edu/gc/en/wemo/.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.