



Contribution to the Theme Section 'Latest advances in research on fish early life stages'

# MPA network design based on graph theory and emergent properties of larval dispersal

Andres Ospina-Alvarez<sup>1,\*</sup>, Silvia de Juan<sup>2</sup>, Josep Alós<sup>1</sup>, Gotzon Basterretxea<sup>1</sup>, Alexandre Alonso-Fernández<sup>3</sup>, Guillermo Follana-Berná<sup>1</sup>, Miquel Palmer<sup>1</sup>, Ignacio A. Catalán<sup>1</sup>

<sup>1</sup>Mediterranean Institute for Advanced Studies (IMEDEA-CSIC/UIB), C/ Miquel Marques 21, CP 07190 Esporles, Balearic Islands, Spain

<sup>2</sup>Marine Science Institute (ICM-CSIC), Passeig Marítim de la Barceloneta, 37-49, CP 08003 Barcelona, Catalunya, Spain

<sup>3</sup>Marine Research Institute (IIM-CSIC), C/ Eduardo Cabello 6, CP 36208 Vigo, Pontevedra, Spain

**ABSTRACT:** Despite the recognised effectiveness of networks of marine protected areas (MPAs) as a biodiversity conservation instrument, MPA network design frequently disregards the importance of connectivity patterns. In the case of sedentary marine populations, connectivity stems not only from the stochastic nature of the physical environment that affects dispersal of early life stages, but also from the spawning stock attributes that affect reproductive output (e.g. passive eggs and larvae) and survivorship. Early life stages are virtually impossible to track in the ocean. Therefore, numerical ocean current simulations coupled with egg and larval Lagrangian transport models remain the most common approach for the assessment of marine larval connectivity. Inferred larval connectivity may differ depending on the type of connectivity considered; consequently, the prioritisation of sites for the conservation of marine populations might also differ. Here, we introduce a framework for evaluating and designing MPA networks based on the identification of connectivity hotspots using graph theoretic analysis. As a case study, we used a network of open-access areas and MPAs off Mallorca Island (Spain), and tested its effectiveness for the protection of the painted comber *Serranus scriba*. Outputs from network analysis were used to (1) identify critical areas for improving overall larval connectivity, (2) assess the impact of species' biological parameters in network connectivity and (3) explore alternative MPA configurations to improve average network connectivity. Results demonstrate the potential of graph theory to identify non-trivial egg/larval dispersal patterns and emerging collective properties of the MPA network, which are relevant for increasing protection efficiency.

**KEY WORDS:** Larval connectivity · MPA network · Larval dispersal · Larval transport · Management

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## 1. INTRODUCTION

In ecology, connectivity involves the exchange of individuals among populations and, thereby, the dispersal ability and the spatial and temporal scales over which a population of a given species is connected with other populations (Armsworth 2002, Strathmann et al. 2002). Most marine species have a pelagic early life stage in which individuals (i.e. eggs,

spores, larvae, juveniles) drift away from natal locations transported by ocean currents. For many species, these early life stages represent the most important, or even the only mechanism of dispersal (Walford 1938, Norcross & Shaw 1984). Although marine connectivity often refers only to a part of 'reproductive resilience' (Lowerre-Barbieri et al. 2017), it remains a key component of the system affecting recruitment and, as a consequence, long-

\*Corresponding author: aospina.co@me.com

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term population dynamics and persistence (Travis & Dytham 1998, Siegel et al. 2003, Watson et al. 2012). As such, connectivity is of great interest for the management of marine ecosystems and a key variable to consider in the scale, spacing and spatial structure of marine protected areas (MPAs) (Lubchenco et al. 2003, Botsford et al. 2003, 2009b, Fogarty & Botsford 2007).

The identification of population connectivity patterns is, however, challenging since the dispersal of early life stages is highly influenced by the stochastic nature of the physical environment (Siegel et al. 2008) and by multiple biological factors affecting the reproductive output of the spawning stock biomass, like timing of spawning, egg physiology, pelagic larval duration (PLD), larval behaviour and/or larval mortality (Hinckley et al. 2001, Galarza et al. 2009, Ospina-Alvarez et al. 2012a, 2018, Morgan 2014, Donahue et al. 2015). While displacement routes of large organisms (i.e. adult fish) can be assessed using individual-tracking devices, planktonic individuals such as eggs and larvae are virtually impossible to track in the ocean (but see Paris et al. 2013b), notably limiting our ability to characterise their dispersal (Pineda 2000, Armsworth 2002, Kinlan & Gaines 2003, Siegel et al. 2003, Cowen et al. 2006, Cowen & Sponaugle 2009). This limitation has encouraged the use of a suite of indirect methods to reconstruct probable dispersal pathways, such as the analysis of geochemical signatures in calcified structures (Thorrold et al. 2007) and genetic structure assessments (Hedgecock et al. 2007). However, numerical ocean current simulations coupled with egg and larval Lagrangian transport algorithms (i.e. individual based models, IBMs) remain the most common approach for the assessment of marine larval connectivity (Werner et al. 2007, Catalán et al. 2013, Alós et al. 2014, Ospina-Alvarez et al. 2015, Blanco et al. 2019).

Larval connectivity derived from these IBMs can be interpreted using 2 measures: potential and realised larval connectivity (Watson et al. 2010). Potential larval connectivity refers to the probability of connection between a natal site or spawning area and a destination or nursery area. In contrast, realised larval connectivity refers to the number of larvae travelling from spawning to nursery sites (Watson et al. 2010). Realised larval connectivity can be estimated using potential connectivity weighted by relevant biological and environmental information (Kough & Paris 2015). For example, an estimate of realised connectivity can be obtained by weighting potential larval connectivity with observed or modelled spatial egg production (see review by Low-

erre-Barbieri et al. 2017). These estimates can be improved by including biological aspects such as maternal effects (like body size), reproductive timing, spawning seasonality or individual spawning times (Hixon et al. 2014, Gwinn et al. 2015). Realised larval connectivity provides spatially explicit information on the ability of a set of sites to hold connected populations. Therefore, it can provide valuable information for the management of coastal resources (Ospina-Alvarez et al. 2020). However, it is rarely considered in the design of MPA networks (but see Watson et al. 2010).

The effectiveness of an MPA network critically depends upon the consideration of connectivity patterns, source–sink dynamics and rates of population replenishment (Botsford et al. 2009a,b, Gaines et al. 2010, Lagabrielle et al. 2014). Therefore, connectivity values estimated through IBMs can provide insights into the design of MPA networks. However, conventional connectivity matrices generated by larval transport IBMs only provide a partial representation of the complexity of the connectivity, and omit parts such as identification of key locations that act as genetic corridors or central populations that feed many others. In this context, graph theory (i.e. the mathematical study of the interaction of a system of connected elements) is a valuable approach for analysing MPA network performance, as it provides a simplified and quantitative view of the multiple factors involved in the exchange among system elements (Conklin et al. 2018, Henry et al. 2018, Friesen et al. 2019, Kininmonth et al. 2019).

In graph theory, a system of connected elements, a 'graph', can be defined as a 'network'. Network elements are modelled as 'vertices' or 'nodes', and the 'arcs' or 'edges' of the graph are the connections or links in the network. In a network of marine reserves, the graph represents the network itself, with each area being a vertex or node, and the probability of connection or flow of individuals between areas being the arcs or edges (Dale & Fortin 2010). Graph theory provides insights into the system's properties and identifies critical nodes with high centrality (i.e. connected to many other areas) or clusters of well-connected nodes with high potential genetic flow and acting as bridges between distant populations (Treml et al. 2008, Kininmonth et al. 2010, Jacobi & Jonsson 2011, Friesen et al. 2019). MPA network design based on connectivity studies and graph theory have increased in recent years (Treml et al. 2008, Friesen et al. 2019, Kininmonth et al. 2019). However, most studies fail to adopt an objective approach for selecting the most

adequate centrality measures to identify important nodes in an MPA network. The difficulty lies in the fact that each node could be important from a different point of view depending on the definition of 'importance'. According to Freeman (1978 p. 217): 'There is certainly no unanimity on exactly what centrality is or on its conceptual foundations, and there is very little agreement on the proper procedure for its measurement'.

The methodological framework introduced in this study allowed us to address several questions: (1) Does the importance of sites for population connectivity differ when demographic characteristics and available habitat are coupled to larval transport models? (2) Does the importance of sites for population connectivity differ when considering either (a) the probability or flow of individuals or (b) centrality measures from graph theoretic analyses? (3) Is it possible to design an MPA network that maximises net larval productivity and net larval supply and simultaneously avoids fragmentation between sub-populations? For this purpose, we first analysed the potential and realised connectivity and the emergent properties of an ensemble of coastal species inhabiting an MPA network, in which the respective sub-populations are potentially interconnected (e.g. in terms of dispersive/retentive associations between

areas) through early life stages (Basterretxea et al. 2012). As a novelty, our approach explores differences between the potential and realised networks, and provides an ecological interpretation for the centrality measures analysed. This approach sets the baseline for a wider adoption of coupled connectivity-graph theory models in marine conservation and planning.

## 2. METHODS

Our case study involves the south-eastern coast of Mallorca Island, in the Western Mediterranean Sea (Fig. 1). In this region, we identified 12 coastal sites (hereafter nodes) managed under 2 different regimes: MPAs and open-access areas (OAA) (Table 1, Fig. 1). In total, 5 MPAs protect the most important ecological assets of the island (e.g. well preserved seagrass meadows, rocky reefs), including the National Marine-Terrestrial Park of Cabrera (a fully no-take MPA for recreational fisheries since 1991). For this study, 2 small, neighbouring MPAs (Malgrats and Toro) were considered as a single MPA. A complete description of environmental and hydrodynamic characteristics of the area can be found in Basterretxea et al. (2012).

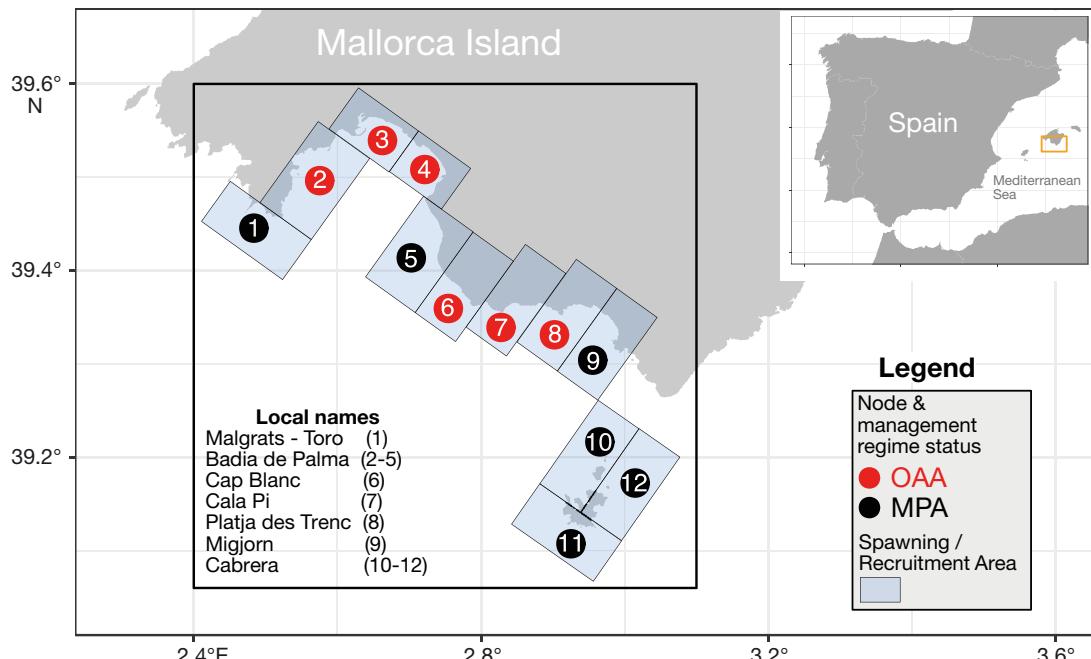


Fig. 1. Study area; orange box in inset, top-right, shows the general location within the Mediterranean Sea. The 12 nodes and management regime status are shown in the main map. MPA: marine protected area; OAA: open-access area. Blue shaded rectangles: zones established as spawning and recruiting areas within which the number of exported larvae and the number of larvae recruited were summarised in model simulations

Table 1. Areas (nodes) included in this study, their geographic location and management regime type: marine protected area (MPA) or open access area (OAA). The available habitat and extension of protected area in each node ( $\text{km}^2$ ) and the size and abundance of the painted comber *Serranus scriba* are indicated. Manag.: management

Node ID	Node name	Latitude, longitude	Manag. regime	Available habitat ( $\text{km}^2$ )	Sea surface under protection ( $\text{km}^2$ )	Fish size (cm; mean $\pm$ SD, N)	Fish abundance (ind. $\text{km}^2$ habitat; mean $\pm$ SD)
1	Malgrats-Toro	39.445°N, 2.468°E	MPA	0.75	2.25	135 $\pm$ 29.73 214	4531.36 $\pm$ 2758.46
2	Badia de Palma	39.495°N, 2.574°E	OAA	9.74		124 $\pm$ 27.68 467	96651.25 $\pm$ 46475.54
3	Badia de Palma	39.538°N, 2.658°E	OAA	8.08		124 $\pm$ 30.64 279	68074.11 $\pm$ 16431.04
4	Badia de Palma	39.502°N, 2.720°E	OAA	18.12		121 $\pm$ 29.76 607	152634.46 $\pm$ 36841.35
5	Badia de Palma	39.405°N, 2.701°E	MPA	9.24	23.94	144 $\pm$ 24.95 135	111311.57 $\pm$ 73869.36
6	Cap Blanc	39.358°N, 2.753°E	OAA	1.32		143 $\pm$ 26.91 238	8215.92 $\pm$ 5417.97
7	Cala Pi	39.333°N, 2.823°E	OAA	5.76		119 $\pm$ 25.56 84	64827.08 $\pm$ 26730.27
8	Platja des Trenc	39.328°N, 2.904°E	OAA	14.69		120 $\pm$ 24.77 37	127115.42 $\pm$ 100846.30
9	Migjorn	39.308°N, 2.966°E	MPA	10.47	223.32	112 $\pm$ 27.36 63	96173.66 $\pm$ 46896.00
10	Cabrera	39.198°N, 2.945°E	MPA	4.51		151 $\pm$ 27.72 354	71691.32 $\pm$ 17304.12
11	Cabrera	39.116°N, 2.914°E	MPA	0.98	86.8	164 $\pm$ 26.89 28	15518.97 $\pm$ 3745.81
12	Cabrera	39.162°N, 3.010°E	MPA	3.3		163 $\pm$ 24.42 14	52523.67 $\pm$ 12677.63

## 2.1. Hydrodynamic model

The coupled hydrodynamic–biological IBM used in this work has been previously described and validated (Basterretxea et al. 2012). Some outstanding features of the modelling approach include simulation of the hydrodynamics around Mallorca Island using a 3-dimensional density-resolving model based on the Princeton Ocean Model, with a resolution of 200 m in the horizontal and 25 sigma layers in the vertical, from 2000–2009. The model was executed offline and included wind forcing using 12 h maps for the same period.

## 2.2. Potential larval exchange matrix

A total of 19 325 passive tracers were released at weekly intervals from 200 m equispaced grid points located over seagrass/rocky bottoms (<40 m depth) for a 6 mo period (March–August) each year. The depth of release of the particles was random within the first 10 m of the water column. Particles were treated as passive, neutrally buoyant, flowing near

the surface being freely transported by the currents for 21 d. A reflective boundary condition was used to prevent particles from moving onto land. At the end of this period the simulation was stopped. The final position (latitude, longitude and depth) of the passive tracers was used to determine their fate. Larvae within the 12 previously defined areas were assumed to successfully settle. A potential larval matrix was obtained, representing the probability of connection between the 12 sites. This matrix can be associated to an ensemble of coastal fish species inhabiting the rocky, sand and seagrass meadows of the Mediterranean Sea, with summer spawning preferences and a PLD of 21 d (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m560p309\\_supp.pdf](http://www.int-res.com/articles/suppl/m560p309_supp.pdf)).

## 2.3. Realised larval exchange matrix

The painted comber *Serranus scriba* was selected as a model species for calculating the realised larval exchange matrix in this modelling approach because its breeding season spans from May–August in the Balearic Islands (Alonso-Fernández

et al. 2011). Moreover, its dispersal is restricted to early life stages (March et al. 2010) that are pelagic for ca. 3 wk (Macpherson & Raventós 2006). Here, we developed a total egg production model based on the individual which incorporates valuable information of basic reproductive parameters of *S. scriba*, like size- and site-dependent fecundity or a long spawning season, as revealed by empirical data (Alonso-Fernández et al. 2011, Alós et al. 2013, 2014). Potential fecundity (oocytes female<sup>-1</sup>), density (ind. m<sup>-2</sup>), proportion of females and proportion of mature females were used as proxies in the model to assess the total egg abundance (for a detailed model explanation, see Text S1 in the Supplement). The model output was used to calculate the realised larval exchange matrix by weighting the potential larval matrix with the spatial variability in egg abundance (oocytes m<sup>-2</sup>). As a consequence, egg abundance is a function of adult population abundance and reproductive characteristics, which are a function of the extent of available habitat (rocky and seagrass meadows down to 40 m depth) and the level of protection (MPA vs. OAA; see Table 1). Since information on vertical movements or the orientation of larvae towards sound or light stimuli for the painted comber is non-existent, directed horizontal movement and the vertical movement of the larvae were not parameterised in the hydrodynamic simulations.

#### 2.4. Matrices, graphs and networks as representations of connected systems

Any adjacency matrix can be represented as a graph with its nodes and edges and, consequently, they are equivalent representations of a connected system. Hereafter, we will refer to connected larval flow systems as larval connectivity networks. The potential larval exchange matrix, and its correspondent graph, represents the larval connectivity network of an ensemble of species with a common PLD (Table S1). The realised larval exchange matrix, and its correspondent graph, represents the larval connectivity network of the painted comber as the model species. Although the visual representation of adjacency matrices on their own provides valuable information about links within the entire network (i.e. probabilities or absolute numbers), the use of graph theory provides key information about the role of each node within a larval connectivity network (Fig. S1) (Minor & Urban 2008). To explore the potential of graph theory methods, we calculated centrality

measures to understand the effect of the distinct levels of connectivity derived from potential and realised larval connectivity networks.

#### 2.5. Roadmap for the selection of retention indices and centrality measures

A roadmap was established for the selection of retention indices and centrality measures based on their usefulness and importance for conservation, recreational fisheries or management. This roadmap is summarised as follows (Fig. 2): (1) obtain the larval connectivity network (e.g. by species, functional groups, etc.); (2) select the retention indices and centrality measures that can be calculated according to the characteristics of each connectivity network (e.g. Strength can only be calculated in weighted networks, or Closeness cannot be calculated in disconnected networks); (3) calculate indices and measures that may be relevant to conservation, recreational fisheries or management (see rationale column in Tables 2 & 3); (4) conduct exploratory data analysis to assist decisions on which indices and measures are informative (e.g. summary statistics, correlation analysis, etc.); (5) the indices and measures are normalised and the nodes (locations) of the network are ranked globally; (6) management decisions can be made, and management scenarios designed according to the overall ranking of the nodes; and (7) the structure of the resulting connectivity network can be analysed and discussed according to the conservation, recreational fisheries or management objectives.

#### 2.6. Retention indices and centrality measures

Following this roadmap (Fig. 2), 3 retention indices and 9 centrality measures were considered to have potential relevance to conservation, recreational fisheries or management. To capture hydrodynamic retention and, consequently, larval retention in our system, we calculated 3 different retention indices for the potential and realised larval connectivity networks following Lett et al. (2015): Local Retention (LR), Relative Local Retention (RLR) and Self-Recruitment (SR). Retention indices are defined in Table 2 according to Lett et al. (2015).

With the aim of highlighting the most important nodes for larval connectivity within the network, we calculated 9 measures of centrality for the potential and realised networks: In-Strength; Out-Strength;

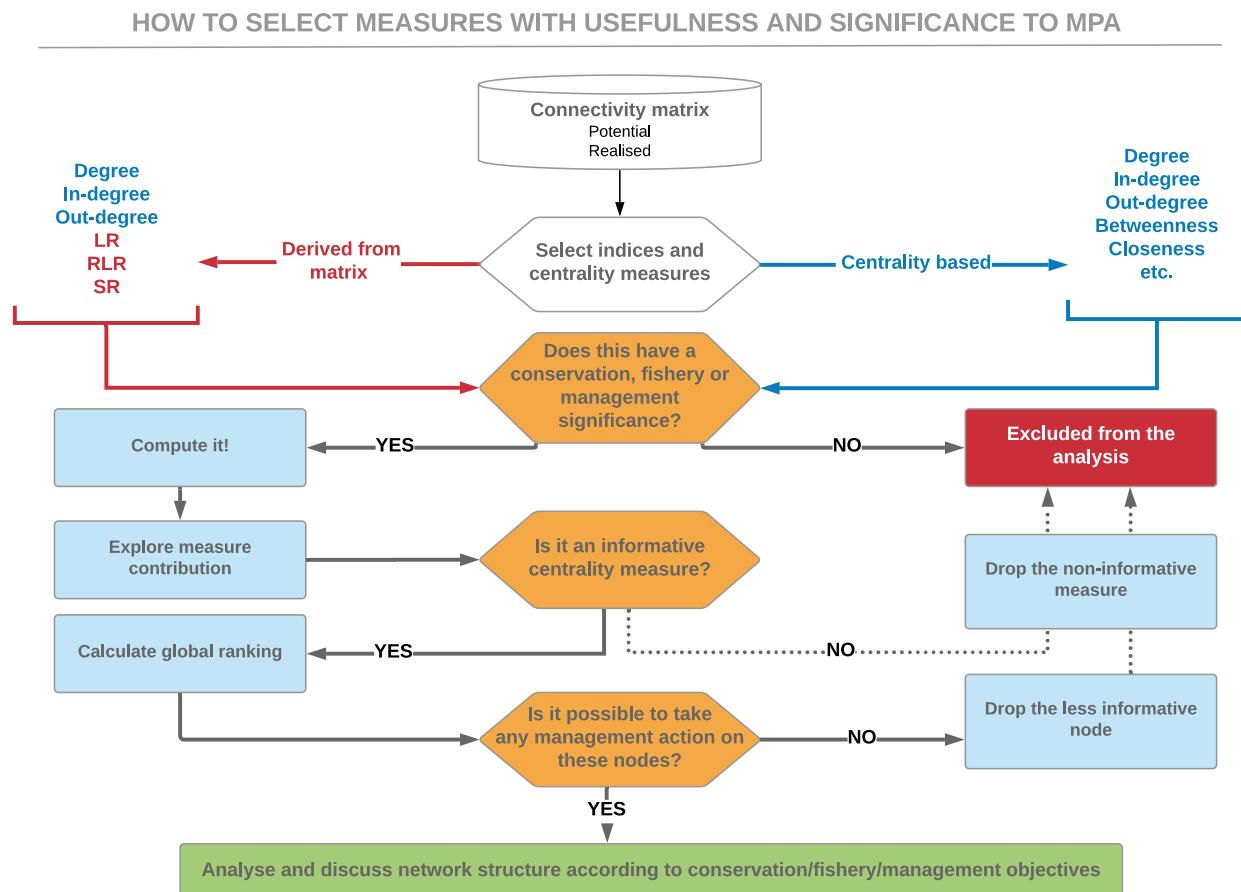


Fig. 2. Selection criteria for retention indices and centrality measures based on usefulness and significance for conservation, recreational fisheries or management. LR: Local Retention; RLR: Relative Local Retention; SR: Self-Recruitment

Table 2. Self-persistence indices of local marine populations (as presented by Lett et al. 2015)

Index	Definition	Calculation	Rationale
Local Retention (LR)	The ratio of locally produced settlement to local egg production	LR is equal to the diagonal elements of the connectivity matrix	LR does not depend on egg production in the different habitat patches, meaning it is independent of temporal changes in adult population size
Relative Local Retention (RLR)	The ratio of locally produced settlement to all settlement of local origin	RLR is equal to the diagonal elements of the connectivity matrix divided by the sum of the corresponding column of the connectivity matrix	RLR does not depend on egg production, but it does depend on the connectivity between the focal patch and the ensemble of patches in the system
Self-Recruitment (SR)	The ratio of locally produced settlement to settlement of all origins at a site	If egg production is uniform over sites, then SR is equal to the diagonal elements of the connectivity matrix divided by the sum of the corresponding row of the connectivity matrix. If not, then the elements of the dispersal matrix must be weighted by the number of eggs produced	SR depends on egg production in the different habitat patches (relative to that of the focal patch) and therefore on temporal changes in population size. SR also depends on connectivity between every patch and the focal patch

Table 3. Measures of centrality, definitions and rationales in a context of ecological-larval connectivity. See references for additional information. The formula used in each centrality measurement can be found in the documentation of the 'igraph' package for R

Measure	Reference	Definition	Rationale
Strength	Barrat et al. (2004)	Also named weighted degree. The node degree is the number of relations (edges) of the nodes. In weighted networks, node Strength is the sum of weights of links connected to the node	Strength indicates a node is involved in many important (by weight) interactions with other nodes. Nodes with high Strength can act as kestones, since they are connected by egg production and recruitment to many neighbouring nodes
In-Strength	Barrat et al. (2004)	In directed networks, the In-Strength is the sum of inward link weights	Nodes with high In-Strength can act as important nursery areas, sensitive recruitment or settlement zones
Out-Strength	Barrat et al. (2004)	In directed networks, the Out-Strength is the sum of outward link weights	Nodes with high Out-Strength can act as essential spawning habitats. Genetically, sub-populations inhabiting nodes with high Out-Strength have a high probability of spreading genes to other sub-population in the network
Closeness	Freeman (1978)	Closeness centrality indicates how long it will take for information from a given node to reach other nodes in the network	Nodes with a higher Closeness have a high probability of exporting propagules to their nearest neighbouring nodes
Betweenness	Freeman (1979)	Betweenness centrality is a measure of the influence of a node over the flow of information between every pair of nodes under the assumption that information primarily flows over the shortest paths between them	While high release of propagules and high recruitment of larvae is important, it is not everything. Nodes with high Betweenness centralities have been termed 'bottlenecks' or 'bridges', and they prevent the fragmentation of the network. A node acting as a bridge between 2 well-differentiated subpopulations should have a high Betweenness
Eigenvector centrality	Bonacich (1987)	The Eigenvector centrality network metric takes into consideration not only how many connections a node has (i.e. its degree or Strength), but also the centrality of the vertices that it is connected to	This is a measure of the influence of a node in a network. In general, a connection to a well-connected node is more important than a connection to a poorly connected node. High Eigenvector centralities indicate those nodes with a high-productivity and high-recruitment that are connected to other high-productivity and high-recruitment nodes
Kleinberg's Hub centrality score a.k.a. Hub score)	Kleinberg (2000)	The Hub score of a node shows how many highly informative nodes or authoritative nodes this node is pointing to	Nodes with high Hub scores are those nodes that recruit larvae from many other nodes in the network. In this case, this metric indicates nodes that act as nursery areas and are well-connected to other areas in the network
Kleinberg's Authority centrality score (a.k.a. Authority score)	Kleinberg (2000)	The Authority score of a node is a measure of the amount of valuable information that this node holds	Nodes with high Authority scores indicate nodes that export successful propagules to many other nodes in the network. These are nodes that act as a well-connected source of propagules to other nodes in the network
Page Rank	Brin & Page (2000)	Algorithm developed by Larry Page and Sergey Brin, founders of Google. Page rank works by assigning importance to a webpage (node) if important pages (other nodes) point to it	The interpretation is similar to that of the Hub score. The approximate estimation of the importance of a node is based on the number and quality (weight) of the links pointing to it. The most important nodes are likely to recruit more larvae from other nodes in the network

Strength; Betweenness, Eigenvector centrality; Closeness; Kleinberg's Hub centrality score (hereafter Hub score); Kleinberg's Authority centrality score (hereafter Authority score); and Page Rank. These central-

ity measures were selected as being potentially useful in larval connectivity studies, and came from a first selection that included all existing measures of centrality, identified from a review of the existing litera-

ture. A full description of each centrality measure selected, their scope and ecological interpretation and references to the original source, is provided in Table 3. Note that Out-Strength and In-Strength correspond to the sum of all eggs released and larvae recruited from each node, respectively, and Strength corresponds to the sum of In-Strength and Out-Strength. In consequence, these 3 centrality measures can be calculated either from a network or directly from an adjacency matrix. Higher values in centrality measures indicate greater ‘connectivity’ (*sensu lato*). Connectivity is not understood as larval connectivity but as connectivity between the nodes of the network. Therefore, each centrality measure informs node connectivity properties within the network and provides a different ecological interpretation of network connectivity. The selection and prioritisation of one measure over the other should be carefully considered depending on local management and conservation targets (Fig. 2, Table 3).

To facilitate interpretation of the ranking of the nodes in a network, firstly, each index or centrality measurement was normalised between 0 and 1, with 1 corresponding to the highest connectivity value; secondly, the nodes were sorted in a descending order, with those with the highest connectivity measures at the top. We also calculated edge Betweenness centrality, a measure of arc centrality, defined as the number of the shortest paths that go through an edge in a graph or network (Girvan & Newman 2002). An arc with a high edge Betweenness centrality score represents a bridging connector between 2 parts of a network, the removal of which can affect communication between many pairs of nodes through the shorter paths between them.

Following the roadmap described in Section 2.5 (Fig. 2), indices and centrality measures were used to design a scenario where some OAAs could be converted into no-take areas and vice versa. The biological parameters observed at Cabrera MPA (Nodes 10–12) were used to scale up egg production in the OAAs to be converted to no-take. To convert no-take into ‘open to fisheries’ areas, the average biological parameters of the OAAs were used. The characteristics and structure of the network were explored and the impact of protection on larval network connectivity was discussed based on the decisions made.

## 2.7. Community detection

In graph theory, it is possible to identify groups of nodes (i.e. modules) that probably share common

properties and/or play similar roles within the network. In networks where the distribution of links is globally and locally inhomogeneous, some nodes have higher concentrations of links within special groups of nodes and low concentrations between these groups. Here, we considered the approach to community detection using edge weights (i.e. connection probability or larval number; Brandes et al. 2008). When 2 or more network graphs are compared, the weight differences among pairs result in differences in cluster formation. Therefore, we quantified network modularity; the existence of groups of locations that are highly interconnected among themselves by proximity of links, and that are poorly connected to locations in other modules (Guimerà & Nunes Amaral 2005, Reichardt & Bornholdt 2006). Then, we calculated the optimal community structure for the graph, in terms of maximal modularity score, to determine clustering organisation and to identify communities (following Brandes et al. 2008). The number of communities and membership of each node were used to visually display network structure.

All analyses were performed using R v.3.6.0 (R Core Team 2019). Matrix, network graph and community detection analyses were performed using R packages ‘igraph’ v.1.2.4.1 and ‘ConnMatTools’ v.0.3.3 (Csardi & Nepusz 2006, Kaplan et al. 2017). Network visualisations were made with R packages ‘mapdata’ v.2.3.0, ‘ggplot2’ v.3.2.1 and ‘ggraph’ v.2.0.0 (Chang 2012, Wickham 2016).

## 3. RESULTS

### 3.1. Retention and self-recruitment

The nodes, ranked according to their relative retention indices for potential and realised larval connectivity and for the scenario networks, are shown in Tables S2–S4. In the case of the LR index, where sorting is based on absolute numbers and not on proportions, a slightly different ranking of the nodes in the potential and realised networks was observed; however, Nodes 3 and 4 were positioned as the most locally retentive in both networks (Fig. 3). These results are because Nodes 3 and 4 are in the zone with the highest hydrodynamic retention, and where egg production is also the highest for any node in the network. LR is sensitive to local patch (node) gamete production, but not to gamete production from all metapopulations (the whole network). Therefore, LR only provides information about local processes (i.e. node processes).

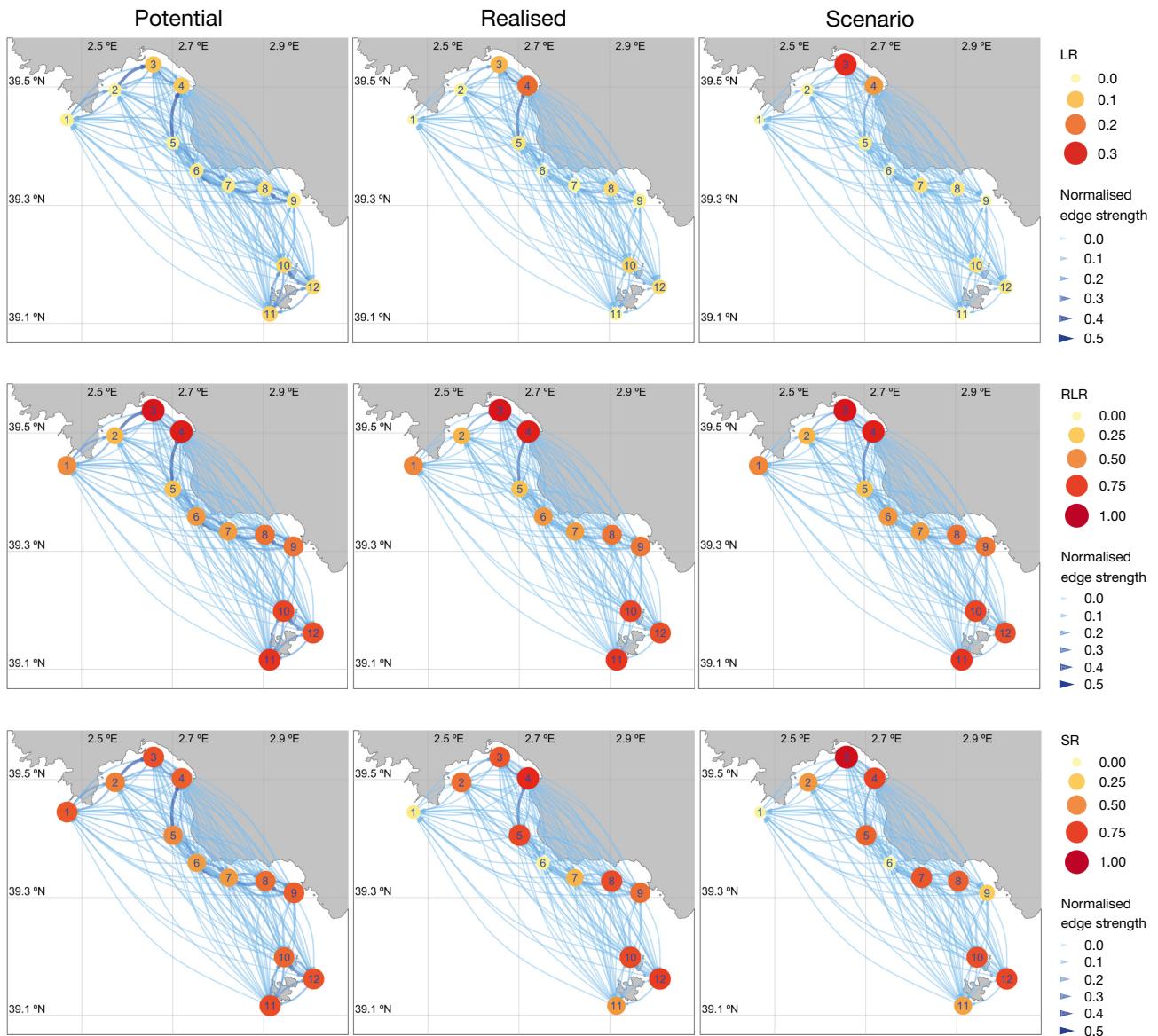


Fig. 3. Local Recruitment (LR, top), Relative Local Recruitment (RLR, middle) and Self-Recruitment (SR, bottom) indices for the potential, realised and scenario larval connectivity networks. Node size and colour symbolise index; edge width and colour symbolise normalised edge strength

Nodes 3 and 4, located in the inner Palma Bay, showed the highest RLR in both the potential and realised larval connectivity networks. Indeed, the same RLR node rank was obtained for these 2 networks since this index is relative to the reproductive output of the whole network; the results did not differ if either probabilities or measured demographic weights based of the species were used (Fig. 3).

SR, unlike RLR, is an index relative to the number of larvae arriving and not to the gamete production of each node. In a system where egg production is not uniform and initial density is known, SR provides valuable information on the relative importance of

each node in the larval connectivity system. The main SR differences between the potential and realised networks occurred in Nodes 5, 10 and 12, which were ranked higher in the realised network, whereas Node 3 descended in the rank (Fig. 3).

### 3.2. Analysis of centrality measures

Out-Strength, In-Strength and Strength (the sum of the first 2) are measures of centrality, with a marked influence in larval retention. The nodes highlighted as important for these centrality measures are those

with the highest values of self-connection (i.e. LR) in the potential and realised networks (Figs. 3 & S2).

### 3.2.1. Potential larval connectivity network

In the case of the potential larval connectivity network, Nodes 3 and 4 were the most important nodes when considering the Out-Strength, i.e. the release of propagules that reach some recruitment node. If self-loops (i.e. self-connections, LR) are not considered, the nodes with the highest probability of emitting successful propagules were 5 and 7. Nodes 3 and 4 were also highlighted as those with the highest probability of being successful nursery areas (Table S2, In-Strength column, Fig. S2).

In a network, a high Closeness value indicates a higher probability of information propagation from one node to all other nodes in the network. In a larval connectivity network, this probability will be higher for those nodes that occupy areas of the network where hydrodynamics facilitates larval transport to all other nodes. Accordingly, in the potential larval connectivity network, the nodes with highest Closeness were 6 and 7, followed by 5 (Fig. 4). There was a moderately high correlation between the Closeness

and Betweenness measures ( $r = 0.78$ ; Fig. 5); Nodes 6 and 7 also exhibited the highest Betweenness, indicating their importance as 'bridges' between the nodes located north and south of their location (Fig. 6a, Table S2). The connections between the pairs of nodes  $8 \rightarrow 7$ ,  $7 \rightarrow 6$ ,  $9 \rightarrow 8$ ,  $6 \rightarrow 7$  and  $10 \rightarrow 9$  exhibited the highest edge Betweenness within the network. Excluding the self-loops, the strongest connections were  $5 \rightarrow 4$ ,  $2 \rightarrow 3$ ,  $7 \rightarrow 6$  and  $5 \rightarrow 6$ . These routes are the ones that concentrate the largest flow of larvae between the different nodes of the potential network. There is a strong inverse correlation between Closeness and the SR index ( $r = -0.90$ ; Fig. 5), which suggests that Closeness is a useful measure of centrality since it allows the identification of nodes that facilitate global connectivity in networks with a strong larval retention influence.

Continuing with the potential larval connectivity network, the nodes with the highest Eigenvector, revealing the influence of a node in the network, were 3 and 9, which also had high SR values (Figs. 3 & 4). Indeed, there is a strong correlation between these 2 metrics ( $r = 0.90$ ; Fig. 5). Nodes 10, 11 and 12 had the highest Hub score, while Nodes 1, 2 and 3 had the highest Authority score (Fig. 7). Nodes 1, 2 and 3 were also highlighted by Page Rank (Fig. S3). These

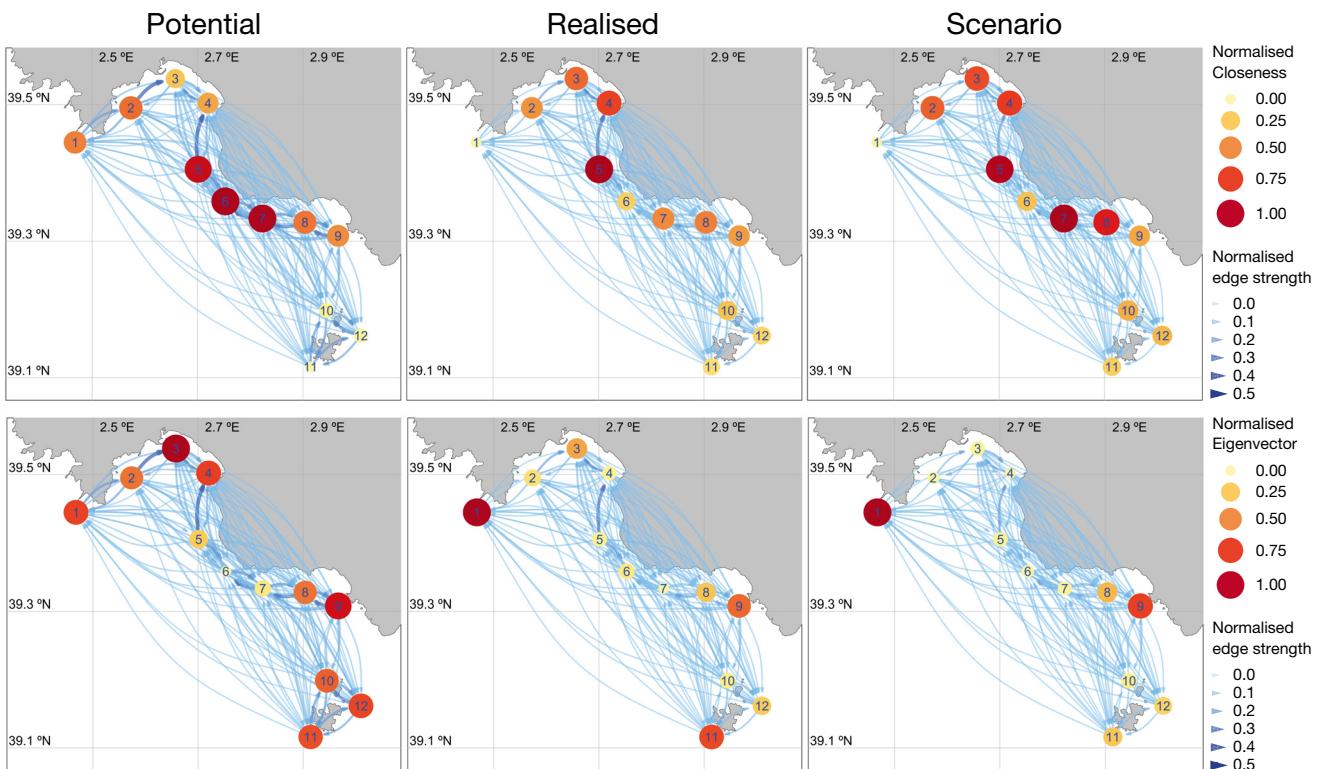


Fig. 4. Closeness (top) and Eigenvector (bottom) centrality measures for the potential, realised and scenario larval connectivity networks. Node size and colour symbolise the centrality measure and edge width and colour symbolise normalised edge strength

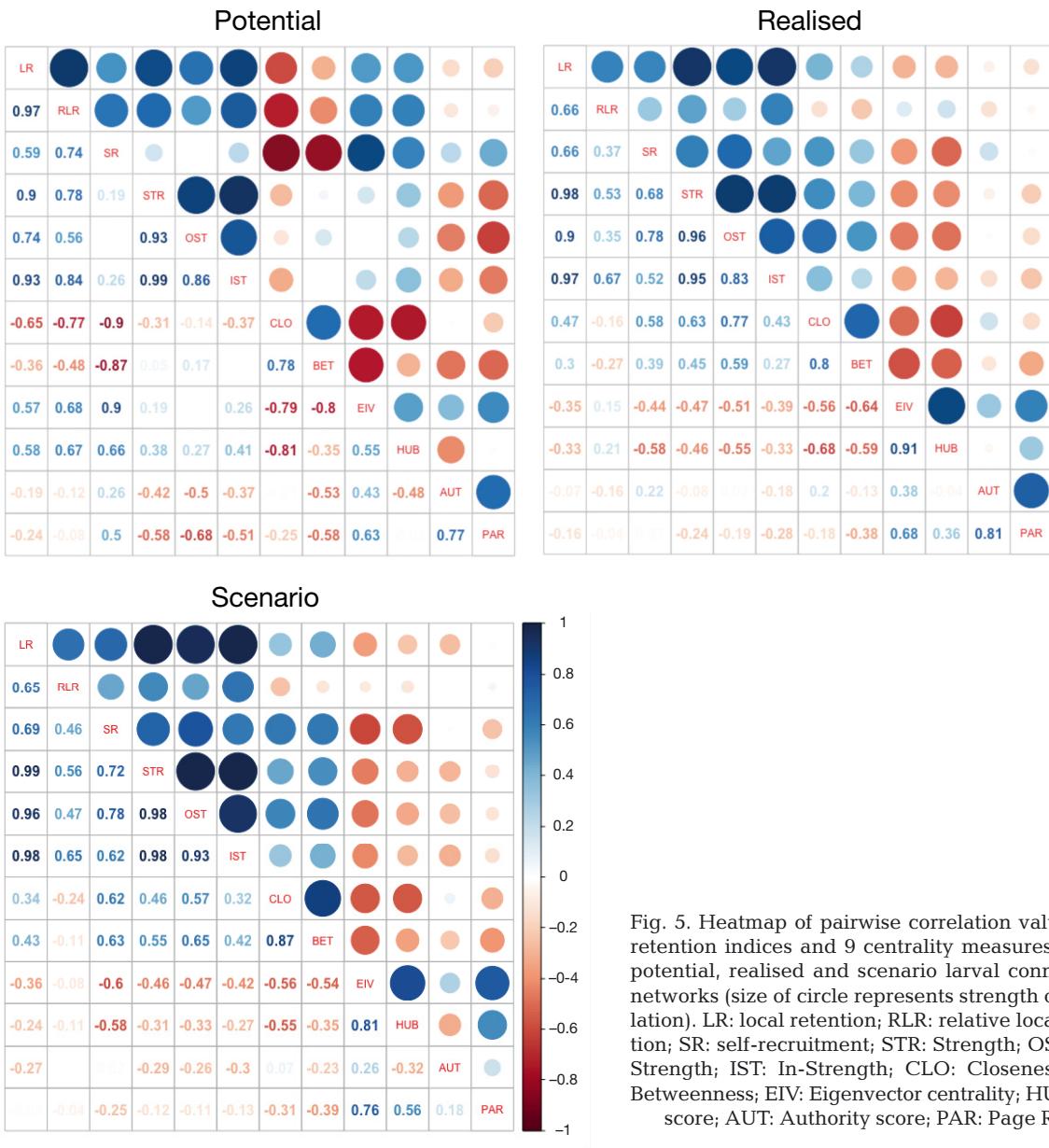


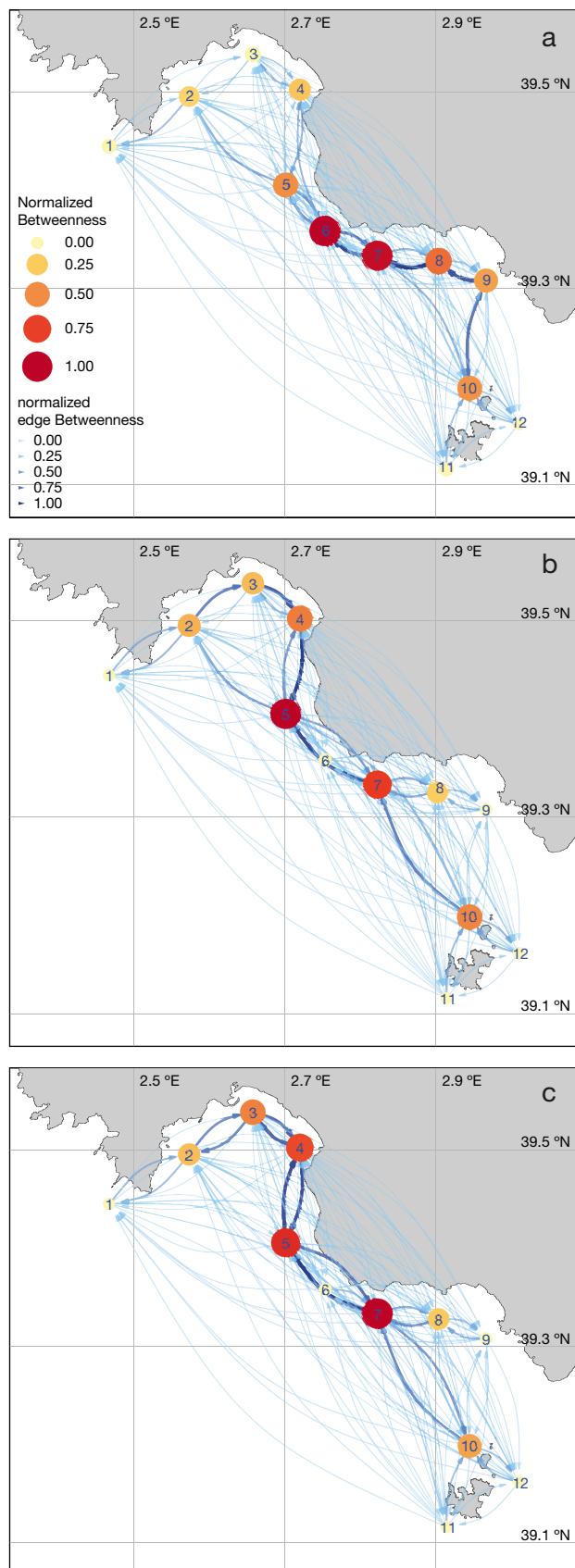
Fig. 5. Heatmap of pairwise correlation values of 3 retention indices and 9 centrality measures for the potential, realised and scenario larval connectivity networks (size of circle represents strength of correlation). LR: local retention; RLR: relative local retention; SR: self-recruitment; STR: Strength; OST: Out-Strength; IST: In-Strength; CLO: Closeness; BET: Betweenness; EIV: Eigenvector centrality; HUB: Hub score; AUT: Authority score; PAR: Page Rank

4 measures (Eigenvector, Hub- and Authority score and Page Rank) could be useful to identify critical nodes in a connectivity network. For example, Node 1, with low release and larval recruitment values, had a high Authority score and Page Rank (Table S2). This suggests that although the weight of its connections to other nodes is low, these other nodes have the highest connections in the network.

### 3.2.2. Realised larval connectivity network

In the case of the realised larval connectivity network, Node 4 held the highest Strength and In-Strength coinciding with what was observed in the

potential network (Tables S2 & S3, Fig. S2). The node with the highest probability of emitting successful larvae was Node 4 (5 if self-loops are not considered). According to Closeness, the incorporation of demographic information shifts the importance of nodes to those where more eggs are produced. Nodes 5, 4 and 3 had the highest Closeness, i.e. the highest potential for connecting their larvae to all the other nodes in the network (Fig. 4). Betweenness was partly correlated with Closeness centrality ( $r = 0.80$ ). Regarding Betweenness, the most important nodes in this network were 5 and 7 (Fig. 6b). Surprisingly, the node with the highest Betweenness in the potential network (Node 6) had the lowest values in the realised network. In the realised network, the nodes with a



high Betweenness were distributed both in the periphery and in the geographic centre of the network, indicating a higher cohesion between distant nodes in the network promoted by these 'bridge' nodes. The connections between the pairs of nodes  $4 \rightarrow 5$ ,  $7 \rightarrow 5$ ,  $3 \rightarrow 4$ ,  $10 \rightarrow 7$  and  $2 \rightarrow 3$  exhibited the highest edge Betweenness within the network. The strongest connections, excluding self-loops, were  $5 \rightarrow 4$ ,  $5 \rightarrow 6$ ,  $4 \rightarrow 3$ ,  $2 \rightarrow 3$  and  $8 \rightarrow 7$ . It is important to note that the high edge Betweenness of the 9–10 node pair in the potential network was not observed in the realised network, while Node 10 formed a new bridge with Node 7 (see Fig. 6a,b).

The 4 measures that highlight the importance of the nodes according to their relationship to other nodes in a network (i.e. Eigenvector, Hub- and Authority score and Page Rank) selected some of the same nodes as critical in both the potential and realised networks. Node 1 was the most important node in the realised network regarding Eigenvector, Hub score and Page Rank, and it ranked high in Authority score, after Nodes 9 and 8 (Table S3, Figs. 4 & 7). There was an almost total coincidence in the classification of the nodes according to Page Rank for the 2 networks (potential and realised), indicating that this measure of centrality is not sensitive to the inclusion of demographic information, or that it is a measure relative to egg production (similar to the RLR index).

### 3.2.3. Larval connectivity network in the simulated scenario

In order to test the influence of node protection on network connectivity, we simulated a scenario where OAA Nodes 3 and 7 were converted to no-take areas through the assignment of the biological parameters observed in Cabrera MPA Nodes 10–12. Otherwise, no-take Nodes 1 and 9 were 'open to fisheries' by the assignment of the average biological parameters observed in OAAs. We explored the structure of the

Fig. 6. Betweenness centrality in the (a) potential larval connectivity network, (b) realised larval connectivity network and (c) larval connectivity network scenario. Circle size and colour: importance of each node in maintaining network connectivity (the higher the value, the more likely a node is to act as a bridge between 2 sub-populations); edge width: strength of the connection between 2 nodes. In (c) open-access Nodes 3 and 7 were converted to no-take (marine protected area) and no-take Nodes 1 and 9 were 'open to fisheries' (open access areas)

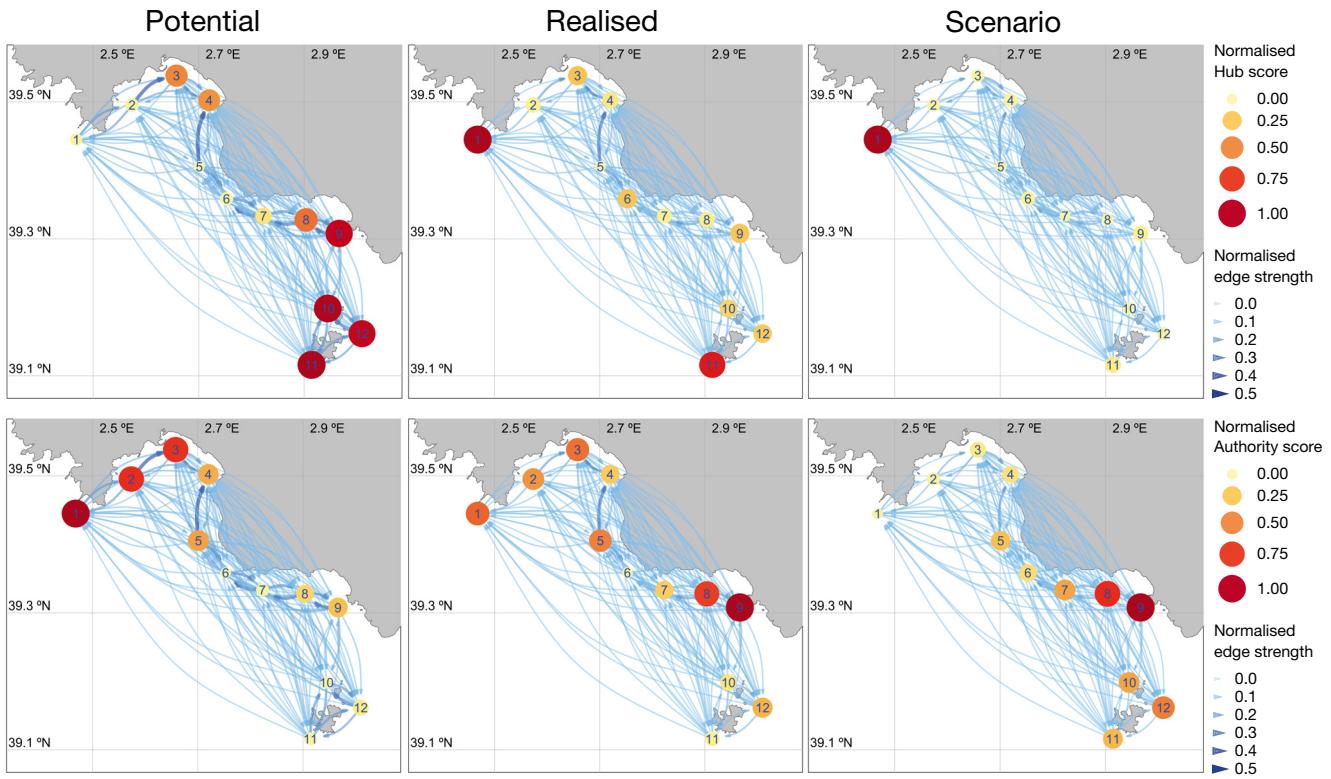


Fig. 7. Kleinberg's Hub (top) and Kleinberg's Authority (bottom) centrality scores for the potential, realised and scenario larval connectivity networks. Node size and colour symbolise the centrality score and edge width and colour symbolise normalised edge strength

network in this scenario and generally observed higher scores of LR, RLR and SR indices (Fig. 3) and of Strength, Out-Strength and In-Strength for Nodes 3 and 7, and higher connectivity measures for Node 7 (particularly Closeness and Betweenness; Figs. 4 & 6c, Table S4). Otherwise, Nodes 1 and 9 obtained similar scores. Overall, this scenario obtained an improved connectivity throughout the nodes of the realised larval connectivity network (e.g. see Authority score in Tables S3 & S4, Fig. 7).

### 3.3. Community detection

A total of 5 communities were detected in both the potential and realised larval connectivity networks, whereas only 4 communities were detected in the scenario network (Fig. 8). The community formed by Nodes 1, 2 and 3 was persistent in all 3 networks, as was the community formed by Nodes 10, 11 and 12. However, Nodes 4–9 shifted their community membership across the networks. Node 4, which remained isolated in the potential and realised networks, formed a new community with Node 5 in the simulated scenario.

## 4. DISCUSSION

Larval transport is a key factor to consider in MPA network design. Optimal sites regarding larval connectivity metrics are not always easy to identify, particularly in complex scenarios constituted by intricate geographical settings, heterogeneous habitats, or where strong variations in physical ocean conditions occur. Our results show that, in these settings, the combination of larval connectivity patterns in complex marine systems and the network emergent properties (centrality measures) from graph theory may optimise decisions on the design and management of MPA networks.

Graph theory allows spatially explicit representation of a complex, inter-connected ecological system (Saunders et al. 2016) because different populations, represented as nodes, are connected by links that represent population connectivity pathways (Loro et al. 2015). As shown in the present study, measures like Betweenness and Closeness are good descriptors of MPA network properties, which is not explicit in traditional cartography. The adequacy of these measurements depends on the management or conservation targets and the resources to be managed. For example, when managing a network of reserves, often

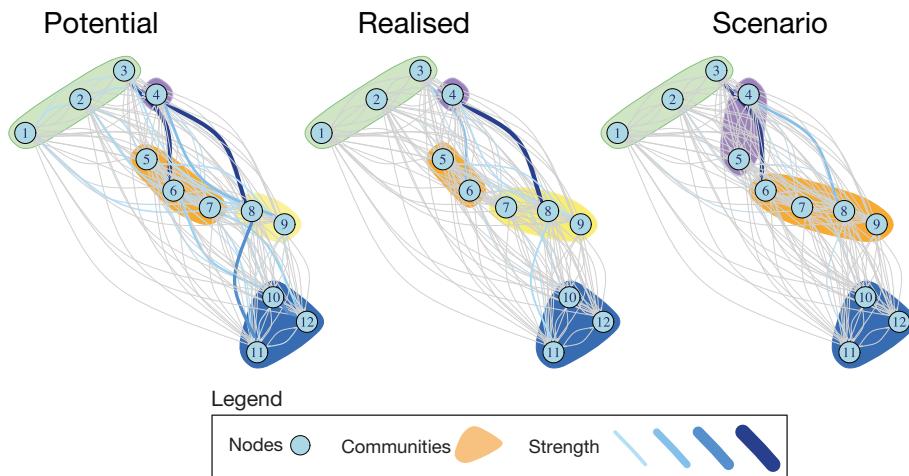


Fig. 8. Graph-based community detection results for the potential, realised and scenario larval connectivity networks. The network communities were calculated finding the optimal community structure by maximising the modularity measure over all possible partitions. Note that community here does not refer to biological communities but to a subset of nodes within the graph such that connections between the nodes are denser than connections with the rest of the network. Colours used to differentiate different communities

the objective is to maximise biological connectivity (Andrello et al. 2015), either by facilitating the mobility of adult organisms or by ensuring the departure, arrival and mobility between nodes of larvae or propagules (i.e. recruits). In this case, local flow patterns and the biological features of the organisms, including their PLD and reproductive behaviour, play a crucial role. In a broad sense, optimal sites for conservation should meet at least 3 basic conditions: (1) enhanced larval production; (2) increased larval recruitment; and (3) high connectivity amongst sites to ensure larval flow and avoid the isolation of populations.

We demonstrated that applying graph theory enables us to gain a deeper insight into egg/larval dispersal network structure and function in a complex system. For example, betweenness centrality identified nodes that have strategic importance for channelling a large flow of propagules (high Betweenness), such as Nodes 5–8 that are in a hydrodynamically active area close to a cape (Fig. 1). The incorporation of spatially explicit information on reproductive output and graph theory analysis enabled the identification of nodes acting as stepping-stones within the complete network (Betweenness centrality), as well as the main paths through which the larvae are transported (edge-Betweenness). For example, a recent study used Betweenness to identify key nodes that act as gateways to dispersal in an MPA–OAA network in an archipelago in the Western Indian Ocean (Gamoyo et al. 2019). At the same time, Closeness captures how close a node is to the ‘central region’ of the network. But here, ‘central region’ does not correspond to the geographical centre but rather to the

central source of larvae dissemination. This ‘central region’ can change from species to species; therefore, the Closeness value for each node will change for each realised larval connectivity network when species-specific demographic information is incorporated (Fig. 4). Hence, it is possible to identify the best- and worst-connected nodes (using Closeness) independently of their spatial location.

If egg production is uniform throughout the network, differences in centrality measures should not be expected. However, demographic differences between species in an ecosystem should be expected. For example, in nature, individuals tend to aggregate where conditions are more favourable. Marked differences in population reproductive parameters (e.g. batch fecundity, maternal effects, etc.) have been observed in *Serranus scriba* at relatively short distances (a few km; Alós et al. 2013). This spatial variability highlights the necessity of including demographic parameters when estimating connectivity. Other factors like larval behaviour are also relevant, yet not always available. For example, vertical migration (Ospina-Alvarez et al. 2012b, Daigle et al. 2016); directionality in swimming in response to the sound of waves breaking on shore (Tolimieri et al. 2000, Montgomery et al. 2006) or to chemical stimuli (Sweatman 1988, Paris et al. 2013a); and aggregation under floating objects (Shanks 1983, Tully & Ceidigh 1989, Ohta & Tachihara 2004) have been shown to modify the trajectories and final destination of fish larvae. Our study relied on *S. scriba* due to availability of biological data on the species in the study area, but the spatial optimisation of MPAs in other case

studies should incorporate a set of species representative of the species pool per habitat type in the region (Blanco et al. 2019).

Despite these limitations, the potential connectivity network is highly relevant, as it can be used in the absence of detailed biological information of the key species, or species pool, in the area of interest. However, incorporating biological parameters of a key species allowed us to obtain a more realistic representation of the connectivity patterns and a better understanding of stock dynamics (Morgan & Fisher 2010, Kell et al. 2016). The comparison of the 2 networks (potential vs. realised) evidences changes in the relative importance of nodes as stepping stones. For example, in our realised connectivity network, Node 5 emerged as a key node, while the importance of Node 6, a key component of the potential network, decreased drastically. In the case study, this is relevant because Node 5 is in fact a marine reserve (Fig. 1) that, according to the centrality measures chosen, acts well as a bridge between communities (Fig. 8) and as a node with high egg exportation and subsequent high larval recruitment rates. We observed how Betweenness and Closeness centrality ranked differently the important nodes in the realised connectivity matrix. We also observed how the bridge links between stepping-stone nodes and the classification of the best-connected sites (according to their Closeness; Fig. 4) changed between these networks, despite the case study being a small network dominated by high retention and SR.

MPA network design involves making decisions about the allocation of protected areas, interspersed by areas open to fisheries (or under more permissive fisheries restriction regimes). The alternative scenario showed potential benefits for the network performance, particularly improving the Betweenness in Palma Bay (Nodes 2–5). It also achieved a better balance of Out-Strength and In-Strength measures in the southern cape area (Node 7). Still, as revealed by Strength, Out-Strength and Betweenness, Nodes 3–5 are crucial for the performance of the network. However, Node 7 gained relevance in maintaining the connectivity with the more peripheral nodes, including the Cabrera Archipelago MPA (Nodes 10–12). By allocating MPAs in the best performing sites in terms of larval connectivity, ecological connectivity through the network is improved and, therefore, the resilience of the whole spawner-recruit system is strengthened. We also showed how closing sites to fishing activities leads to different patterns of connectivity or groupings of sites. Management decisions based on centrality measures can increase network resilience by allowing, through

simple analysis, decision-making in networks composed of several management units (Fig. 8).

The graph analysis performed over the realised connectivity network helps in understanding some ecological processes (e.g. gene flow, colonisation, invasion; Moilanen 2011) and demonstrates that the incorporation of biological data provides an additional and valuable source of information to assist management decisions. A key advantage of graph analysis is the information provided by centrality measures, which allow us to identify the most critical nodes acting as bridges between communities. We encourage scientists and decision-makers to choose within the set of centrality measures derived from graph theory, those that best define their case study according to their ecological significance. This will assist in the adoption of the 'reproductive system' concept (Lowerre-Barbieri et al. 2017) as a more realistic framework to analyse population resilience through time, and produce a more detailed view of the connectivity patterns in meta-populations of marine species.

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*Editorial responsibility:* Rebecca Asch (*Guest Editor*),  
Greenville, North Carolina, USA

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