



Weak biodiversity connectivity in the European network of no-take marine protected areas

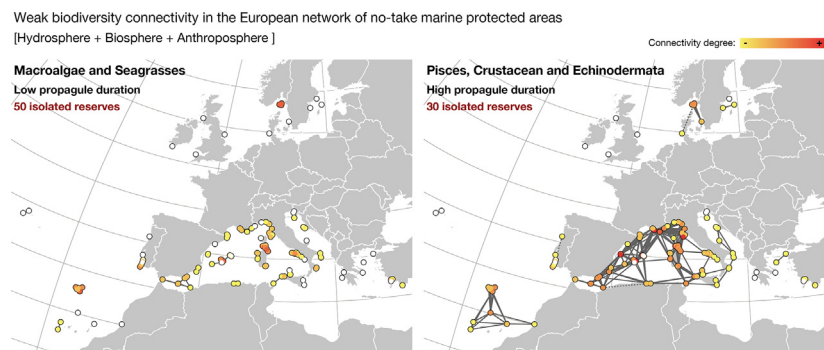
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HIGHLIGHTS

- Networks of Marine Protected Areas (MPAs) protect biodiversity across all ranges.
- The European network of MPAs concentrates almost half of the world's MPAs.
- The European network of MPAs was previously considered to be well-connected.
- Biophysical modelling shows weak connectivity in the European network of MPAs.
- Vulnerable regions require additional reserves to promote connectivity corridors.

GRAPHICAL ABSTRACT



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ABSTRACT

The need for international cooperation in marine resource management and conservation has been reflected in the increasing number of agreements aiming for effective and well-connected networks of Marine Protected Areas (MPAs). However, the extent to which individual MPAs are connected remains mostly unknown. Here, we use a biophysical model tuned with empirical data on species dispersal ecology to predict connectivity of a vast spectrum of biodiversity in the European network of marine reserves (i.e., no-take MPAs). Our results highlight the correlation between empirical propagule duration data and connectivity potential and show weak network connectivity and strong isolation for major ecological groups, resulting from the lack of direct connectivity corridors between reserves over vast regions. The particularly high isolation predicted for ecosystem structuring species (e.g., corals, sponges, macroalgae and seagrass) might potentially undermine biodiversity conservation efforts if local retention is insufficient and unmanaged populations are at risk. Isolation might also be problematic for populations' persistence in the light of climate change and expected species range shifts. Our findings provide novel insights for management directives, highlighting the location of regions requiring additional marine reserves to function as stepping-stone connectivity corridors.

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1. Introduction

Marine Protected Areas (MPAs) are one of the most widespread tools for ocean resource management and conservation, used to reduce, prevent and reverse ongoing marine biodiversity declines (Gaines et al., 2010). MPAs increase resilience of ecosystems, improving capacity to cope with global environmental changes (Micheli et al., 2012), and

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contribute to promote restoration of marine populations by protecting critical habitats and spawning biomass, supplying propagule and adult spillover to adjacent unprotected sites (Caselle et al., 2015). Among multiple features influencing MPA performance, their protection level is particularly important (Zupan et al., 2018), with meta-analysis studies showing that no-take MPAs (i.e., no extractive activities allowed) provide greater benefits (i.e., greater densities of organisms, higher biomass) when compared to partially protected areas (Lester and Halpern, 2008; Sala and Giakoumi, 2017; Sciberras et al., 2013). To enhance protection benefits, networks of individual MPAs operating synergistically are increasingly preferred over single MPAs, as they comprehensively protect integrated ranges of distributions across the spectrum of marine biodiversity (Gaines et al., 2010; Grorud-Colvert et al., 2014).

Most MPAs are implemented and managed locally, at regional or national levels, yet, marine biodiversity is connected beyond political or legal jurisdictions (Ramesh et al., 2019). The need for international co-operation in resource management and conservation is reflected in the uprisings number of agreements aiming for the implementation of effective, global-scale MPA networks. One of the pivotal criteria for effective MPA networks is the establishment and maximization of connectivity links between individual MPAs (Woodley et al., 2012), through dispersal of eggs, larvae, juveniles and/or adults (Magris et al., 2018). This criterion was emphasized in recent studies addressing connectivity and climate change in the scope of marine conservation planning (Magris et al., 2014), and also in the Convention on Biological Diversity target 11 (also known as the Aichi Target 11) that specifically called for the protection of 10% of ecologically representative marine habitats by the year 2020, under effectively managed and well-connected MPAs, a target now figuring 30% by 2030 (Sala et al., 2018).

Similarly to terrestrial ones, networks of MPAs can promote connectivity corridors that enhance population persistence under environmental changes (Fung et al., 2017). For instance, the effect of massive mortality events at the ecosystem level (e.g., heatwaves; Garrabou et al., 2009) can be reversed by replenishing impacted key species from well-connected source locations (Bonin et al., 2016). Still, connectivity along MPA networks changes significantly with dispersal ecology, as planktonic propagule duration (PD), a proxy of dispersal distances, can vary from few hours to hundreds of days (Faurby and Barber, 2012; Shanks et al., 2003; but see Bay et al., 2006; Riginos et al., 2011). Species like corals and macroalgae, generally with reduced PD, are likely to benefit from denser networks of MPAs, while fish and invertebrates, with longer PD, can still be connected over sparse networks (Shanks et al., 2003; Trembl et al., 2012). In this framework, species without planktonic life stages are not under consideration, and one cannot neglect that connectivity is a process occurring in the long-term, benefiting from stepping-stones, i.e., source and sink locations promoting multi-generational connectivity events (Buonomo et al., 2016).

The extent to which MPA networks are connected and able to provide ecological benefits to marine biodiversity remains mostly unknown. Connectivity is often estimated indirectly, through genetic and chemical element analyses (Gillanders, 2005; Hellberg et al., 2002), and commonly for single species or strict ecological groups (Alberto et al., 2010; Assis et al., 2018b; Johansson et al., 2015; Maggs et al., 2008; Pujolar et al., 2013). A recent approach is the use of bio-physical dispersal models, which allow covering broad spatial and temporal scales, as well as multiple taxa, and have recurrently shown a good agreement with empirical connectivity estimates (Assis et al., 2015, 2018a; Buonomo et al., 2016; Cunha et al., 2017; Pujolar et al., 2013). These models simulate virtual oceanographic environments where propagules are advected by trajectories of ocean currents, while incorporating empirical biological components like PD to increase the realism of connectivity processes.

Here we predict the biodiversity connectivity of the European network of no-take MPAs (from now on referred to as marine reserves) by developing a bio-physical model for multiple taxa, and over large temporal and spatial scales (e.g., Assis et al., 2015, 2018b; Buonomo

et al., 2016; Cunha et al., 2017; Lourenço et al., 2017). This was coupled with graph theory to allow considering multigenerational stepping-stone processes in the estimates of reserve connectivity/isolation (e.g., Andrello et al., 2017b; Bunn et al., 2000). Our results highlight that the European reserve network is poorly connected and disaggregated, missing direct connectivity corridors, particularly for key ecological groups with shorter dispersal potential. The general pattern of network disaggregation, with several isolated or poorly accessible reserves, undermines effective connectivity for marine biodiversity, particularly relevant in light of climate change integrated conservation strategies.

2. Methods

Biodiversity connectivity of the European network of marine reserves was predicted with a bio-physical model for a broad span of PD, ranging from 1 to 200 days (i.e., to cover the vast spectrum of marine ecological groups).

2.1. Study region and reserve network

We focus on the European context, as it concentrates ~50% of the global MPAs (Marine Conservation Institute, 2019) and it is based on well-developed marine policies and management (Rilov et al., 2019). This included the broad geographic region where the European network of MPAs is located as well as additional neighboring regions that may be used as stepping-stone connectivity sites, i.e., from the Norwegian Sea to the Canary Islands, including the Azores and Madeira archipelagos, the Atlantic coast of Morocco and the Mediterranean Sea.

The strongest protection level provided by marine reserves was chosen because it represents the highest conservation value for biodiversity, showing greater benefits and yielding higher densities of organisms relative to other types with lower protection degree (Giakoumi et al., 2017; Lester and Halpern, 2008; Sala and Giakoumi, 2017). In fact, marine reserves are less impacted by commercial trawling (Sala and Giakoumi, 2017) and biological invasions seem to be reduced by high levels of protection (Giakoumi and Pey, 2017). Additionally, despite the general lack of information regarding relative enforcement levels, studies conducted on European waters indicate that over 88% of marine reserves present medium to high levels of enforcement (Giakoumi et al., 2017). Together, these general traits, assisting on biodiversity conservation and network performance, allow removing potential confounding effects while estimating biodiversity connectivity (Dureuil et al., 2018; Eigaard et al., 2015; Sala and Giakoumi, 2017).

The Atlas of Marine Protection (Marine Conservation Institute, 2019) was used as a starting point for assembling a spatial database of marine reserves (polygons matching MPA limits). An additional baseline search (Zupan et al., 2018) was conducted at the country level to ensure all existing reserves were included in the study. This information allowed defining the actual location, size and shape of each marine reserve.

2.2. Marine taxa and ecological groups

To examine whether the European reserve network is providing effective connectivity for multiple taxa and ecological groups, a database on empirical marine species PD was compiled from the published literature (e.g., Shanks et al., 2003), covering Cnidaria, Tunicata, Porifera, Macroalgae, Seagrass, Bryozoa, Mollusca, Polychaeta, Pisces, Crustacea and Echinodermata. Specific search criteria were used, following the keywords rule: “propagule duration” or “pelagic duration” or “larval duration” or “planktonic duration”. All resulting references were reviewed and selected whenever they met the criteria of (1) having PD information (2) for the marine groups considered (3) in the North Atlantic Ocean or the Mediterranean Sea. This process resulted in a database comprising 441 species, with PD values ranging from 1 to 198 days

(mean = 29.95 ± 32.47 days; Fig. 1; S2). To facilitate the overall interpretation of connectivity patterns, species were grouped into 4 higher taxon/ecological groups according to their PD (please refer to the results section).

2.3. Connectivity model

Estimates of connectivity between the European marine reserves were inferred with a bio-physical model (Assis et al., 2015, 2018b; Buonomo et al., 2016; Cunha et al., 2017) that uses data from the Hybrid Coordinate Ocean Model (HYCOM), a high-resolution hindcast of ocean velocity fields, forced by wind stress, wind speed, precipitation and heat flux (Chassignet et al., 2007). The bio-physical model integrating HYCOM data resolves key oceanographic processes (Lett et al., 2008) and allows to properly estimate biodiversity connectivity and oceanographic/biogeographic barriers, as previously validated with genetic and demographic data for macroalgae, mussels, limpets, fish, crustaceans, echinoderms and seagrasses (Assis et al., 2015, 2018b; Buonomo et al., 2016; Cunha et al., 2017; Klein et al., 2016; Lourenço et al., 2017; Nicastro et al., 2019; Ntuli et al., 2020). In this line of modeling, propagules (e.g., spores, seeds, rafts, eggs and larvae) are assumed to drift passively with ocean currents, which, although might not precisely reflect small scale movements, allows detecting connectivity patterns at broader scales (Assis et al., 2018b; Shanks et al., 2003), which is the focus of our study.

Individual particles simulating propagules were daily released throughout a complete year from source/sink sites located 1 km apart along the limits of each reserve polygon. A high-resolution polygon was used to define landmasses (Haklay and Weber, 2008). The model determined the geographical position of each particle at every hour of simulation, using bilinear interpolation over the ocean velocity fields to smooth individual trajectories. Particles were allowed to drift on the virtual environment for up to 200 days until they eventually

ended up on land, on a reserve (i.e., a source/sink site), or got lost in the open ocean. Individual trajectories were aggregated to develop pairwise matrices of probability of connectivity between all reserves, by dividing the number of particles released from reserve *i* that reached reserve *j*, by the total number of particles released from reserve *i*. In this process, local retention, as a proxy for population persistence (Burgess et al., 2014), was considered by assessing the particles that were retained in source sites, even when previously advected to open areas. To account for interannual variability, the model performed individual simulations per year, for the 10-year period 2008–2017.

2.4. Network analyses

We used a graph-theory approach to measure and visualize connectivity patterns between reserves (Andreello et al., 2017b; Bunn et al., 2000). This is particularly useful for detecting stepping-stone links throughout the network (Buonomo et al., 2016). A graph is defined by two basic elements, the nodes and the edges connecting nodes (Rozenfeld et al., 2008). The pairwise connectivity matrix averaging the 10-year period of simulations structured the graph nodes (individual reserves) and the strength of edges (probability of connectivity). Network connectivity was inferred at the reserve level by determining (1) isolation, as the reserves with no edge connections, (2) degree centrality, as the number of edge connections per reserve and (3) accessibility, as the minimum number of pathways necessary to bridge one reserve with all alternative reserves (i.e., the Shimmel Index, or the inverse of closeness centrality; Newman, 2010). Nodes with high accessibility index contribute for long connectivity corridors, thus attenuating the compactness and fragmentation of the network (Newman, 2010). At the network level, we determined (4) the maximum number of network components formed by closed edge connections (i.e., number of clusters). Together, these indices aim to infer the relative connectivity/fragmentation degree of the overall European

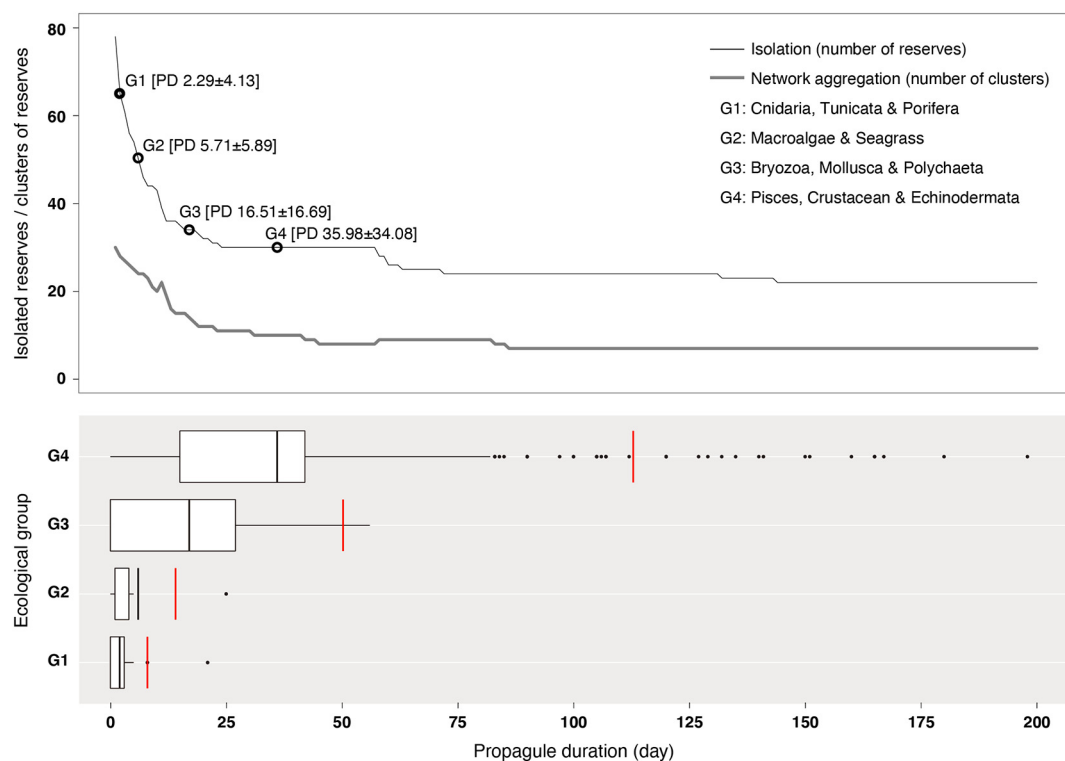


Fig. 1. (top panel) Number of reserve aggregations (i.e., clusters; thick line) and number of isolated reserves (thin line) as a function of propagule duration (PD). Black circles depict the mean PD of each ecological group. (lower panel) Distribution of propagule duration per ecological group. Vertical lines in boxplots depict the mean (black) and the extreme 95th percentile (red) of PD values across species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reserve network, an approach that contrasts with studies more focused in evaluating the actual contribution of individual protected areas in structuring connectivity flow and stepping-stones processes, which generally apply alternative indices like betweenness centrality (Costa et al., 2017).

All graph results were produced individually per PD (i.e., from 1 to 200 day), with particular focus on the average and extreme 95th percentile of the PD of each ecological group (see results section).

3. Results

3.1. European reserve network

The Atlas of Marine Protection contained a total of 7627 European and neighboring MPAs, of which 159 were listed as marine reserves. The database was further enriched with a thorough search, resulting in 172 reserves (2.25% of the total European MPAs; S1). The majority of reserves was concentrated in the Mediterranean Sea (76%), while the remaining were located in the Northeastern Atlantic and the North/Baltic Sea (14% and 10%, respectively). These reserves are mostly distributed along coastlines and do not include deep offshore waters (average depth of reserves: 42.65 m; 95% of reserves depth distribution shallower than 150.39 m depth; S1).

3.2. Marine taxa and ecological groups

The database of propagule duration (PD) per higher taxon/ecological group showed: (G1) Cnidaria, Tunicata and Porifera with mean PD 2.29 ± 4.13 days ($n = 33$; median: 0.8 days), (G2) Macroalgae and Seagrass with mean PD of 5.71 ± 5.89 days ($n = 17$; median: 4 days), (G3) Bryozoa, Mollusca and Polychaeta with mean PD of 16.51 ± 16.69 ($n = 53$; median: 10 days) and (G4) Pisces, Crustacea and Echinodermata with mean PD of 35.98 ± 34.08 days ($n = 338$; median: 25; Fig. 1).

3.3. Network connectivity

The bio-physical model ran daily over a 10-year period, releasing a total of 3,033,150 particles (S3). Analyses showed a positive correlation between increasing PD and reserve network connectivity. Increasing PD from 1 to 200 days was translated into a decrease in the number of isolated reserves (from 78 to 22; Fig. 1; S4) and their distinct aggregations (structured clusters from 30 to 7; Fig. 1; S4), and an increase in the average degree centrality (connections per reserve from 1.17 to 11.73; Fig. 2; S4) and network accessibility (Shimbel index from 1.03 to 1.64; S4).

Potential connectivity, i.e., the probability of propagule transport from source to sink locations, was associated to the PD periods of the

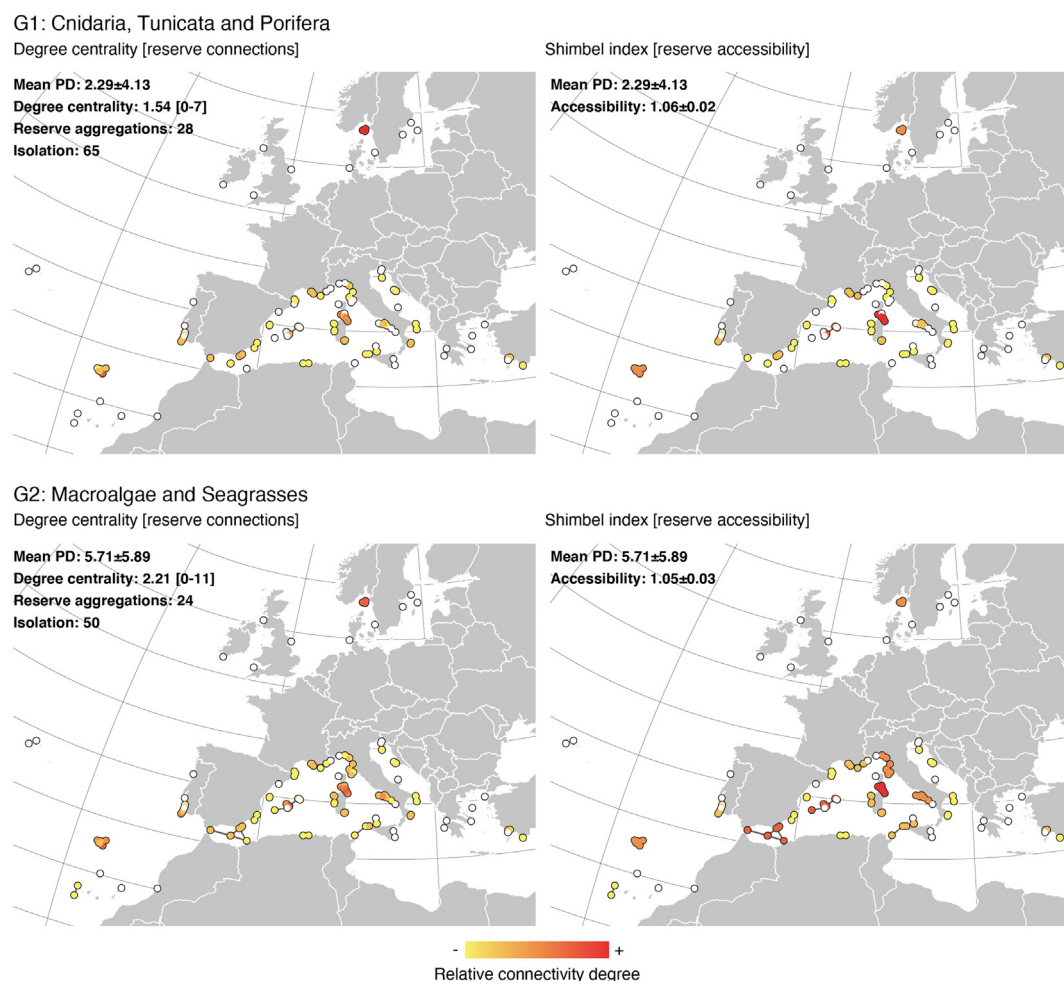


Fig. 2. Potential biodiversity connectivity of the European network of marine reserves estimated with the average propagule duration (PD) of ecosystem structuring species of (G1) Cnidaria, Tunicata and Porifera, and (G2) Macroalgae and Seagrass. Reserves are depicted as circles, with color gradients reflecting the relative degree centrality and Shimbel index (white for isolated reserves with no connectivity links). Lines between reserves represent potential connectivity links and not actual dispersal trajectories. The total number of isolated reserves and reserve aggregations (i.e., clusters) are shown per group.

contrasting ecological groups. As anticipated, groups with shorter PDs were more subject to network fragmentation, higher reserve isolation, as well as lower degree centrality and reserve accessibility. The lowest PD of G1 (Cnidaria, Tunicata and Porifera) and G2 (Macroalgae and Seagrass) structured fragmented networks with 24–28 distinct aggregations (i.e., clusters), 50–65 isolated reserves (up to 38% of all) and 1.54–2.21 average connections per reserve (Fig. 2). Higher degree centrality and reserve accessibility of G1 and G2 were mostly located in the Alboran Sea, Madeira (Portugal), Sardinia and Corsica (Italy) islands and Skagerrak (Fig. 2). The higher PD of G3 (Bryozoa, Mollusca and Polychaeta) and G4 (Pisces, Crustacea and Echinodermata) allowed reserves to cluster across broader oceanographic regions. In particular, connectivity is likely between reserves within Madeira, Canary Islands and Morocco and also across the Western Mediterranean Sea (G4 further links to the Adriatic Sea; Fig. 3). Connectivity patterns of both G3 and G4 structured 10–14 distinct reserve aggregations with 30–34 isolated reserves (up to 20% of all) and 3.36–4.65 average connections per reserve (Fig. 3). Degree centrality and reserve accessibility of G3 and G4 were predominantly higher in the Western Mediterranean Sea, from Gibraltar to southern Italy.

The PD were not homogeneous within ecological groups and extreme values were observed. The extreme 95th percentile of PD resulted in increasing connectivity potential across ecological groups (Fig. 4). In particular, the Western Mediterranean connectivity increased for high dispersive species, with G4 being able to cross the Gibraltar straight and link the Western Mediterranean and the NE Atlantic reserves

(Fig. 4). Yet, potential connectivity still isolates those reserves located in the broad sections of the Baltic, Kattegat and Celtic Seas, and in most Eastern Mediterranean Sea (Fig. 4), leaving 24 to 44 isolated reserves (up to 25%), depending on the ecological group considered (S4).

4. Discussion

The European network of MPAs, which concentrates half of the existing protected sites of the world, is safeguarded by well-developed marine policies and was previously considered to be one of the most well connected networks in the world (Andrello et al., 2017a; Marine Conservation Institute, 2019; Rilov et al., 2019). Yet, our study focusing on marine reserves, areas with the highest conservation value, predicted poor network connectivity for propagule stages, with the formation of distinct clusters over broad oceanographic regions and strong isolation/inaccessibility of marine reserves. This information is key for marine biodiversity conservation and management (Balbar and Metaxas, 2019; Magris et al., 2014), but it was unknown until now. Vast connectivity gaps are pointed out, created by the lack of stepping-stone reserves and connectivity corridors. These refer to regions where species are unlikely to interconnect marine reserves, regardless of their inherent propagule duration, ecological group, habitat or climatic niche requirements defining putative ranges (e.g., rocky reef vs. sandy bottoms or cold-temperate vs. warm-temperate). The overall pattern of isolation potentially limits marine conservation and might trigger cascading effects to entire ecosystems. Although areas

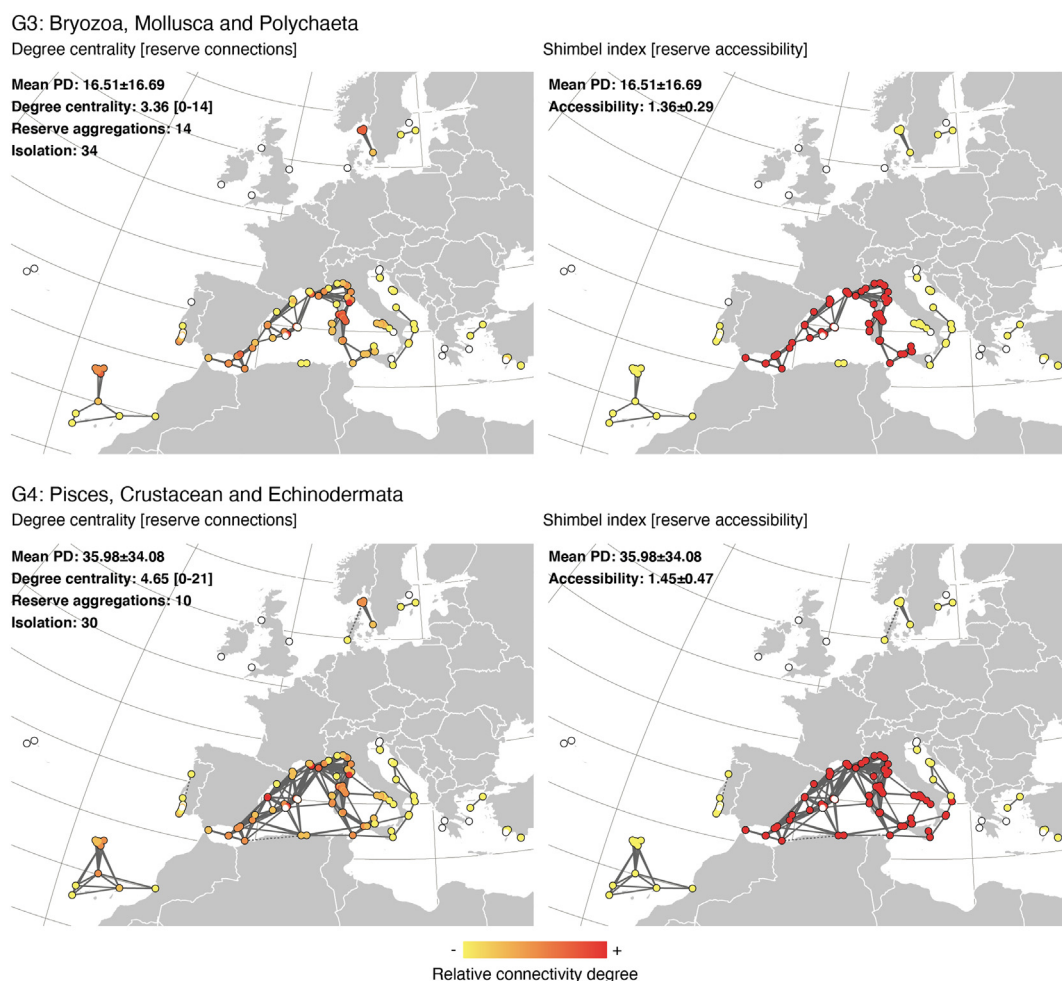


Fig. 3. Potential biodiversity connectivity of the European network of marine reserves estimated with the average propagule duration (PD) of species of (G3) Bryozoa, Mollusca and Polychaeta, and (G4) Pisces, Crustacea and Echinodermata. Reserves are depicted as circles, with color gradients reflecting the relative degree centrality and Shimbel index (white for isolated reserves with no connectivity links). Lines between reserves represent potential connectivity links and not actual dispersal trajectories. The total number of isolated reserves and reserve aggregations (i.e., clusters) are shown per group.

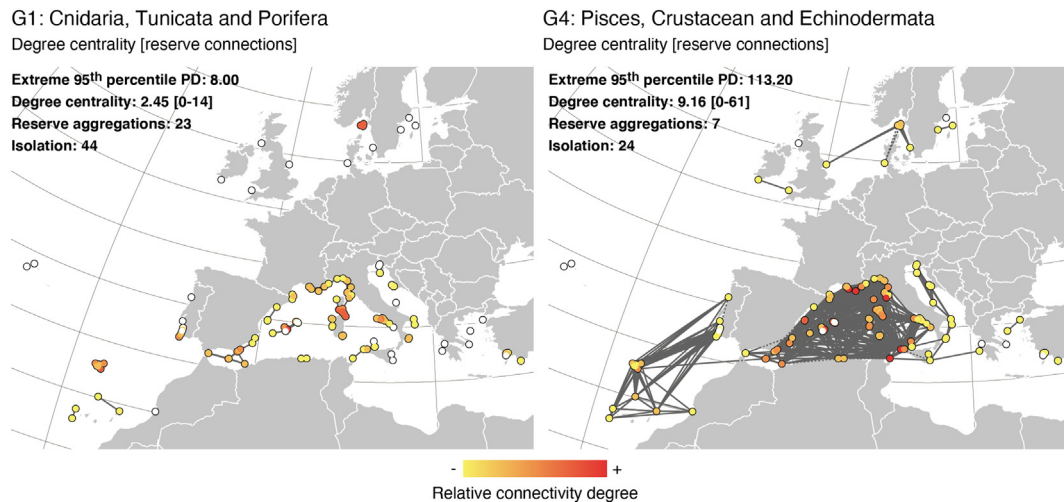


Fig. 4. Potential biodiversity connectivity of the European network of marine reserves estimated with the extreme 95th percentile propagule duration (PD) of contrasting groups of (G1) Cnidaria, Tunicata, Porifera and Echinodermata and (G4) Pisces, Crustacea and Echinodermata. Reserves are depicted as circles, with color gradients reflecting the relative degree centrality (white for isolated reserves with no connectivity links). Lines between reserves represent potential connectivity links and not actual dispersal trajectories. The total number of isolated reserves and reserve aggregations (i.e., clusters) are shown per group.

outside the modelled marine reserves may also promote population connectivity, eventually acting as additional stepping-stones, their efficiency as such is highly dependent on the pressures they endure and therefore might only be relevant for a few species. Sporadic events might also act as connectivity sources (Siegel et al., 2008), yet, given their stochastic nature (Assis et al., 2018b), they probably have a minor role on ensuring functional connectivity on the long-term and therefore are unlikely to sustain network resilience.

The modelling approach implemented, based on high-resolution ocean circulation data, provided unique information about the potential connectivity of the European marine reserve network. The novelty of using a broad range of PD characterizing marine biodiversity provided a global overview of MPA gaps across major groups. It also allowed verifying how marine reserve connectivity correlated positively with species' dispersal potential, as previously shown for particular ecological groups (e.g., Selkoe and Toonen, 2011), and how initial connections formed between adjacent reserves increased in number and expanded in distance with larger PD (Faurby and Barber, 2012; Krueck et al., 2017; Shanks et al., 2003). Ecosystem structuring species of corals, tunicates, sponges, macroalgae and seagrasses, characterized by short PD, showed reduced direct connectivity, restricted to distinct reserve aggregations (i.e., clusters) with poor accessibility, and high probability of isolation, while species with longer PD, such as fish and crustaceans, potentially connect more reserves across the network and over greater distances. Such relationship between dispersal potential and spatial population structure is in line with previous studies (Shanks et al., 2003; Treml et al., 2012) and corroborates broadscale genetic patterns across ecological groups. Corals (Pilczynska et al., 2019), macroalgae (Assis et al., 2018b; Nicastro et al., 2019), seagrasses (Alberto et al., 2008) and sponges (Duran et al., 2004) exhibit well-defined genetic structure over shorter distances, when compared to longer PD species such as fish (Klein et al., 2016; Viret et al., 2018), echinoderms (Maltagliati et al., 2010) and crustaceans (Heras et al., 2019), which tend to be more genetically homogeneous across large water masses, although not completely panmictic (Schunter et al., 2011). Contrasting to the main approach and dispersal ecology considered in our study, are species that can actively swim against the prevalent trajectories of ocean currents (e.g., performing large migrations or ontogenetic shifts in habitat use; Abecasis et al., 2009; Almpandidou et al., 2019; Briscoe et al., 2016). These have the potential to further reduce population differentiation across large water masses (e.g., hundreds of kilometers; Bowen and Karl, 2007; Silva et al., 2014).

The estimates of biodiversity connectivity considered key ecological traits (i.e., propagule duration) and oceanographic patterns/processes (e.g., eddies and fronts; Manel et al., 2019), as well as the actual number, relative shape, size and spatial arrangement of marine reserves. Additional drivers like active larval behavior and competency, settlement success, marine debris and translocations, as well as habitat type and quality may also play an important role (Anadón et al., 2013; Faillettaz et al., 2018; Manel et al., 2019). For instance, the simulations estimated connectivity whenever a propagule reached a marine reserve, and not after the full time of dedicated planktonic phases (potentially important for groups like fish; Leis, 2015). Not taking into account such drivers might have biased the estimates, however, their incorporation into biophysical modelling is still challenging, particularly when considering that some may strongly vary between species, individuals of the same species or even the same development stage (e.g., behavior and competency; Endo et al., 2019). While only a European-wide assessment across marine genetic biodiversity could bring to light the potential limitations, previous multi-disciplinary studies coupling our biophysical model with independent empirical genetic and demographic information for species with contrasting propagule duration systematically provided evidence on the central role of propagule duration, oceanographic transport and barriers shaping population connectivity/isolation, and keeping or diluting the intra-specific signatures of past demographic changes (Assis et al., 2018b; Buonomo et al., 2016; Lourenço et al., 2017; Nicastro et al., 2019; Ntuli et al., 2020; Pascual et al., 2017).

The predicted low connectivity patterns highlight the need for additional reserves for proper network dispersal across European oceanographic regions. Connectivity links were found between Madeira Archipelago, Canary Islands and Morocco and across the Western Mediterranean Sea, but broad regions remained isolated, regardless of the ecological group or PD considered. In particular, striking isolation over vast regions in the Eastern Mediterranean (e.g., Aegean Sea) and the NE Atlantic, resulting from the absence of marine reserves over thousands of kilometers, from Turkey to Tunisia (~4000 km) and Denmark to Portugal (~3000 km), may undermine biodiversity conservation efforts if local retention is insufficient and unmanaged populations are at risk. Importantly, key structuring species (e.g., corals, tunicates, sponges, macroalgae and seagrass) with limited dispersal potential (i.e., reduced propagule duration; PD), may be subjected to high network fragmentation. Even for the few species with longer PD (95th percentile of extreme PD; Fig. 4), or in a hypothetical extreme PD of

200 days (S4), the absence/limited number of stepping-stone reserves, as well as their uneven distribution in space, isolates the Baltic, Kattegat and Celtic Seas, and most of the Eastern Mediterranean Sea, leaving up to 25% of reserves with no connectivity links. New reserves implemented in between such regions would create key corridors improving connectivity of the network as a whole. Additionally, some of the connectivity gaps identified in our study (e.g., in the Mediterranean), in line with the priority conservation areas proposed by Magris et al. (2018) to maximize connectivity and the effectiveness of conservation plans, have also been recognized as relevant areas for conservation due to their ecological importance (Abdulla et al., 2009; Giakoumi et al., 2011). In this perspective, our results might assist the development of more coherent reserve networks through transboundary conservation (i.e., different states aiming to protect common resources; Katsanevakis et al., 2020), help tuning optimal network configurations maximizing connectivity (Daigle et al., 2020; Magris et al., 2018) and integrate systematic conservation planning procedures for reserve site selection, an approach rarely considered at the European level (Fraschetti et al., 2018; Katsanevakis et al., 2020) but acknowledged by international agreements (Balbar and Metaxas, 2019). Notwithstanding the relevance of connectivity towards the effectiveness of MPA networks, other aspects such as representativity and replication of conservation features, socio-economic costs, and ecological and biological importance also need to be considered during design processes (Gaines et al., 2010; Roberts et al., 2001; Timonet and Abecasis, 2020; Woodley et al., 2012).

The highest reserve density and degree of potential connectivity, both in terms of reserve connections and accessibility, was observed in the Western Mediterranean Sea. This may be encouraging for fisheries resource management, as many commercially targeted species with longer PDs may be highly connected across the region. One such case is the Dusky Grouper *Epinephelus marginatus*, for which an additional biophysical model mimicked our results (Andrelo et al., 2013), or the seabream *Diplodus vulgaris* (Di Franco et al., 2015). Despite higher connectivity potential, the conservation of these species relies on the maintenance of essential habitats structured by Cnidaria, Porifera, Macroalgae and Seagrasses (Lefcheck et al., 2019; Vassallo et al., 2013), the least connected ecological groups that highly benefit from strict protection. Such groups might thus be prioritized as targets for marine connectivity and adequate management (inside and outside reserves), given their role for other ecological groups, that despite having higher dispersal capacity could still become limited by habitat availability. Additionally, even the areas with denser reserve coverage, higher linkage and accessibility (e.g., Balearic and Ligurian Seas), show isolation within clustered networks (please refer to S4 for a list of reserves that remained isolated during the whole simulation). Our results allow linking this pattern to reserve size (but not shape; S4), with the largest reserves more likely to be connected regardless of the species PD. Larger reserves release more propagules relatively to smaller ones, while at the same time, increase the likelihood of receiving propagules from other reserves. Additional studies focusing on fisheries management further stress the relevance of reserve size for population density and network design (Belharet et al., 2020; Claudet et al., 2008).

The generally low connectivity between reserves predicted across ecological groups may have negative consequences for the demography and evolutionary potential of local populations. While local retention may allow the persistence of local populations (Burgess et al., 2014), the lack of gene flow from other populations can produce inbreeding depression, increasing risk of population extinction and reduce the adaptive potential to changing environments (Charlesworth and Willis, 2009). This has much relevance in the scope of ongoing and anticipated global changes (Reusch et al., 2005). Mass mortality events and distributional range shifts, already observed along the lower latitudes of the Atlantic Ocean and in the Mediterranean Sea (Garrahou et al., 2019; Horta e Costa et al., 2014), are expected to increase for all

ecological groups (Assis et al., 2018a; Cheung et al., 2009; García Molinos et al., 2016). The lack of reserve connectivity between the East-Western Mediterranean or along the NE Atlantic may impair proper conservation of the least warm-adapted species and their gene pools. At the same time, increasing ocean temperatures may accelerate metabolic responses, shortening PD and therefore connectivity potential (Rossi et al., 2019). Such a reduction may downgrade the already poor network connectivity inferred for all taxa.

Guaranteeing a functional network through the implementation of new reserves seems vital for ecosystem resilience. Similarly to terrestrial migration corridors (Ward et al., 2020), stepping-stone reserves guarantee safe passages for species and genes shifting ranges within physiological tolerance limits (i.e., available habitat conditions). Against these expectations, we show gaps in reserve coverage in regions of high biodiversity (e.g., eastern Mediterranean Sea; Tortonese, 1985) or coastal corridors for poleward shifts (e.g., Iberian Peninsula and English Channel; Burrows et al., 2011). The latter regions are also recognized as glacial refugia harboring richer and ancient gene pools for numerous marine species (Maggs et al., 2008), making their conservation even more crucial. Assuming a scenario where marine reserves are the only hubs serving as source and sink areas, the estimated gaps in connectivity suggest that marine populations are likely subject to higher risk of local extinctions owing to lower probability of being rescued by neighboring populations. This hypothesis might not be completely realistic, as additional areas with different levels of protection may further support and connect populations. Also, despite the effort of assembling the most comprehensive database of marine reserves at the European level, some might not have been included in the analyses, as protection levels can be unreported (Mazaris et al., 2018). Thus, our results provide a what-if scenario where properly documented reserves allow narrowing biodiversity connectivity estimates to the actual topology of the European network of marine reserves. As we reach the deadline of the international Aichi target, this evaluation is timely, providing key insights for the creation of future management directives by drawing attention to potentially isolated reserves and regions with poor network coverage, where additional protection should be implemented. These regions may further interact with the negative impacts of global climate change (Hannah et al., 2002), as well as local stressors like water pollution (Abessa et al., 2018) and marine invasions (Giakoumi and Pey, 2017). While global change mitigation seems strictly dependent on the broad compliance of the Paris Agreement (UN Framework Convention on Climate Change), limiting greenhouse gas emissions and setting warming below 1.5 °C on average, local stressors might be controlled with managers acting a priori, since it is virtually impossible to prevent their negative impacts once established (Abessa et al., 2018).

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CRedit authorship contribution statement

J. Assis, E. Fragkopoulou and D. Abecasis conceived the study. J. Assis and M. Gandra conducted the analyses. J. Assis and E. Fragkopoulou drafted the manuscript with support of D. Abecasis, E. A. Serrão and B. Horta e Costa.

Data availability

Shapefiles for geographic information systems with high-resolution digitized polygons of MPA available in Figshare: <https://doi.org/10.6084/m9.figshare.12173610>.

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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