



Cross-scale connectivity of macrobenthic communities in a patchy network of habitats: The Mesophotic Biogenic Habitats of the Northern Adriatic Sea

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ABSTRACT

Connectivity is a fundamental ecological property affecting stability, resilience and recovery of marine populations, in particular in networks of patchy habitats as the Mesophotic Biogenic Habitats of the Northern Adriatic Sea. Specific information on the dispersal behaviour of many species living in these habitats is lacking, thus the connectivity simulations were performed over different pelagic propagules duration and different reproductive seasons of six consecutive years, covering most of the possible dispersal behaviour variability. The connectivity simulations were analysed with graph analysis methods by characterizing each connectivity graph with several structural measures and by identifying sites with greatest individual and group centrality. We tested the hypothesis that geographic proximity of sites cannot be a proxy for the connectivity and that hydrodynamic connectivity is statistically significantly related to the observed beta diversity among the studied sites. Results showed that species with different pelagic propagules duration follow greatly different dispersal dynamics, and that the network of studied outcrops is only partially connected to coastal benthic populations. Our results also made possible a critical appraisal of the current conservation strategies, evidencing gaps in the existing network of protected Mesophotic Biogenic Habitats in the Northern Adriatic Sea. We suggest possible improvements for an efficient preservation strategy of these unique biodiversity hotspots by including a fundamental ecological process, the dispersal connectivity, into the process of decision making for conservation.

1. Introduction

Connectivity by dispersal, i.e. the exchange of early life stages (larvae, spores, eggs, zygotes) among populations, is a fundamental process in ecology (Cowen et al., 2007) shaping the structure and resilience of communities in a specific area (Borthagaray et al., 2009; Fogarty and Botsford, 2007; Levin and Lubchenko, 2008; Magris et al., 2016; Sponaugle et al., 2002; Standish et al., 2014). It increases local genetic diversity through inflow of recruits from other populations, and thus it improves the ability of metapopulations to resist to stress conditions induced by perturbations or climate changes (Bray et al., 2017; Melià et al., 2016; Rattray et al., 2016; Trembl and Halpin, 2012). Habitat fragmentation on the contrary leads to genetic drifts/bottlenecks by inbreeding, carrying capacity reduction and population decline, ending up with a lower potential of recovery to perturbations (Jones et al., 2007). Nevertheless, high connectivity can also cause a rapid spread of diseases, pests, pollution, invasive species or other unwanted effects

(Cabanelas-Reboredo et al., 2019; Carlson et al., 2017; Perry et al., 2017; Roy et al., 2016). Therefore, intermediate levels of connectivity might better preserve the resilience of a community (Field and Parrott, 2017; Minor and Urban, 2008). The effects of the connectivity depend on the time scale: at short time scales connectivity is important for the successful dispersal of juveniles and their settlement in barren habitat patches, at intermediate time scales connectivity affects migration and resilience of metapopulations, while at long time scales it favours the possibility of species to escape adverse environmental conditions, changing their distributional range (Minor and Urban, 2008; Rudnick et al., 2012). Connectivity is thus an ecological process that acts across multiple scales, and all these need to be considered in order to maintain successful, resilient and diversified populations (Bennett et al., 2009; Magris et al., 2016).

Connectivity in the sea is critically dependent on the ocean currents, their direction and velocity. This is particularly true for passive propagules, but also for species with actively swimming larvae, since the

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transport induced by currents generally spans over much larger scales than their swimming capacity. The spatial scales are important also for the connectivity in the marine environment (Bishop et al., 2017), which is characterized by great variability and multiple scale features. Large scale hydrodynamic structures, such as persistent mean flows or basin and sub basin-scale gyres, may impact large scale patterns of connectivity (Clarke and Li, 2004), while small scale or short-lived hydrodynamic features would affect mainly local connectivity. Connectivity mediated by currents is of critical relevance for the dispersal of benthic species with reduced or no motility, or for species living in a fragmented habitat, since the propagules of these species need to find a habitat suitable for settlement and survival (Adams et al., 2014; D'Agostini et al., 2015; Pineda et al., 2007). The study of connectivity is also important for the design and management of networks of Marine Protected Areas (MPAs) (Airamé et al., 2003; Carlson et al., 2016; Corell et al., 2012; Largier, 2003; Magris et al., 2016; Marti-Puig et al., 2013; Olds et al., 2012; Rattray et al., 2016), to understand the paths of dispersal for commercially important fish resources (Sciascia et al., 2018), for the design of successful restoration projects (Baums, 2008; Bode et al., 2006; Jacob et al., 2018; Lipcius et al., 2008; Rudnick et al., 2012), and to understand the effects of the ocean sprawl on marine ecosystems (Bishop et al., 2017).

For a long time it was assumed that marine species have the ability to disperse over great distances (Caley et al., 1996; Kinlan and Gaines, 2003; Thiel and Gutow, 2005), but further studies showed the importance of self-recruitment (Magris et al., 2016; Swearer et al., 2002) and of medium-scale connectivity (10–100 km) on local populations (Becker et al., 2007; Borthagaray et al., 2009; Rattray et al., 2016). The direct observation of connectivity of marine species poses several problems due to the accessibility of the study sites, the variability and complexity of the marine environment, the costs associated with underwater research, but also because of the small size and high mortality of many species' propagules (Becker et al., 2007; Levin, 2006, 1990; Magris et al., 2016; Thorrold et al., 2007). Controlled experiments addressing propagules movement and dispersal at the relevant temporal/spatial scales are also extremely difficult to realize. Scarce or absent commercial interest for many marine species only adds up to this, preventing the availability of substantial funding for the study of dispersal mechanics, such as the time and abundance of spawning, the behaviour and duration of propagules in water, the dynamics of settlement, recruitment and interactions at the arrival site. It has been shown that even congeneric species sharing general life traits and pelagic larval duration may differ in the time of spawning and reproductive adults distribution, thus impacting the scale and dynamics of dispersal (Carson et al., 2010). This is arguably all the more true for metacommunities made by species belonging to different taxa and where the main goal of connectivity studies is the preservation of the communities as a whole (Airamé et al., 2003). Multispecies connectivity studies should necessarily be cross-scale and extending over the spawning periods of all the considered species (Magris et al., 2016).

Many methods to investigate connectivity in marine ecosystem can be used (Becker et al., 2007; Guizien et al., 2014; Hedgecock et al., 2007; Jones et al., 1999; Levin, 2006; Padrón and Guizien, 2016; Palumbi, 2003; Pringle, 2003; Schiavina et al., 2014; Swearer et al., 1999; Thorrold et al., 2007; Werner et al., 2007). In particular, the use of experimental Lagrangian drifters (Monzón-Argüello et al., 2010; Sciascia et al., 2018) for the study of complex marine ecosystem is not easily feasible, since such studies are limited to the surface layer and require a relevant observational effort spanning over a long time-range, with high release frequency, both in space and time, in order to account for spatial and temporal variability. On the other hand, numerical models of marine circulation analysed with a Lagrangian approach (Cowen et al., 2006, 2000; Drake et al., 2011; Magris et al., 2016; North et al., 2008; Rattray et al., 2016; Roughan et al., 2011; van Sebille et al., 2018) represent an indirect method especially well-suited for connectivity estimations of multiple species across different sites (Cowen et al., 2006;

Magris et al., 2016). In fact, modelling tools allow the design and setting of many different scenarios to track virtual particles over a large variety of spatial and temporal scales (Bray et al., 2017; Carlson et al., 2016; Magris et al., 2016). The validity of the numerical approach relies on some crucial features, such as the use of high spatial and temporal resolution, as well as on an accurate parameterization, in particular concerning the sub-grid scale processes. Special care must be given when setting up 3D simulations for mesophotic connectivity, with respect to purely superficial studies, because less observations are available below the surface to validate three-dimensional currents and virtual drifter trajectories.

At present, several connectivity studies have been carried out in the Mediterranean Sea, with focus mainly on large scale connectivity, fish population, and connectivity between MPAs (Andrello et al., 2013; Berline et al., 2014; Calò et al., 2013; Di Franco et al., 2016; Dubois et al., 2016; Guizien et al., 2014; Padrón and Guizien, 2016; Rattray et al., 2016; Rossi et al., 2014; Schunter et al., 2011). However, connectivity studies performed in the Adriatic Sea were limited mainly to large scales (Andrello et al., 2013; Dubois et al., 2016; Rossi et al., 2014), to the Southern Adriatic basin (Carlson et al., 2016; Pujolar et al., 2013; Rattray et al., 2016; Sciascia et al., 2018), to a few species (Melià et al., 2016; Schiavina et al., 2014; Sciascia et al., 2018), to surface transport (Carlson et al., 2016), or to specific seasons (Bray et al., 2017; Carlson et al., 2016; Melià et al., 2016). Only three studies addressed cross-scale and multispecies connectivity in the Adriatic (Bray et al., 2017; Melià et al., 2016; Rattray et al., 2016). Our study is the first one to be focused specifically on the Northern Adriatic Sea (NAS), by using a high-resolution 3D hydrodynamic and transport model and a Lagrangian approach.

We applied this approach to study the connectivity of the Mesophotic Biogenic Habitats (MBHs) of the NAS. The MBHs are a network of outcrops arranged in a scattered mosaic on a siliciclastic seafloor, from 10 to 40 m depth (Tosi et al., 2017). They host many algae and animals, which cannot thrive on the surrounding soft and flat bottoms, thus representing important biodiversity hotspots (Falace et al., 2015). The principal bioconstructors are calcareous algae, bryozoans, molluscs, serpulids and scleractinians, while among other invertebrates prevail populations of suspension feeders, such as sponges, anthozoans, hydroids, polychaetes and ascidians (Curjel et al., 2012; Falace et al., 2015; Ponti et al., 2014, 2011). The MBHs assemblages have a significant degree of similarity with the coralligenous, a Mediterranean priority habitat in the framework of the Marine Strategy (MSFD, 2008/56/EC), although their overall structure shows unique features (Falace et al., 2015). They also act as important spawning areas, nurseries and refuges for many species targeted by commercial fishery (Fortibuoni et al., 2017; Tonin, 2018). The further understanding of the fundamental dynamics of dispersal might improve the results of the Lagrangian approach to marine connectivity by including in the model the larval behaviour and duration as free-swimming plankton, and the habitat preferences of species (Cowen et al., 2006; Magris et al., 2016). However, such information for the majority of species inhabiting MBHs is fragmentary at best or completely lacking. Thus, connectivity simulations over different Pelagic Propagules Duration (PPD) and different reproductive seasons were performed, in order to cover most of the possible dispersal behaviour variability.

Since 2015 a restricted number of biogenic outcrops in the NAS benefits of a legal protection within the framework of the European Habitats Directive (92/43/EEC). Their inclusion in the European Natura 2000 network as Sites of Community Importance (SCIs) acknowledges the need to protect these habitats in order to preserve their unique assemblages, mitigate the effects of climate change and local stressors (i.e. dystrophic crises, mucilage, dredging, fishing or anchoring) on them (Bevilacqua et al., 2020; Falace et al., 2015), and thus their ability to deliver important ecosystem services (Fraschetti et al., 2009; Tonin, 2018). The proper criteria for the selection of the minimum viable number of outcrops to be protected in such a large, heterogenous and

patchy habitat, is challenging for policy makers. The establishment of the protected areas in 2015 was focused basically on the presence of a few threatened or endangered species listed in the Annex II of the Habitats Directive. Appropriate descriptors related to functional and ecological processes are still seldom taken into account in the planning of biodiversity conservation measures, but they should also be considered (Bennett et al., 2009; Jacobi and Jonsson, 2011; Pressey et al., 2007). Knowledge of the connectivity among outcrops can assist in the design of an effective network of protected areas, triggering more successful management, conservation and restoration plans (Airamé et al., 2003; Andrello et al., 2013; Bray et al., 2017; Bunn et al., 2000; Carlson et al., 2016; Di Franco et al., 2016; Jacobi and Jonsson, 2011; Pujolar et al., 2013). With this study, evidence is provided on how an important ecological process, such as the potential passive dispersal, can be included in the decision making process for conservation (Bennett et al., 2009; Minor and Urban, 2008; Pressey et al., 2007).

Therefore, the objectives of the present paper are: 1) to estimate the hydrodynamic connectivity among the biogenic outcrops and with coastal segments across different spatial/temporal scales in the NAS; 2) to test the hypothesis that the geographic proximity of sites cannot be a proxy for connectivity and that hydrodynamic connectivity is significantly related to the pattern of diversity observed on the biogenic outcrops; 3) to critically evaluate the existing network of protected areas from the point of view of current-mediated dispersal; 4) to propose a strategy for the inclusion of connectivity in the decision making process for conservation of the MBHs in the NAS.

2. Methods

2.1. Study area

The NAS is the northernmost part of the Mediterranean Sea (Fig. 1). The basin is surrounded by mainland areas that exhibit sharp contrasts in tectonism, topography, climate, and fluvial inputs. A ragged coastline with some deep fjords characterizes the south-eastern coast along the Istria peninsula. The north-eastern coast, along the Karstic plateau, is regular and high, with several submarine freshwater springs close to the shore. The north-western and south-western coasts are sedimentary and contain some coastal lagoons (Grado-Marano, Caorle and Venice), and

several important river estuaries (Isonzo-Soča, Tagliamento, Piave, Adige), ending in the big delta of the Po river. The bottom is composed of soft sediments of riverine origin, dotted by MBHs. These biogenic outcrops display a broad range of geomorphologies and extent (1–1000 m²), from flat elongated forms, to structures that can reach the height of several meters, to scattered conglomerates of small rocks (Gordini et al., 2012). The oceanography of the NAS is characterized by wide seasonal and inter-annual variability in temperature, salinity and inorganic nutrients concentrations (Solidoro et al., 2009). The general circulation in the NAS is cyclonic, with a northward flow along the eastern side and a southward return flow along the Italian coast on the western side (Artegiani et al., 1997; Poulain, 1999; Ursella et al., 2018). However, the strong hydrologic and meteorological variability can induce remarkable differences from the average scenario, with basin scale recirculation during strong Bora wind episodes (Kuzmić et al., 2007), offshore penetration of the Po freshwater plume (Jeffries and Lee, 2007), and intense mesoscale dynamics (Cushman-Roisin et al., 2007).

2.2. Connectivity simulations

The hydrodynamic connectivity between 33 biogenic outcrops were analysed (Fig. 1, Suppl. Table 1). The structure and biodiversity of the microbenthic communities on these outcrops were reported in Falace et al. (2015). The connections between the outcrops and the mainland were investigated by dividing the coast into 10 segments, based on geomorphological features, which affect biological communities, and on coastline orientation, which influences the direction of particle advection (Fig. 1).

The hydrodynamic connectivity was studied by using a numerical approach, tracking tri-dimensional Lagrangian particles with the LTRANS Zlev model (Larval TRANSPORT, Laurent et al., 2020), based on LTRANS v.2b (Mitchell, 2013; North et al., 2008, 2011; Schlag and North, 2012). LTRANS Zlev was coupled with the three dimensional flow fields produced by the finite volume, non-hydrostatic, Massachusetts Institute of Technology general circulation model (MITgcm, Marshall et al., 1997), applied to the NAS in the framework of the CADEAU project (Silvestri et al., 2020). The validation of the implementation of the three-dimensional advection and interpolation algorithms of LTRANS-Zlev was performed on an idealized flow (Laurent

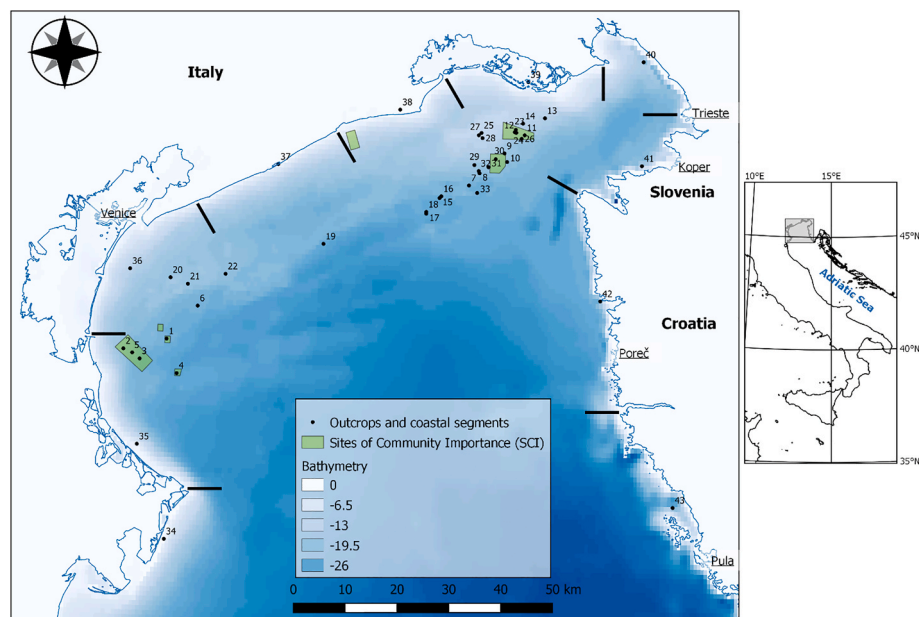


Fig. 1. Study area. Black dots show the position of the MBHs used in this study. Black lines show approximate boundaries of coastal segments used for the connectivity simulations. Green polygons show the position of the Natura 2000 Sites of Community Importance (SCIs). Refer to Suppl. Table 1 for the correspondence between numbers and names of the study sites and coastal segments.

et al., 2020) reproducing a cyclonic gyre in a mid-latitude closed basin (Cossarini et al., 2017).

Our MITgcm setup for the NAS is a higher resolution downscaling of the Adriatic model described in Querin et al. (2016) and references therein, with further upgrades (i.e., hydrodynamic variables dumped at daily temporal resolution) in respect to the version available on the CADEAU project website (<http://www.bio.isprambiente.it/cadeau/>). The computational grid of the hydrodynamic model spans north of latitude 43.5° N, with a horizontal resolution of 1/128° (about 600 m and 850 m in the zonal and meridional direction, respectively). In this study, we focused on the northernmost part of the domain. Due to the strong environmental variability of the system and the high resolution of the simulation, the model is run in non-hydrostatic mode, with a vertical discretization consisting of 27 unequally spaced levels, with thickness varying from 1.5 m (surface layer) to 21.4 m (bottom layer). We used the Leith-Smagorinsky and KPP schemes for the horizontal and vertical parameterizations of turbulence. Grid resolution and model set-up guarantee a proper simulation of the main basin and sub-basin scale (mesoscale) features of the NAS (i.e., full eddy resolving simulations) and allows to model the most energetic turbulent structures. However, the smallest (sub-grid scale) and less energetic structures cannot be reproduced, but their effects on the system are taken into account by the turbulence parameterization of the hydrodynamic model.

Model configuration explicitly considers the 19 major rivers flowing into the basin. Daily discharge rates are available for the Po, Isonzo-Soča and Timavo rivers, while the other flow rates have been derived from up-to-date climatologies, modulated in order to have the maximum and minimum values in spring/autumn and summer/winter, respectively. The meteorological forcing (hourly fields of air temperature, pressure and humidity, wind velocity, heat fluxes and precipitation) was obtained from the 2.8 km resolution COSMO-2I model, run by the Emilia-Romagna Environmental Protection Agency (ARPA-EMR, Struttura IdroMeteoClima).

The simulation time period covers 6 consecutive years (2013–2018), in order to investigate a broad range of hydrodynamic and thermohaline features. Initial conditions are derived from a previous simulation (characterized by the same resolution, but a different setup) of the period 2006–2012, while daily open boundary conditions are extracted from the regional Mediterranean Copernicus Marine Environment Monitoring Service (CMEMS - <https://marine.copernicus.eu>) applied to the southern side of the domain. The model also assimilates sea surface temperature from CMEMS satellite products by using a nudging algorithm. The model neglects tides and short gravity waves (wind waves). Further details on the MITgcm implementation for the NAS are provided in Silvestri et al. (2020).

The daily flow fields of the MITgcm were interpolated by the Lagrangian model LTRANS Zlev to compute the three-dimensional paths of the particles using a fourth order Runge-Kutta scheme for particles advection with a timestep of 120 s. Reflective horizontal boundary conditions were applied along the coastal borders of the domain, while sticky boundaries were considered along the open-sea borders. Particles eventually advected across the seafloor (bottom boundary) were simply replaced in the water domain, to be advected further.

In order to take into account the different reproductive and spreading habits of MBHs benthic species, hydrodynamic connectivity was assessed by simulating different PPDs (3 h, 1 day, 3 days, 1 week, 2 weeks, 32 days) and reproductive seasons (Winter, Spring, Summer, Autumn), hence effectively simulating the connectivity over different spatial scales of the domain. We assumed the larval production as homogenous and tracked evenly distributed Lagrangian particles as generic passive tracers (i.e., particles that do not have influence on the hydrodynamic flow field, neither by changing the density, nor the viscosity of the fluid). The connectivity during each season was independently studied by releasing particles over the whole season (three months) and following their advection for each of the six PPDs.

Two distinct simulations represented in Fig. 2 were set up, to study

the connectivity of organisms coming from either the outcrops (Fig. 2 left) or from the coast (Fig. 2 right). In simulation A one particle was released from each outcrop location (1.5 m above the sea bottom) every 30 min for 91 consecutive days of each season. Similarly, in simulation B, the particles were released once a day along the coastal segments at intervals of about 341 m. In both cases, every particle was tracked during each PPD and considered to have reached a possible settlement site whenever during the time interval associated to every PPD it would pass either 1) within the volume defined by a cylinder of 300 m radius and of 5 m height above the bottom, located in the centre of any other outcrop or 2) within a 1 km wide strip along the coastline, as schematically represented in Fig. 2. During the simulated time period (6 years), for each season a total of 26,208 particles was released from each outcrop, and between 30,360 and 112,608 particles from the coastal segments, according to the different length and complexity of the coastline (Suppl. Table 2). We computed 24 connectivity matrices, i.e. one for each PPD and for each season, summing all particles connecting each source and each sink site during the whole 6 years period of simulations.

2.3. Graph analysis methods

For each selected PPD, the simulated dispersal routes can be viewed as sets of nodes (i.e. the release and arrival sites) connected by edges (i.e. the paths connecting sites) (Borgatti, 2005; Bunn et al., 2000; Dale and Fortin, 2010; Urban and Keitt, 2001). The number of particles moving along an edge represents the “edge weight” which is different in the two directions of an edge. Thus, for each PPD and season a directed and weighted graph was constructed, for a total of 24 graphs (see Fig. 3 and Suppl. Figs. 1-3).

The connectivity can be summarized in a binary matrix or in an adjacency matrix, and can be analysed with the graphs analysis method, borrowed from social network science (Carrington et al., 2005; Dale and Fortin, 2010; Minor and Urban, 2008; Treml et al., 2008; Urban and Keitt, 2001; Urban et al., 2009). A binary matrix is an $n \times n$ matrix of 0 and 1, where n is the number of nodes: 0 denotes the absence of an edge between two nodes and 1 denotes the presence of an edge between two nodes. On the binary matrix of each of the 24 graphs we performed three structural measures: connectedness (*Conn*), graph hierarchy (*Hier*) and efficiency (*Eff*) (Everett and Krackhardt, 2012; Krackhardt, 1994) (Table 1).

A graph is fully connected, if it is possible to reach each node starting from any node of the graph, or disconnected, if several sub-graphs or isolated nodes exist. *Conn* is computed as

$$Conn = 1 - \left(\frac{V}{N \times \frac{N-1}{2}} \right) \quad (1)$$

where N is the total number of nodes in a graph and V is the number of pairs of nodes that are not mutually reachable.

Hier is the measure of the order in the graph, i.e. whether edges between nodes are mainly symmetrical or asymmetrical. If they are symmetrical the particles can flow between two nodes in both directions, if they are asymmetrical, particles can only flow in one direction along an edge. *Hier* is computed as

$$Hier = 1 - \left(\frac{W}{maxW} \right) \quad (2)$$

where W is the number of pairs of nodes symmetrically linked and $maxW$ is the number of all pairs of connected nodes.

Eff is related to the number of multiple paths between nodes existing in a graph and computed as

$$Eff = 1 - \left(\frac{Z}{maxZ} \right) \quad (3)$$

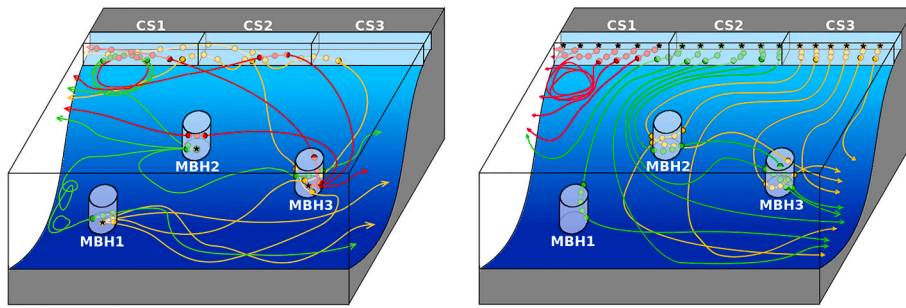


Fig. 2. Schematic representation of virtual particles released from three outcrops identified as MBH1, MBH2 and MBH3 (left), and from three distinct coastline segments identified by CS1, CS2 and CS3 (right). The white semi-transparent cylinders and rectangular parallelepipeds represent respectively the volume around every outcrop, and the volume delimited by the strip of 1 km from the coastline. The coloured dots represent each time a particle passes through one of these volumes, and the sum of these events over six years between each source and each sink site are the entries for the 24 connectivity matrices (one for each PPD and for each season).

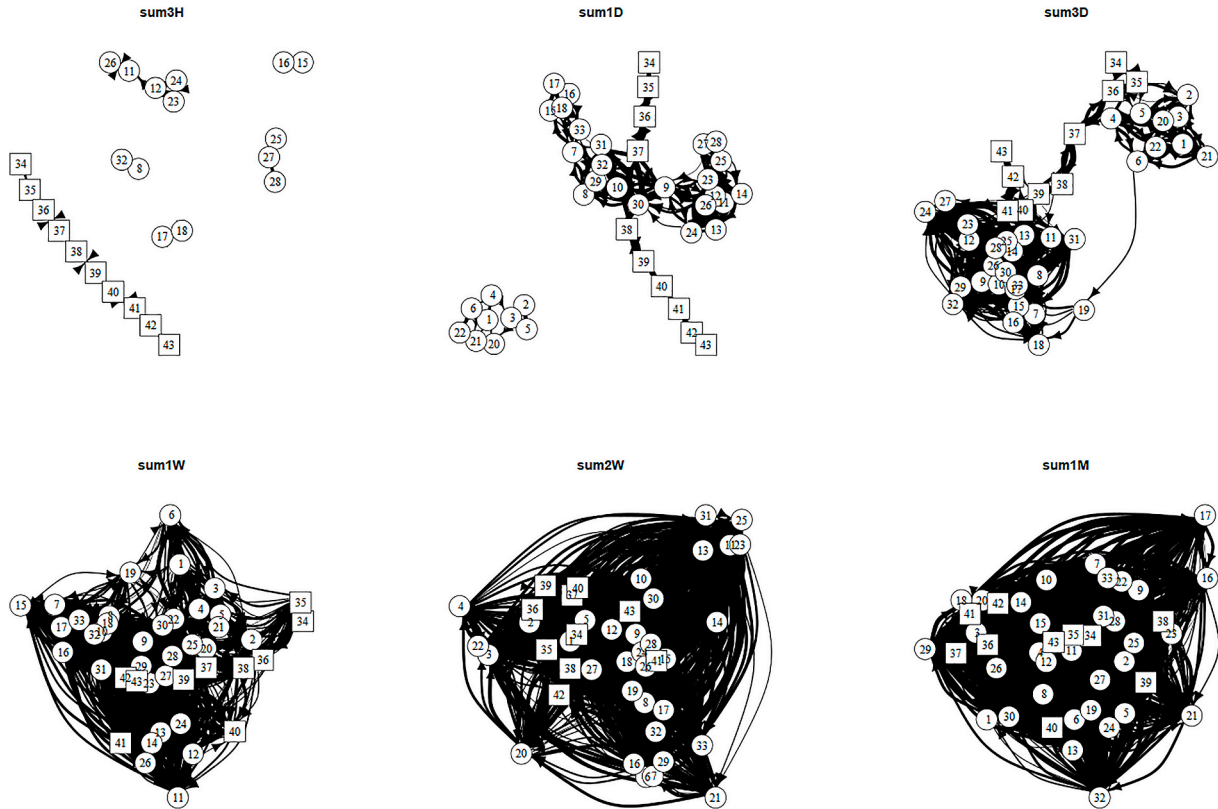


Fig. 3. Connectivity graphs for summer at different PPDs. The width of the edges is proportional to the logarithm of the number of particles flowing in one direction between two nodes. Isolated nodes have been omitted. Titles above the graphs indicate the PPD, from top-left to bottom right: 3H = 3 h, 1D = 1 day, 3D = 3 days, 1W = 1 week, 2W = 2 weeks, 1M = 32 days. Circles = biogenic outcrops, squares = coastal segments. See [Suppl. Table 1](#) for the correspondence between numbers and names of the outcrops and of the coastal segments, and [Fig. 1](#) for the geographic position of the outcrops and of the coastal segments.

where Z is the number of links in excess of $N - 1$ ($N - 1$ is the minimum number of links to have all nodes of the graph connected) and $maxZ$ is the maximum number of links possible in excess of $N - 1$.

Eff is not a desirable property in ecology. The more are ecological networks redundant, and thus less efficient according to the above definition, the more they are stable and resilient (Field and Parrott, 2017; Hodgson et al., 2015; Levin and Lubchenco, 2008): if one of the nodes is removed, for instance an element of a trophic food web or a patch in a fragmented habitat, many different paths would still exist linking the remaining nodes. Thus, to characterize the MBHs networks, we preferred to define redundancy (*Red*) as (Table 1):

$$Red = 1 - Eff = 1 - \left(1 - \left(\frac{Z}{maxZ} \right) \right) = \frac{Z}{maxZ} \quad (4)$$

All three measures have values between 0 and 1. The Sna package for R (Handcock et al., 2003) was used to perform structural measure computations.

An adjacency matrix is an $n \times n$ matrix, where each non-null entry represents the weight of an existing edge between two nodes. The potential self-recruitment *Self* (Table 1) was estimated as the diagonal elements of the adjacency matrices for each PPD and each season and expressed as percentage of the total amount of particles released from each site (Magris et al., 2016; Tremblay et al., 2012).

On the adjacency matrix of each of the 24 graphs the M-reach closeness centrality (MC) (An and Liu, 2016; Borgatti, 2005) was applied, to examine the relative importance of each node in the network (Table 1). The MC for a node i out of N is computed as:

$$MC_i = \frac{\sum_{j \in F} d_{ij}^{-1}}{d \times (N - 1)} + \frac{\sum_{j \in H} d_{ji}^{-1}}{d \times (N - 1)} \quad (5)$$

where F and H are the sets of nodes reachable from or to node i via M steps, respectively, d_{ij} is the distance between nodes i and j along edges of the graph, and d is the maximum d_{ij} across all pairs of nodes. MC_i consists of two components: the outgoing centrality, which considers

Table 1

List of connectivity metrics computed on connectivity graphs for each PPD and season, with a short explanation of their ecological interpretation, and the original literature reference.

METRICS	ACRONYM	ECOLOGICAL INTERPRETATION	REFERENCE
Connectedness	<i>Conn</i>	Overall connectedness of the sites, existence of separate sub-networks of sites linked by dispersal.	Krackhardt (1994)
Hierarchy	<i>Hier</i>	Preferential direction of dispersal, i.e. the asymmetrical linkage strength of dispersal.	Krackhardt (1994)
Redundancy	<i>Red</i>	A measure of the number of alternative paths of dispersal in a network of sites.	This paper, based on Efficiency as defined in Krackhardt (1994)
Self-recruitment	<i>Self</i>	Self-sustainability capacity of a population.	Tremblé et al. (2012)
M-reach closeness centrality	<i>MC</i>	Identification of stepping-stone sites and of the most used dispersal pathways.	Borgatti (2005)

edges reaching out from a certain node, and the ingoing centrality, which considers edges reaching a node from other nodes (hereafter referred as the source and sink centrality, respectively). Note that source and sink site terms indicate respectively the site of origin and the site of arrival of particles, without any deeper ecological meaning (Pulliam, 2000). To calculate *MC*, the distances d_{ij} along the edges on the graph should reflect the topological proximity of a pair of nodes. Thus, we first inverted the values in the adjacency matrices, so that a higher number of particles reaching a sink site from a source site resulted in a shorter distance with a closer relationship between the two sites. In this way the interpretation of the adjacency matrix of connectivity in terms of ecological distances is straightforward. We set $M = \text{Inf}$, i.e. all nodes of a connected graph can be reached from every other node (An and Liu, 2016).

To select the most important nodes of the whole network (i.e. a subset of nodes with the highest group centrality) we applied the greedy algorithm for key players selection (Borgatti, 2006; An and Liu, 2016). The centrality measure used was again the *MC* with $M = \text{Inf}$ and for an optimal resolution we fixed *a priori* at 10 the number of sites, starting the search from the set of sites with the highest MC_i . All other options were set to the default of the key player R package (An and Liu, 2016) used for both, the computation of individual centrality and for the key player nodes search.

Graph figures (Fig. 3 and Suppl. Figs. 1-3) were drawn using igraph package for R (Csardi and Nepusz, 2005).

2.4. Relationships between absolute connectivity, geographic distance and β_w

We defined the Absolute Connectivity index (*AbsConn*) for each pair of sites as the total sum of particles exchanged between these two nodes, regardless of the total amount of particles released or received from other sources:

$$AbsConn_{ij} = Connectivity_{i \rightarrow j} + Connectivity_{j \rightarrow i} \quad (6)$$

where $AbsConn_{ij}$ is the absolute connectivity between sites i and j , $Connectivity_{i \rightarrow j}$ is the number of particles leaving site i and reaching site j , $Connectivity_{j \rightarrow i}$ is the number of particles leaving site j and reaching site i in the same time interval. It can be considered as a measure of dispersal proximity mediated by hydrodynamics, i.e. the higher the *AbsConn* value, the more two sites are able to exchange particles.

On the presence-absence matrix of the 33 outcrops macrobenthic assemblages (Falace et al., 2015) the Whittaker's beta diversity β_w

measure for pair of locations (Koleff et al., 2003) was calculated:

$$\beta_w = \frac{a + b + c}{\frac{2a+b+c}{2}} - 1 \quad (7)$$

where a is the number of species common to the two sites, and b and c the numbers of species found only in either one of the two sites. β_w values fall between 0 and 1.

The Pearson's product-moment correlation for all pairs of sites was computed between β_w , geographic distance, and *AbsConn* for each reproductive season and each PPD.

To calculate the effect of passive dispersal proximity, as expressed by *AbsConn*, and compare it to the predictive power of the simple geographic distance on β_w , two multiple linear regression models were built: the first one had as predictors only the *AbsConn* for each season and each PPD, in the second one the geographic distance between locations was added. The best parsimonious models were identified with a stepwise selection of variables based on the generalized Akaike Information Criterion (AIC) (Venables and Ripley, 2002). The relative importance of the variables in the parsimonious regression models was assessed by lmg method (Grömping, 2007; Lindeman et al., 1980), using the Relaimpo package for R (Grömping, 2006). The 95% confidence intervals were computed with 1000 random bootstrap runs (Efron and Tibshirani, 1986).

3. Results

3.1. Graph analysis

Many outcrops are very close to each other and they exchange large amounts of particles, therefore a visualization in the true geographical space produced tangled graphics even for short PPDs. We chose to visualize the connectivity graphs with a topological visualization, in which nodes are positioned based on their dispersal proximity: nodes sharing edges with high weights are close to each other in this visualization (Fig. 3 and Suppl. Figs. 1-3) and the width of directed edges is proportional to the logarithm of the number of particles moving along them. Such visualization is more meaningful than that based on the true geographical space, since it emphasizes the existence of clusters of sites linked by dispersal and allows for a better positioning of the nodes on the 2D plane.

At PPDs shorter than 3 days (1 day in Autumn) the system was made up of several mutually disconnected subgraphs, with several isolated nodes (they were omitted from Fig. 3 and Suppl. Figs. 1-3). Coastal segments were connected to one another, but mainly disconnected from the MBHs for PPDs shorter than 3 days. At higher PPDs the connectivity graphs grew increasingly complex becoming more difficult to analyse them visually.

Conn increased with PPDs and the graphs resulted fully connected at PPD 1 day in Autumn, and PPD 3 days for all other seasons (Table 2). *Hier* was relatively high for short PPDs but fell to 0 at PPD 3 days for all seasons except for Spring (Table 2). The lowest *Red* values were for PPDs from 3 h to 3 days and grew larger for PPDs of 1 and 2 weeks. At PPD of 1 month the *Red* values were almost 1 for all seasons (Table 2).

For MBHs *Self* was 100% at PPD = 3 h but fell to between 16.94 and 43.41% at PPD = 1 day, and to one tenth of these values (1.43–4.07%) at PPD = 3 days (Table 3). For coastal segments *Self* was much higher than for MBHs (Table 3): it was 100% at PPD = 3 h, but still at PPD = 1 day the great majority of the particles released from each of the coastal segments was in a 1 km wide stretch along the same segments. From PPD = 3 days the coastal segments of the Istrian peninsula and the Gulf of Trieste (41–43) showed always much higher *Self* values than the coastal segments located along the Italian coast on the western side. Mean *Self* values were constantly higher in Spring and Summer for both MBHs sites and coastal segments (Table 4).

Suppl. Table 3 shows the top five sites in order of descending total M-

Table 2

Conn, *Hier* and *Red* values for each PPD and season. PPD times are indicated as 3H = 3 h, 1D = 1 day, 3D = 3 days, 1W = 1 week, 2W = 2 weeks, 1M = 32 days.

PPD	Winter	Spring	Summer	Autumn
CONN				
3H	0.07	0.05	0.07	0.07
1D	0.66	0.35	0.37	1
3D	1	1	1	1
1W	1	1	1	1
2W	1	1	1	1
1M	1	1	1	1
HIER				
3H	0.27	0.25	0.40	0.05
1D	0.44	0.04	0.26	0.51
3D	0	0.38	0	0
1W	0	0	0	0
2W	0	0	0	0
1M	0	0	0	0
RED				
3H	0.22	0.20	0.15	0.19
1D	0.15	0.26	0.24	0.12
3D	0.30	0.23	0.22	0.26
1W	0.58	0.41	0.45	0.54
2W	0.78	0.64	0.71	0.73
1M	0.98	0.96	0.97	0.96

Table 3

Mean *Self* values for each site and each PPD as percentage of all particles released at each site. Bold = maximum *Self* for each PPD. Italics = minimum *Self* for each PPD. *Self* values for PPD = 3 h are omitted.

SITE	1D	3D	1W	2W	1M
1	21.11	1.67	1.07	0.72	0.53
2	20.07	2.63	1.68	0.91	0.53
3	21.63	1.85	1.24	0.87	0.49
4	22.74	1.86	1.24	0.59	0.48
5	17.61	1.70	1.73	1.10	0.62
6	21.09	1.76	1.27	0.81	0.54
7	42.96	4.07	2.19	0.99	0.58
8	35.35	3.49	1.58	1.13	0.59
9	37.61	2.70	1.40	0.70	0.21
10	37.55	2.84	1.28	0.64	0.27
11	42.63	2.85	1.12	0.52	0.25
12	36.42	2.60	1.00	0.44	0.25
13	41.25	2.35	1.10	0.51	0.34
14	34.82	2.81	1.61	0.57	0.42
15	29.60	3.08	1.79	0.82	0.40
16	31.87	3.00	1.71	0.83	0.39
17	27.68	2.61	1.26	0.92	0.46
18	23.44	2.25	1.26	0.64	0.35
19	33.57	2.65	1.90	0.93	0.42
20	18.47	1.97	1.14	0.52	0.37
21	16.94	1.43	0.94	0.56	0.35
22	24.93	2.12	0.92	0.64	0.38
23	36.30	2.82	1.26	0.49	0.29
24	24.49	1.98	0.78	0.37	0.23
25	36.35	2.06	0.84	0.46	0.21
26	43.41	3.02	1.27	0.54	0.21
27	38.01	2.66	1.27	0.47	0.24
28	41.53	2.81	1.05	0.49	0.24
29	32.44	3.52	1.64	0.72	0.31
30	37.89	2.76	0.95	0.50	0.20
31	33.70	3.02	1.12	0.57	0.28
32	34.47	3.62	1.85	0.79	0.38
33	42.36	3.15	1.61	0.80	0.45
34	92.85	46.59	17.30	6.58	3.00
35	92.37	61.81	37.20	16.34	4.98
36	95.56	66.08	40.54	19.02	6.99
37	92.82	36.50	10.53	2.41	0.98
38	95.80	47.62	12.94	3.23	1.00
39	98.16	59.58	23.57	7.19	2.13
40	95.77	58.29	36.77	19.83	8.83
41	98.43	86.73	68.02	45.84	26.60
42	98.71	83.02	58.08	33.66	16.92
43	99.61	85.48	66.14	43.77	25.52

reach closeness centrality (MC_i) value and their source and sink centrality components, separately for MBH sites and coastal segments.

The key player selection was made considering only nodes representing biogenic outcrops, not the coastal segments, since the goal was to identify possible gaps/improvements for the network of biogenic outcrops protected within the Natura 2000 sites. A total of 16 different nodes were selected, each selected for 8 or more times in the 24 possible combinations of season and PPD (Table 5 and Fig. 4).

3.2. Correlations and multiple regression models

Geographic distance was positively and significantly correlated with β_w (Suppl. Table 4). Pearson's correlation coefficients between *AbsConn* values and the geographic distance were all negative and significant, but for Autumn at 1 month, and they generally decreased with increasing PPD. The correlations between absolute connectivity values (*AbsConn*) and β_w were always significant and negative, but for PPD = 3 h in all season because of the high self-retention of particles at this PPD. The lowest values of the correlation coefficient were observed for either PPD = 1 week or PPD = 2 weeks.

The regression model of β_w on geographic distance and the 24 *AbsConn* components had showed an $R^2 = 0.24$ (p-value < 0.001). The stepwise selection based on AIC selected geographic distance and 6 significant *AbsConn* as the best predictors in a model with an $R^2 = 0.23$. The highest relative importance was that of the *AbsConn* in Autumn at 1 month and 1 week, followed by geographic distance and by *AbsConn* of Summer at 3 days (Fig. 5, top).

The model with only the 24 *AbsConn* components showed only a slight decrease in the explained variance ($R^2 = 0.22$, p-value < 0.001). The stepwise selection based on the AIC resulted in an optimal parsimonious model with only 8 relevant variables, explaining an $R^2 = 0.21$. Among them, the highest relative importance was that of the *AbsConn* in Autumn at 1 month and 1 week, followed by the *AbsConn* in Winter at 1 month, and by the *AbsConn* in Summer at 3 days (Fig. 5, bottom).

4. Discussion

The knowledge on spreading habits (i.e. period of reproduction, amount of spawning material, pelagic period duration, etc.) is lacking or episodic at best for most marine species (Bradbury et al., 2008; Gaines et al., 2007; Kinlan and Gaines, 2003; Magris et al., 2016; Selkoe and Toonen, 2011). The communities on the biogenic outcrops in the NAS are no exception to this. Nevertheless, based on the lists of species (Falace et al., 2015), and on the available literature, we choose to consider PPDs as short as 3 h to PPDs as long as 1 month. Short PPDs are characteristic of macroalgae, whose spores mainly settle within a couple of days (Bradbury et al., 2008; Santelices, 1990; Selkoe and Toonen,

Table 4

Mean *Self* value over all MBHs and all coastal segments for each season and each PPD as percentage of all particles released at each site. Bold = maximum *Self* for each PPD. Italics = minimum *Self* for each PPD. *Self* values for PPD = 3 h are omitted.

MARINE BIOGENIC HABITATS				
	WINTER	SPRING	SUMMER	AUTUMN
1D	28.44	35.59	32.57	29.49
3D	2.26	3.13	2.62	2.37
1W	<i>1.13</i>	1.67	1.41	1.14
2W	0.59	0.96	0.72	<i>0.45</i>
1M	0.28	0.61	0.44	<i>0.16</i>
COASTAL SEGMENTS				
	WINTER	SPRING	SUMMER	AUTUMN
1D	95.59	96.20	97.14	<i>95.10</i>
3D	60.01	65.41	68.28	58.98
1W	34.51	39.93	40.82	33.18
2W	18.35	22.69	22.01	<i>16.09</i>
1M	8.95	12.27	10.48	<i>7.08</i>

Table 5

Nodes with best group centrality in all seasons and all PPDs. The number in the first column corresponds to the site numbers in Figs. 1 and 4, and in Suppl. Table 1. N = total number of combinations of season and PPD in which the node was selected. PPD durations are indicated as 3H = 3 h, 1D = 1 day, 3D = 3 days, 1W = 1 week, 2W 2 weeks, 1M = 32 days.

SITE	N	3H	1D	3D	1W	2W	1M
27	14	Spring, Summer, Autumn	All seasons	Winter, Autumn	Spring, Summer, Autumn	Summer	Spring
4	13	Spring	Winter, Autumn	Winter, Autumn	Winter, Autumn	Winter, Spring, Autumn	Winter, Spring, Autumn
19	12			Spring, Summer, Autumn	Winter, Summer, Autumn	Winter, Spring	All seasons
2	11	All seasons				Winter, Spring, Autumn	All seasons
5	11		All seasons	All seasons	Winter, Spring, Summer		
22	11			Winter, Autumn	Winter, Summer, Autumn	Winter, Summer, Autumn	Winter, Summer, Autumn
13	10		Spring	All seasons	Spring, Summer	All seasons	All seasons
14	10		Spring	All seasons	All seasons	Autumn	
18	10	Spring, Summer, Autumn	Winter	Spring, Autumn	Winter	Spring, Summer	Spring
16	9	All seasons	Winter, Spring	Winter, Spring, Autumn			
1	8	All seasons			Spring, Summer	Summer	Spring
8	8	Winter, Summer, Autumn			Spring, Summer	Spring	Winter, Autumn
17	8	Winter	Spring, Summer, Autumn	Winter, Summer	Spring		Autumn
24	8	Winter, Spring, Autumn	All seasons				Autumn
29	8	Winter	Winter, Autumn		Autumn	Summer	Winter, Spring, Summer
33	8				Winter	Winter, Summer, Autumn	All seasons

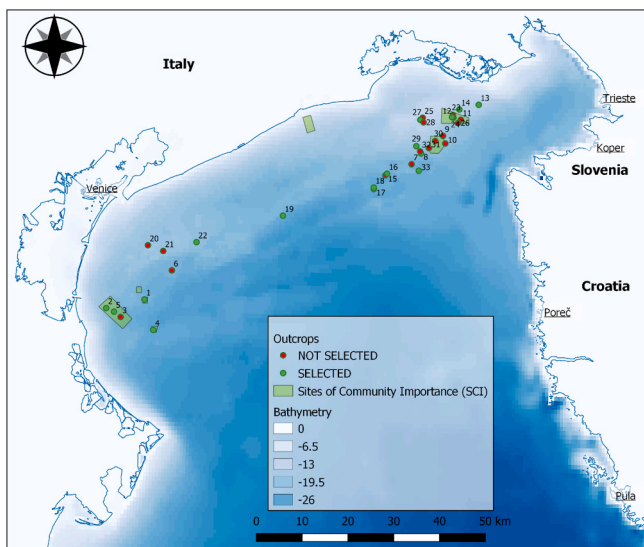


Fig. 4. Best choice of sites to be protected in order to guarantee cross-scale connectivity of the studied system. Green dots show the position of most selected sites in the key players selection procedure for all PPDs and seasons, red dots show the position of the other sites in the study. Green polygons show the position of Natura (2000) Sites of Community Importance (SCIs) areas. Refer to Suppl. Table 1 for the correspondence between numbers and names of the study sites.

2011), tunicates with propagules lasting few hours to less than 1 day (Bradbury et al., 2008; Shanks, 2009), and some sponges (i.e. Demospongiae) whose planktonic phase persist less than 3–4 days (Maldonado and Uriz, 1999; Shanks, 2009). Some other species have much longer PPDs (Bradbury et al., 2008; Dethier et al., 2003; Shanks, 2009; Strathmann, 1987), thus their propagules are able to travel hundreds of kilometres (Bray et al., 2017; Shanks, 2009). In case of adverse conditions many species can also extend their PPD to attain a suitable habitat far from the source (Martin and Nilsson, 2007). Some macroalgae (e.g. green algae such as *Codium* spp., *Caulerpa* spp., brown algae such as *Sphacelaria* spp., and red calcareous algae, such as the bioconstructors of

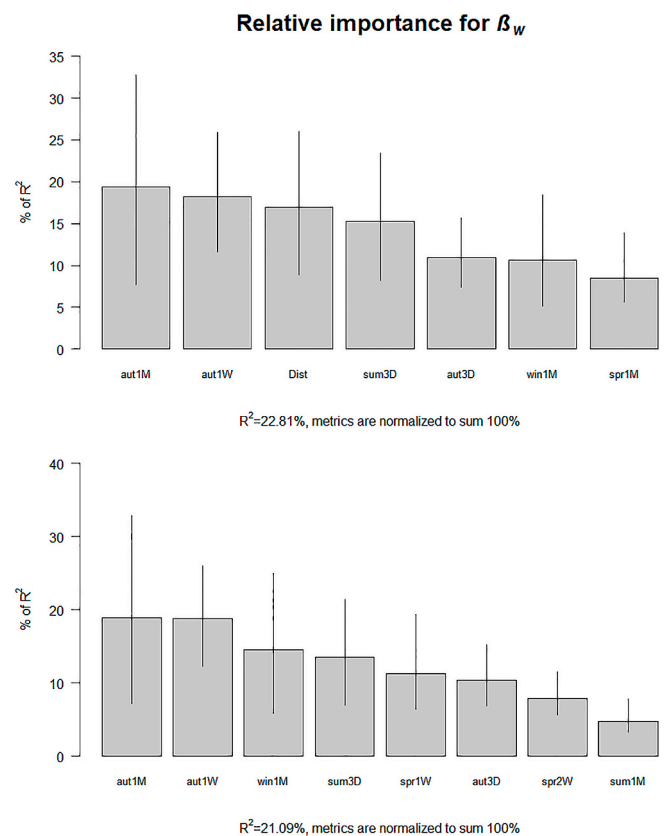


Fig. 5. Relative importance of predictors in the distance + *AbsConn* model (above) and in the *AbsConn* model (below) as calculated using the lmg method. Vertical bars show the 95% bootstrap confidence intervals.

the MBHs in the NAS) and benthic invertebrates (e.g. Porifera, such as *Chondrosia reniformis* and *Tedania anhelans*), can reproduce both sexually and asexually, changing their dispersal capability over different temporal and spatial scales (Di Camillo et al., 2012; Kinlan and Gaines, 2003; Maldonado and Uriz, 1999; van den Hoek, 1987). Finally, due to

large quantities of debris passively transported by the currents in the Adriatic Sea (Carlson et al., 2017), adult specimen travelling from one site to another attached to macro debris may represent another vector of dispersal (Suaria and Aliani, 2014). We believe that our cross-scale approach considers most of the dispersal diversity and does represent a good cross-scale, multi-season proxy for the connectivity of species living on the biogenic outcrops in the NAS. To further improve connectivity simulations more detailed information on specific taxa to be protected would be needed: the individual behaviour of their propagules, the predator-prey interactions, the habitat preferences, the species persistence, and the information on the availability of suitable substratum for settlement (Chan and Walker, 1998; Magris et al., 2016). A further task would be to understand and model the interactions at the arrival site (competition for space, after-settlement mortality before sexual maturity, etc.) (Cowen et al., 2006).

It has been shown that the simulations entirely based on a Lagrangian approach can overestimate the population replenishment from distant sources (Cowen et al., 2000), thus considerations should be made on the dispersal scales of the organisms in order to set up appropriate connectivity simulations (North et al., 2008). The use of a high-resolution 3D hydrodynamic model allowed a more realistic estimate of the connectivity for benthic species that release propagules close to the substrate.

Geographic distance can be considered as a measure of dispersal proximity in particular if there are no physical barriers preventing movements of particles between two sites (Ratray et al., 2016). Furthermore, it may stand for human-mediated (e.g. via boat movements) or secondary dispersal (i.e. dispersal mediated by the drift of mobile adult specimen actively searching new habitats). Its computation is by far easier and faster than running hydrodynamic model simulations, thus we tested the explanatory power of geographic distance compared to that of connectivity with a linear regression model of a measure of beta diversity. Beta diversity, i.e., the variation in species composition among sites in the geographical region of interest (Whittaker, 1972), reflects the outcome of different factors in shaping a community: dispersal, habitat availability, inter- and intraspecific interactions (competition, synergy, mutualism). For the purpose of this study, we used Whittaker's β_w (Koleff et al., 2003), one of the many approaches to measure beta diversity (Anderson et al., 2011; Koleff et al., 2003; Legendre et al., 2005; Legendre and De Cáceres, 2013). Our results (Fig. 5, top) showed that geographic distance is not the main factor determining patterns of beta diversity on the MBHs of the NAS. In fact, the addition of geographic distance to the connectivity components only slightly increases the overall explanatory power of the model of β_w . Passive dispersal by currents, represented by the statistically significant connectivity components retained in the parsimonious model, is significantly related to the observed β_w , and two connectivity components (PPD = 1 month and 1 week in Autumn) showed a bigger relative importance in predicting β_w than distance. These findings are in line with those of Ratray et al. (2016), obtained in the Southern Adriatic Sea and on a bigger scale.

Further, we hypothesised that pairs of outcrops more connected to each other should have more similar assemblages. If there is no correlation between β_w and the connectivity, either the biodiversity observed on the MBHs is not related to passive dispersal by sea currents, or the Lagrangian model used in this study is not appropriate to estimate such dispersal. We defined the mutual dispersal proximity between two sites as the *AbsConn*, i.e. the total exchange of particles between each pair of sites. The significant negative correlations between β_w and *AbsConn* over different seasons and different PPDs, and the relative importance of several connectivity components in the regression model built (Fig. 5, bottom), confirmed that hydrodynamic connectivity is an important factor affecting the macrobenthic assemblages of the studied sites. MBHs in the NAS can thus be considered as a metacommunity at a regional scale resulting from local communities interactions and spatial dynamics (Falace et al., 2015).

Both models of β_w left much of the observed variance not explained. This could be due to a variety of reasons: post-settlement mortality, inter- or intra-specific competition for space, different natural or human-mediated disturbances, past dispersal events history, i.e. rare or sporadic events (sea storms, heat-waves, flow discharges from rivers due to occasional heavy rains) (Bevilacqua et al., 2020), environmental factors affecting propagules survival upon arrival (Allen, 2017; Falace et al., 2015; Fraschetti et al., 2002; Hunt and Scheibling, 1997; Ratray et al., 2016), all factors not accounted for in our models. Nevertheless, a detailed model of beta diversity and the partitioning of its variance (Legendre and Legendre, 2012) among all possible factors was not an objective of this study.

The results of connectivity simulations were analysed by graph analysis methods. The use of graph analysis methods is increasing in ecology (Bray et al., 2017; Bunn et al., 2000; Dale and Fortin, 2010; Magris et al., 2016; Minor and Urban, 2008; Rudnick et al., 2012; Treml et al., 2008; Urban and Keitt, 2001; Urban et al., 2009), and the methods applied in this study proved to be functional tools for exploring patterns of spatial connectivity, summarizing important features of the Northern Adriatic MBHs network. The structural measures applied, *Conn*, *Red* and *Hier*, gave us information on the characteristics of the overall networks considering different seasons and scales (Table 1). For instance, *Conn* revealed that up to 3 days the MBHs and the coastal segments are split in more reciprocally disconnected networks: thus, different meta-community dynamics for each of the sub-networks can be expected. Only in Autumn the full connectedness is achieved already after 1 day. Species with short planktonic phase (e.g. bioconstructors as the non-geniculate calcareous algae) (Bradbury et al., 2008; Maldonado and Uriz, 1999; Santelices, 1990; Selkoe and Toonen, 2011; Shanks, 2009), are more affected and it can be expected that their colonization and population replenishment is confined to self-recruitment or recruitment from sites in close proximity, thus contributing to the observed patchiness of the macrobenthic communities on the Northern Adriatic biogenic outcrops (Curiel et al., 2012; Falace et al., 2015; Ponti et al., 2011).

The *Red* measure has an immediate application in ecology (Table 1): the highest the number of different paths connecting the nodes of a network, the more the network is resilient (Field and Parrott, 2017; Hodgson et al., 2015; Levin and Lubchenco, 2008). In case of accidental loss of a species on one or more MBHs, there would still be enough links between the remaining sites to maintain the propagules dispersal and re-establish the populations. In our case, *Red* was especially high for long PPDs, when all sites were connected and given enough time a particle could find different pathways between each two sites. The lowest values for *Red* were observed for the shortest PPDs, when *Hier* values were high. This indicates the existence of small sub-networks in which due to persistent current directions over short periods of time preferential paths do exist between the nodes. Future genetic studies might corroborate the hypothesis that populations of species with PPDs for which *Red* is high show a remarkable genetic similarity over the study area, in contrast to species with PPDs for which *Red* is low. *Red* is not a desirable property in case of spreading of diseases or of invasive species (Cabanelas-Reboredo et al., 2019; Perry et al., 2017; Roy et al., 2016): in those cases less redundant networks might be more resilient to adverse changes propagating through their nodes.

The *Hier* measure points out the preferential direction of dispersal (Table 1), i.e. the asymmetrical linkage strength (Treml et al., 2008). The sites upstream can act as source for those downstream and may be of higher priority for protection if they host reach and healthy productive populations (Magris et al., 2016). *Hier* values in our study showed that in the Northern Adriatic the general circulation pattern strongly influences the dispersal connectivity on small scales. It is an important measure in particular for species spawning during Bora or Sirocco winds that strongly and almost instantaneously affect the circulation in this area (Kuzmić et al., 2007; Ursella et al., 2007). At longer PPDs there is no hierarchy in the dispersal among MBHs, thus revealing the effects of the variability in the sea currents and in the meteorological conditions in the

NAS: any MBH can act as both, potential source and potential sink. *Hier* is a structural measure, related to the graph as a whole, and does not take into account the weights along the edges connecting the nodes: more specific information on the source/sink potential of each site may be provided by individual centrality measures.

Conn, *Red* and *Hier* are all important measures to assess the preferential path of spreading of alien or harmful species in case of invasion or infection (Cabanellas-Reboredo et al., 2019; Field and Parrott, 2017; Minor and Urban, 2008; Perry et al., 2017; Roy et al., 2016) and of the fate of anthropogenic macro debris or oil spills in case of maritime accidents (Carlson et al., 2017), and should be considered when planning restoration projects across different scales (Fischer et al., 2006; Minor and Urban, 2008).

Self is an indicator of the potential self-recruitment capacity of local populations (Magris et al., 2016; Trembl et al., 2012) and should be taken into account when planning conservation measures (Table 1). It is a metrics that critically depends on the size of the patches considered, since the larger the patches, the more probable is for a particle to stay within the reach of the patch for a longer time. Thus, *Self* values are not comparable between MBHs and coastal segments as defined in this study. From our results and considering that accounting for propagules mortality *Self* would be much probably even lower, it can be safely assumed that after 3 days the self-recruitment capacity of most MBH populations is negligible. Species with PPDs longer than 3 days must rely on replenishment from other sites to guarantee the persistency of their populations. Generally, the MBHs in the north-eastern part of the study area, showed higher *Self* than MBHs in the south-western part. The former are located close to the open end of the Gulf of Trieste and halfway between the two coastlines, in an area characterized by changes and inversions of the general circulation patterns, due to the wind regime and the variable thermohaline structure in the Gulf of Trieste (Cushman-Roisin et al., 2007; Ursella et al., 2007). The latter are close to the Veneto coastline, downstream from the outflow of important rivers (Tagliamento, Livenza, Piave, Sile) considering the general circulation pattern of the NAS, which is cyclonic and parallel to the coast in that area (Artegiani et al., 1997; Ursella et al., 2007). Nevertheless, even in this general framework, sites not far away could show a very different behaviour: this was the case for instance of sites 24 and 28 (Fig. 1) in spring at PPD = 1 day, when a maximum *Self* = 53.16% characterized site 28, and a minimum *Self* = 19.91% characterized site 24. Small scale current variability thus strongly affects the self-recruitment potential in the NAS.

Because of the larger size of the coastal segments compared to the MBHs, as represented in the Lagrangian model, *Self* for coastal segments was much higher than those of MBHs. Starting from PPD = 3 days *Self* for coastal segments showed a marked difference between the eastern and north-eastern coast and the north-western and western coast. High *Self* values in the eastern part of the study area are caused by the absence of important river outflows, the weakness of the currents (due to the deeper bathymetry), and the complexity of the coastal morphology (Artegiani et al., 1997; Ursella et al., 2007). On the contrary, coastal segments in the western part of the study area, and in particular the coastal segment 37, showed remarkably lower *Self* value for high PPDs in all seasons. Thus, the general dynamic of *Self* values for coastal segments mirrors those of the MBHs and confirms that the south-western area can rely less on self-retention of propagules. The seasonal dynamics of *Self* (Table 4) is a result of the weaker basin-scale cyclonic currents and the more intense mesoscale activity, characterized by eddies and flow instabilities, in Spring and Summer compared to Autumn and Winter (Cushman-Roisin et al., 2007; Ursella et al., 2007).

A result of our simulations is that the biotic communities on the coast and on the biogenic outcrops basically follow independent dynamics but for longer PPDs (Fig. 3 and Suppl. Figs. 1-3). This has important consequences on the effective ability of the communities to persist or reconstruct in case of disruptive events. Many biogenic outcrops may be affected by occasional or persistent local pressures, such as bottom

hypoxia (Djakovac et al., 2015; Justić, 1991; Malej and Malačić, 1995), gear cleaning of fishery activities, discharging of sediments dredged in lagoon channels, discharges from urban wastewater pipes (Mozetič et al., 2008; Solis-Weiss et al., 2007), frequent scuba divers or recreational fishermen visits. These factors can cause selective pressure on existing populations, habitat disruption or even mass mortality (Stachowitsch et al., 2007). Recolonization of barren habitats and immigration to an established community are thus affected mainly by the connection with other MBHs, rather than with coastal segments. Such pattern of colonization, modulated by hydrodynamic connectivity among outcrops at different spatial and temporal scales, together with the existence of localized and occasionally recurring impacts, may explain some of the differences observed between communities of neighbouring MBHs (Curiel et al., 2012; Falace et al., 2015; Ponti et al., 2011). An overall decline in species richness along the coasts of the Gulf of Trieste has been observed in the last 20 years, as a result of cumulative effects of human activities and of the frequency of extreme events (Bevilacqua et al., 2020; Falace et al., 2010), while many MBHs still show rich a diversified communities (Falace et al., 2015). The low connectivity existing between the MBHs and the coastal segments, among other factors, may help explain why the MBHs do not act as keystone structures (Bennett et al., 2009) for the coastal populations of the area and do not contribute to their re-establishing.

The individual centrality of nodes in a network elucidate their source or sink potential (Minor and Urban, 2008; Trembl et al., 2008; Urban and Keitt, 2001), i.e. their relevance as stepping-stones (Magris et al., 2016) (Table 1). By identifying the preferred dispersal routes the individual centrality can help define appropriate conservation and management policies to link source and sink sites or to stop the spreading of invasive species or disease vectors (Magris et al., 2016; Perry et al., 2017). Individual centrality can be measured in several ways (Borgatti, 2005; Ortiz-Arroyo and Hussain, 2008), but since each method is suitable for a specific dispersal modality, care should be taken in considering the nature of flow along the network (Borgatti, 2005). From our results (Suppl. Table 3) emerged that the same MBHs showed the highest individual centralities in all seasons and PPDs combinations, and many of them were neighbouring outcrops, actively exchanging particles between them (e.g. sites 12, 23 and 24; sites 25, 27). In some cases, there was a clear distinction in the source/sink behaviour of the sites in different seasons or at different PPDs. These results showed that the persistence of local communities and the possibility of re-population depends critically on the direction and strength of hydrodynamic connectivity in different seasons and over different time-scales. The MBHs of the south-western part of the study area almost never made up to the top five sites based on individual centrality: the density of sites is much smaller in this area and clearly this influences the individual centrality values. Considering this density effect and the fact that basing on individual centrality the same sites are selected for different PPDs and seasons, the individual centrality measure is not the criterion by which to select group of nodes that would guarantee the best connectivity over the whole network: nodes with the highest centrality as a group are not necessarily composed by those with the highest individual centrality (Borgatti, 2006; Ortiz-Arroyo and Hussain, 2008). Specific algorithms, such as the key player selection procedure (Borgatti, 2006; An and Liu, 2016), have to be applied to take into account the edges and nodes to which each node of the subset is connected.

The optimizing of the selection of sites to protect among all possible choices, or the understanding of which node removal would strongly affect a network, has relevant applications for Marine Spatial Planning strategies (Minor and Urban, 2008). Many different algorithms exist for the selection of the best areas or network of areas to protect (Gaines et al., 2010; Green et al., 2014; Jacobi and Jonsson, 2011; Leslie et al., 2003; Williams et al., 2004), but they usually rely only on structural attributes (species richness, habitat type) of biodiversity (Jacobi and Jonsson, 2011; Magris et al., 2016; Pressey et al., 2007). An ecosystem-approach or considerations on relevant ecological processes

are seldom included in the decision making process for conservation (Jacobi and Jonsson, 2011; Minor and Urban, 2008), but their inclusion in conservation strategies, even if challenging, should become systematic (Bennett et al., 2009). The method proposed here, based on graph analysis techniques, is in our opinion particularly suitable for patchy habitats, connected by dispersal (Rudnick et al., 2012), as the MBHs of the NAS. The Northern Adriatic urgently needs priorities for marine spatial planning, since it is subject to several human uses and offshore activities that generate conflicts between economic growth and habitat protection (Bastari et al., 2016). For the establishment of the Natura 2000 sites protecting MBHs in 2015 only habitat types and local species richness were considered, as explicitly requested by the Habitat Directive to EU Member States. To apply species specific and area corrected dispersal metacommunity models (Guizien et al., 2014; Hanski and Ovaskainen, 2000; Urban et al., 2009), firstly a complete mapping of the MBHs in the Northern Adriatic, including their geomorphology (area, shape, height), is needed. The probable existence of additional, not yet localised MBHs may help bridging the distance between coast and biogenic outcrops, as well as among outcrops themselves, changing our understanding of the system dynamics.

With the applied key-players selection procedure 16 MBHs were identified as the most important for guaranteeing the connectivity over the whole network of biogenic outcrops in the present study. Five of these are included in present Natura 2000 areas, where a total of 11 out of the 33 considered MBHs (Fig. 4) are located. Four of the sites already included in the existing protected areas and selected also in our study are located in the south-western part of the NAS, and only one in the north-eastern part where the highest density of sites considered in this study is found. Clearly, in the north-eastern part of the study area, protection efforts should be increased, either by enlarging existing protected areas or by adding other sites to the network of protected areas (e.g. sites 13, 24, 27, 29, 8, 33) (Fig. 4). Furthermore, from our analysis emerged that the protected outcrops in the north-eastern and in the south-western part of the study area are not adequately connected: additional protected areas should be established in-between to enclose additional outcrops (sites 16, 17, 18, 19, 22), and to improve connection in the existing network of SCIs (Fischer et al., 2006). Besides, sites 16, 17, 18 and 22 have been previously identified as having particularly reach and mature communities (Falace et al., 2015), and their protection would guarantee also the protection of biodiversity (Green et al., 2014). Several outcrops are located in closely connected clusters (e.g. sites 15–16, sites 17–18, clusters of sites close to 27 and to 24 respectively) (Fig. 4). By defining new protected areas or enlarging the existing ones, the protection and conservation measures would be extended to multiple neighbouring MBHs, further increasing the conservation and resilience of their communities. Given our lack of knowledge about the real extension of these substrates over the entire NAS, it is difficult to compare our advice to the prescriptions or best practice for the minimal conservation target area (Hanski, 2011; Magris et al., 2016). In any case, the results of the key player selection over a network of habitats as presented here, has to be complemented with the analysis of each site source/sink and self-retention potential, and by measures of structural elements of biodiversity. Even in the absence of a thorough knowledge of species' life histories, such framework would in our opinion considerably improve the conservation decision process in the NAS.

While our results need to be taken cautiously since the possible bias due to the passive nature of the assumed dispersal mechanism, this should not be an excuse to continue in using only information on habitat types and species richness in designing networks of protected areas for the biogenic outcrops in the NAS (Bennett et al., 2009; Magris et al., 2016; Minor and Urban, 2008; Pressey et al., 2007). An integrated approach to the protection of MBHs would benefit also the ecosystem services that are provided by these habitats, especially as far as their role as refuge, spawning and nursery ground for several species of interest for fishery is concerned (Green et al., 2014; Roberts et al., 2001). The establishment of a network of protected areas including outcrops

connected by dispersal, characterized by diverse populations and experiencing different environmental gradients (Fischer et al., 2006; Standish et al., 2014) should be the primary goal. By making use of the knowledge gained in this study, the cross-scale resilience of the whole system can be strengthened (Shanks et al., 2003), and an effective network of protection of the Northern Adriatic MBHs established.

Author contributions

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Declaration of competing interest

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

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Appendix A. Supplementary data

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