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RESEARCH ARTICLE

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# Ecological coherence of Marine Protected Areas: New tools applied to the Baltic Sea network

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## Abstract

1. Spatial connectivity is an essential process to consider in the design and assessment of Marine Protected Areas (MPAs). To help maintain and restore marine populations and communities MPAs should form ecologically coherent networks. How to estimate and implement connectivity in MPA design remains a challenge.
2. Here a new theoretical framework is presented based on biophysical modelling of organism dispersal, combined with a suite of tools to assess different aspects of connectivity that can be integrated in MPA design. As a demonstration, these tools are applied to an MPA network in the Baltic Sea (HELCOM MPA).
3. The tools are based on the connectivity matrix, which summarizes dispersal probabilities, averaged over many years, between all considered areas in the geographic target area. The biophysical model used to estimate connectivity included important biological traits that affect dispersal patterns where different trait combinations and habitat preferences will produce specific connectivity matrices representing different species.
4. Modelled connectivity matrices were used to assess local retention within individual MPAs, which offers indications about the adequacy of size when MPAs are considered in isolation. The connectivity matrix also provides information about source areas to individual MPAs, e.g. sources of larvae or pressures such as contaminants. How well several MPAs act as a network was assessed within a framework of eigenvalue perturbation theory (EPT). With EPT, the optimal MPA network with respect to connectivity can be identified. In addition, EPT can suggest optimal extensions of existing MPA networks to enhance connectivity. Finally, dispersal barriers can be identified based on the connectivity matrix, which may suggest boundaries for management units.
5. The assessment of connectivity for the HELCOM MPA are discussed in terms of possible improvements, but the tools presented here could be applied to any region.

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**KEYWORDS**
Baltic Sea, biophysical model, connectivity, dispersal, ecological coherence, local retention, marine protected area, network

## 1 | INTRODUCTION

Industrial fisheries, coastal land development, climate change, energy production, shipping infrastructure, contaminants, and nutrients combine to cause dramatic changes and losses in habitats and biodiversity, altering the functioning of marine ecosystems and provisions of ecosystem services (Lubchenco, Palumbi, Gaines, & Andelman, 2003; Worm et al., 2006). About 40% of the ocean is today considered strongly impacted by multiple stressors (Halpern et al., 2008; Halpern et al., 2015). The establishment of Marine Protected Areas (MPAs) is now considered an important instrument for ocean and coastal protection (Fenberg et al., 2012; Lester & Halpern, 2008; Roberts & Polunin, 1991), mainly to mitigate effects of extractive and local disturbance on harvested stocks, general biodiversity, and ecosystem services (Worm et al., 2006). MPAs may also enhance resilience to large-scale pressures, e.g. climate change (Micheli et al., 2012).

MPAs were originally a fishery management tool to protect stocks from overfishing and to promote recruitment (Roberts & Polunin, 1991). More recently more MPAs have been established to contribute to ecosystem-based management goals, e.g. maintaining biodiversity and food web structure (Pikitch et al., 2004). Increasingly, MPAs are viewed as networks of managed areas with the goal to achieve 'ecologically coherent' MPAs where a network provides protection of a range of features, e.g. habitats, species, and ecological processes, more efficiently than unconnected, individual MPAs (HELCOM, 2016). Examples of MPA systems in European waters that potentially act as networks are the marine part of Natura 2000 (Council of the European Communities, 1992), and often overlapping with regional sea MPAs within OSPAR (OSPAR, 2011) and HELCOM (HELCOM, 2016), with the goal to protect threatened species and habitats.

Most MPAs and networks of MPAs have been designed with little concern about dispersal and population connectivity (Carr et al., 2017), although there are a few encouraging exceptions (e.g. California Department of Fish and Game, 2009; Moksnes, Jonsson, & Nilsson Jacobi, 2015). To date, an often implicit assumption is that populations within selected MPAs will persist through local recruitment, survival, and reproduction (reviewed by Botsford et al., 2009). The validity of this assumption critically depends on the relative scales of MPA size and dispersal distance of target species (Corell, Moksnes, Engqvist, Döös, & Jonsson, 2012; Moffitt, White, & Botsford, 2011; Palumbi, 2004). A crucial question is whether individual MPAs or networks of MPAs are biologically functional, i.e. whether they have the capacity to sustainably protect target populations. Clearly, life-history traits that influence dispersal distance and connectivity should determine the efficiency of MPAs depending on their size and location (Almany et al., 2009; Moffitt et al., 2011; Shanks, Grantham, & Carr, 2003). About 70% of marine macro-invertebrates (Thorson, 1950) and many demersal fish and macro-algae disperse during early life as small planktonic spores or larvae. Most sedentary marine macro-organisms therefore form partially open local populations (e.g. Caley et al., 1996; Pinsky, Palumbi, Andréfouët, & Purkis, 2012), which has fundamental consequences for the design of MPAs. The sustainability of protected populations requires either: (1) that MPAs are large enough to allow significant self-seeding for persistence; or (2) that MPAs are inter-connected through dispersal or connected to unprotected populations leading to network persistence (Hastings & Botsford, 2006). Thus, in contrast to terrestrial nature reserves, where the location of particular habitats and the presence of habitat corridors are important design criteria (Perault & Lomolino, 2000), marine reserves should additionally consider larval dispersal in relation to MPA size and how well MPAs form an ecologically coherent network (Almany et al., 2009; Gaines, Gaylord, & Largier, 2003).

Many studies have proposed design criteria for MPAs with a focus on MPA size and connectivity in relation to propagule dispersal or adult migration. Adequate MPA size has been estimated from dispersal distance based on mark–recapture (Jones, Milicich, Emslie, & Lunow, 1999), pelagic larval duration (Shanks et al., 2003), genetic divergence (Underwood, Smith, van Oppen, & Gilmour, 2009), genetic assignment (Berument et al., 2012), and through biophysical models that include critical larval traits such as larval drift depth (Corell et al., 2012; Ross, Nimmo-Smith, & Howell, 2017). The assessment of sufficient network connectivity is more challenging and ranges from genetic assignments (Planes, Jones, & Thorrold, 2009), habitat distribution (Sundblad, Bergström, & Sandström, 2011; Virtanen, Viitasalo, Lappalainen, & Moilanen, 2018), and biophysical models combined with metapopulation dynamics (Jonsson, Nilsson Jacobi, & Moksnes, 2016) or network theory (e.g. Treml, Halpin, Urban, & Pratson, 2008). In a series of papers, we have developed a theoretical framework to facilitate the implementation of connectivity in MPA design by using biophysical modelling of larval dispersal that includes species-specific larval traits, and applying eigenvalue perturbation theory (EPT) to select optimally connected MPA networks (Jonsson et al., 2016; Moksnes, Jonsson, Nilsson Jacobi, & Vikström, 2014; Nilsson Jacobi & Jonsson, 2011). The advantage of the EPT technique is that optimal connectivity is directly linked to maximizing the global metapopulation growth rate given some level of protection offered by MPAs (Nilsson Jacobi & Jonsson, 2011; Ovaskainen & Hanski, 2003).

We here demonstrate a series of tools based on biophysical modelling of larval dispersal and the EPT framework to assess important aspects of the ecological coherence of existing and planned extensions of MPA networks. A workflow using these tools is applied to the existing HELCOM MPA network in the Baltic Sea (HELCOM, 2016) to assess local retention as a function of dispersal traits and MPA size, connectivity, and the optimal topology of a *de novo* MPA network, the optimal extension of an existing MPA network, and identification of dispersal barriers.

## 2 | METHODS

### 2.1 | The HELCOM MPA network

The Baltic Sea, bordering nine countries, is one of the most environmentally impacted seas in the world with habitat loss, eutrophication, pollution, and over-fishing (Diaz & Rosenberg, 2008; Reusch et al., 2018). Recent invasions by non-native species also expose the native biota to new biotic challenges (Ojaveer & Kotta, 2015).

**FIGURE 1** Map showing the Baltic Sea (HELCOM definition) with major sub-basins and the HELCOM MPAs as blue polygons. The inset shows an overview of the Baltic Sea within Europe

The low functional diversity of the Baltic marine ecosystem may limit resilience capacity to environmental deterioration with potential loss of essential ecosystem services (Bonsdorff, 2006; Meier et al., 2012; Österblom et al., 2007). The Baltic Sea is also one of the most managed seas (Paasche et al., 2015; Reusch et al., 2018) within several EU directives and the Baltic Marine Environment Protection Commission – Helsinki Commission (HELCOM), which form international governing bodies with the aim to protect the marine environment of the Baltic Sea (e.g. Council of the European Communities, 2008; HELCOM, 2009). The implementation of MPAs is regarded as a key policy measure and a management tool to address multiple threats and to achieve the vision of obtaining a healthy Baltic Sea environment with diverse biological components.

We applied the MPA assessment tools presented here to the HELCOM MPA network (HELCOM, 2016; Figure 1), which is part of the Europe Regional Sea Conventions (EEA, 2015). There is a 94% overlap of the HELCOM MPA (EEA, 2015) with the EU Natura 2000 system (Council of the European Communities, 1992) when considering only those Natura 2000 areas that include descriptions of marine features (EEA, 2015). The HELCOM MPA network has been extended in steps since 1992 and this study considers the configuration of 163 MPAs. Some HELCOM MPAs are located outside the domain of the NEMO-Nordic circulation model used for the biophysical model (e.g. some Danish lagoons) and 12 MPAs were thus excluded from all analyses. About 70% of the HELCOM MPAs have a management plan (www.helcom.fi) specifying any restrictions of use or permit requirements. All included HELCOM MPAs are given in Table S1 (see Supplementary Information).

## 2.2 | Biophysical modelling

The dispersal of organisms (eggs, spores, larvae, or rafting algae) was modelled with a Lagrangian particle-tracking model driven offline with flow fields from an ocean circulation model. The stored ocean transport data were produced with the NEMO-Nordic model (Hordoir et al., 2019), which is a regional configuration of the NEMO ocean engine (Madec, 2016) covering the Baltic Sea and the eastern North Sea. The model has a horizontal spatial resolution of 3.7 km, and 84 vertical levels with depth intervals of 3 m at the surface and 23 m for the deepest layers. At the boundaries, tidal harmonics define the sea surface height and velocities, and Levitus climatology defines temperature and salinity (Levitus & Boyer, 1994). The model has a free surface, and the atmospheric forcing is based on the re-analysis data set ERA40 (Uppala et al., 2005). Climatological data from a number of different databases for the Baltic Sea and the North Sea provided freshwater runoff. Validation of the NEMO-Nordic model has showed that the model is able to correctly represent the sea surface height, both tidally induced and wind driven (Hordoir et al., 2019).

Trajectories of dispersing propagules were simulated with the Lagrangian trajectory model TRACMASS (De Vries & Döös, 2001), which calculates transport of released, virtual particles using stored ocean flow field data produced by the NEMO-Nordic model. The velocity, temperature, and salinity were updated with a regular interval for all grid boxes in the model domain, in this study every 3 hours, and the trajectory calculations were done with a 15-min time step. Particles simulating propagules were released from all model grid cells (3.7 × 3.7 km$^2$) within the HELCOM area that had a mean depth of ≤100 m, although the connectivity for habitats representing depths of ≤10 m and ≤30 m were extracted to illustrate organisms with different adult habitats (Table 1). To simulate organisms with different larval traits (i.e. spawning season, duration of the pelagic dispersal stage, and dispersal depth), virtual particles were released at different times of the year, were allowed to drift for a predetermined period, and their vertical position was locked at predetermined depths. If the actual depth of the ocean basin was less than the determined depth the trajectories resided as deep as possible.

In the present study, simulations of dispersal were carried out for three contrasting combinations of dispersal traits and habitat (depth) restrictions (Table 1), which represent some of the key species in the Baltic Sea. The selected combinations of traits were based on extensive empirical data collected on plankton surveys in the HELCOM area (Corell et al., 2012; Moksnes et al., 2014). The shallow-water organisms with propagules drifting in the surface water for a 5-day period may represent an upper limit for the bladder-wrack (*Fucus vesiculosus*) and meso-grazing isopods (*Idotea* spp.), although this is still not well-known (Jonsson et al., 2018). The second group of deeper living organisms with a 30-day dispersal period and larvae drifting down to 24 m depth may represent blue mussel (*Mytilus edulis* and *M. trossslus*) and Baltic clam (*Limecola balthica*), and deeper living organisms with long larval periods (30–60 days) may represent, e.g. the flounder (*Platichthys flesus*). However, the dispersal traits of many other Baltic organisms can be approximately represented by these three trait

**TABLE 1** Dispersal simulation of the four dispersal trait combinations and habitat restrictions

| Strategy | Spawning time | PLD (days) | Drift depth | Habitat (depth) | Example genera |
|---|---|---|---|---|---|
| 1 | April–September | 5 | 0–2 m | 0–10 m | *Fucus*, *Idotea* |
| 2 | 25% June, 75% July | 50% 20,50% 30 | 25% 0–2 m,50% 10–12 m,25% 24–26 m | 0–30 m | *Mytilus*, *Limecola* |
| 3 | | 50% 30,50% 60 | 25% 0–2 m,75% 10–12 m | 0–30 m | *Platichthys* |

[a] PLD, pelagic larval duration.

combinations (Moksnes et al., 2014). A large number of sources for propagules covering the Baltic Sea was used where the only habitat restriction was determined by depth intervals (Table 1), since habitat information is generally lacking on the scale of the Baltic Sea. From each grid cell, either grid cells attached to the land contour or grid cells with a mean depth satisfying the depth limitations, 49 particles were released (a 7 × 7 array) each spawning month and for the assumed drift depths of each dispersal strategy (Table 1). This was repeated for 8 years (1995–2002), which cover a wide range of the North Atlantic Oscillation index (Hurrell & Deser, 2009), which is known to correlate well with the variability in circulation pattern in the Baltic Sea. In total, 93 million particles were released.

Potential connectivity (Watson et al., 2010) between model grid cells, satisfying the habitat restriction for each dispersal strategy (based on depth intervals, Table 1), was calculated as the proportion of trajectories starting in grid cell *i* and ending in grid cell *j* and then summarized in connectivity matrices for each dispersal strategy. These normalized connectivity matrices were then used as input for calculations of mean dispersal distance, local retention, EPT network analyses, and identification of dispersal barriers (see below).

## 2.3 | Calculation of dispersal distance

The great-circle dispersal distance for propagules spawned within individual MPAs was calculated from the grid cells in the model that overlapped with HELCOM MPAs with a tolerance of 2 km. The weighted mean dispersal distance ($\bar{l}$) from each source grid cell *i* was estimated as:

$$\bar{l}_i = \sum_{i}^{N} C_{ij} \cdot D_{ij}$$

where $C_{ij}$ is a vector with connectivity from grid cell *i* to all other *N* grid cells, and $D_{ij}$ is a vector of geographic distance from grid cell *i* to all other grid cells. If an MPA overlapped with several model grid cells, an overall mean was calculated for each MPA.

From the connectivity matrix, it is also possible to identify the sources and sinks to and from a particular area, e.g. an MPA. Sources may include a tracer of some pressure (e.g. contaminants or suspended matter) or biological propagules. The areas acting as sources to a particular MPA are found as the column sums for the rows representing locations where the MPA overlaps with the model grid cells. Areas acting as sinks from a particular MPA are instead the row sums for the columns representing locations where the MPA overlaps with the model grid cells. As an example, source areas were identified for four selected MPAs (HELCOM MPA No. 105, 115, 142, and 309) based on a connectivity matrix summarizing dispersal in the depth intervals 0–2 m and 10–12 m for 10 days of dispersal. This analysis assumes that an abiotic tracer or biological propagules maintain their position within these depth intervals during transport. The strength of source areas was colour coded in relative units.

## 2.4 | Calculation of local retention

Local retention is here defined as the proportion of propagules spawned and released within an individual MPA that also settled within the same MPA. The elements in the connectivity matrix overlapping with each MPA were extracted and summed to obtain the estimated mean local retention ($\bar{r}$) for each MPA as:

$$\bar{r} = \sum_{1}^{n \cdot n} \mathrm{C}_{\mathrm{MPA,MPA}} \cdot 1/n$$

where $C_{\mathrm{MPA,\ MPA}}$ is a matrix with connectivity for the *n* grid cells located within the MPA.

## 2.5 | Identification of optimal *de novo* MPA network

EPT was applied to the connectivity matrices to select optimal MPA networks (for details see Nilsson Jacobi & Jonsson, 2011). Briefly, this method finds an optimal subset of MPAs, for a defined total area, that maximizes the growth rate of the global metapopulation in the target area when at low abundance, as is typical for threatened populations. Mathematically, protection of a site is modelled by an increase in connectivity between the protected site *i* and all other sites (including the protected site itself) with a proportion $\delta$ (here set to 20% but EPT results are not very sensitive to the choice of $\delta$). The increase in connectivity by $\delta$ can be biologically interpreted in two ways. Either connectivity is increased *from* the protected site *i* to other sites which can be interpreted as a higher production of larvae. This enhanced larval production rate from protected sites is the result of more fecund adults or a higher adult density. The second possibility is that connectivity increases *to* the protected site *i*, which can be interpreted as a higher post-larval survival in the protected site. These two cases lead to identical results when applying EPT for site selection of an optimal MPA network (Nilsson Jacobi & Jonsson, 2011). The EPT framework has also been extended to find optimal consensus MPA networks when the aim is to protect multiple species, which differ in their dispersal strategies (Jonsson et al., 2016). Identification of optimal networks for multiple species requires additional user information about the minimal acceptable protection for each species (see settings in Jonsson et al., 2016).

In addition to dispersal and connectivity, optimal MPA network will also depend on local reproduction and mortality rates, e.g. caused by habitat quality and presence of competitors and predators (Baskett, Micheli, & Levin, 2007). In the present study of the HELCOM MPA network, there is no information about MPA-specific habitat quality or mortality, and it was assumed that there were no spatial differences. However, if spatial information about habitat quality for example is available, this can be easily included in the EPT framework (Berglund, Nilsson Jacobi, & Jonsson, 2012).

## 2.6 | Identification of optimal extension of existing MPA network

It is possible to extend the EPT framework to also include the more realistic scenario where an existing MPA network is extended with new areas, which are selected based on connectivity to maximize the growth rate of the global metapopulation. To achieve this the connectivity was first adjusted for the sites in the existing network by a factor $\delta$ in the same way as described above. In this way, consistency was ensured by assuming that the old and the new network have the same effect. The EPT algorithm is then used to create a priority list based on the adjusted connectivity matrix. The sites that are already protected in the pre-existing network is excluded from the priority list. The remaining list is the final priority list that describes an optimal extension of the existing MPA network.

## 2.7 | Identification of connectivity barriers

A previously developed clustering method was employed to identify partial dispersal barriers from the constructed connectivity matrices (Nilsson Jacobi, André, Döös, & Jonsson, 2012). This theoretical framework finds clusters as a signature of partially isolated subpopulations. Identification of subpopulations is formulated as a minimization problem with a tuneable penalty term that makes it possible to generate population subdivisions with varying degree of dispersal restrictions. Areas that have an internal connectivity above the dispersal restriction are colour coded, and the transitions of colours thus indicate partial dispersal barriers.

# 3 | RESULTS

## 3.1 | Dispersal distance

Dispersal distance and direction calculated from particle trajectories simulated by the biophysical model showed several patterns with increasing mean dispersal distance offshore and along the Baltic Sea–North Sea gradient (Figure 2). There was also a generally increasing dispersal distance across the three dispersal trait combinations correlated to pelagic larval duration, but also influenced by drift depth. Dispersal direction largely followed the cyclonic circulation in each main basin (Figure S1).

Figure 3 shows an example of how connectivity from a biophysical model may be used to identify sources to protected areas, here four selected HELCOM MPAs, for a depth interval of 10–12 m (for a depth interval 0–2 m see Figure S2).

## 3.2 | Local retention in HELCOM MPA

Local persistence of populations within an MPA may critically depend on local retention of propagules. Local retention varied greatly among individual MPAs for all three dispersal trait combinations (Figure 4) although there was a weak overall correlation with MPA area. MPAs smaller than 10 km$^2$ generally showed low local retention. Only 22 (15%) of the MPAs showed local retention >40%. There was also large variation geographically in local retention with a tendency that offshore MPAs had lower local retention than coastal MPAs (Figure 5, Figure S3). As expected, much of the variation in local retention was

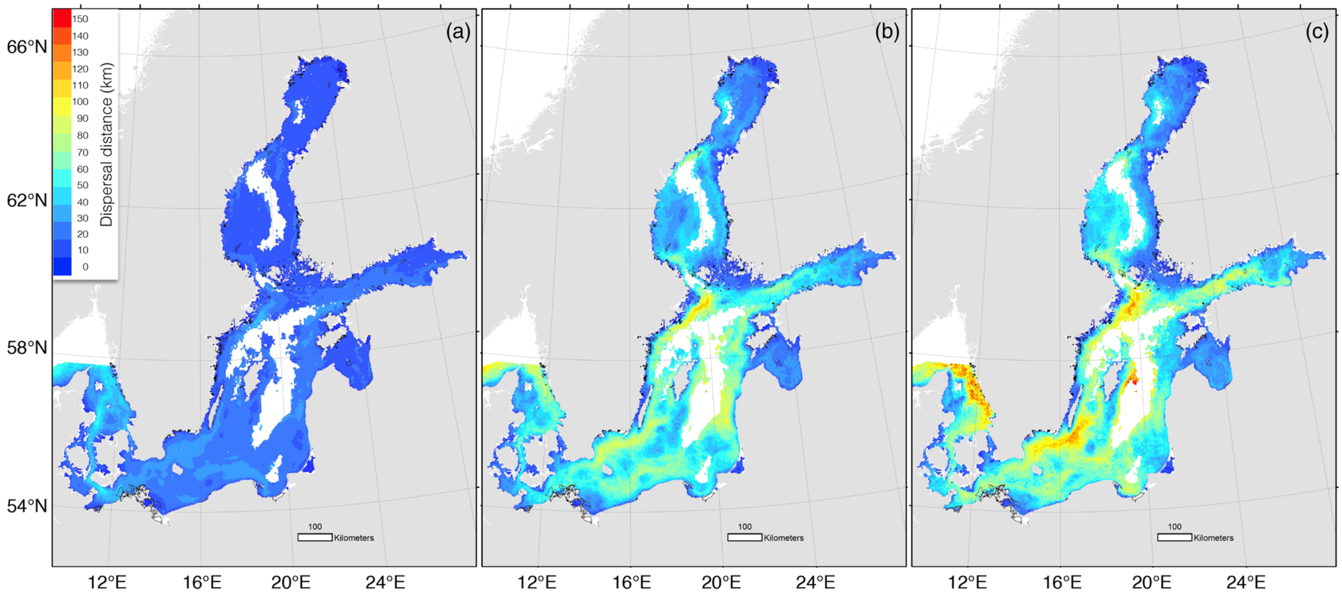

**FIGURE 2** Modelled area-specific average dispersal distance for the three generic dispersal trait combinations in Table 1. (a) Spawning time: 16% for each month between April and September, pelagic larval duration (PLD): 5 days, drift depth: 100% at 0–2 m. (b) Spawning time: 25% June and 75% July, PLD: 30 days, drift depth: 25% at 0–2 m, 50% at 10–12 m, 25% at 24–26 m. (c) Spawning time: 50% April and 50% May, PLD: 50% 30 days and 50% 60 days, drift depth: 25% 0–2 m, 75% 10–12 m

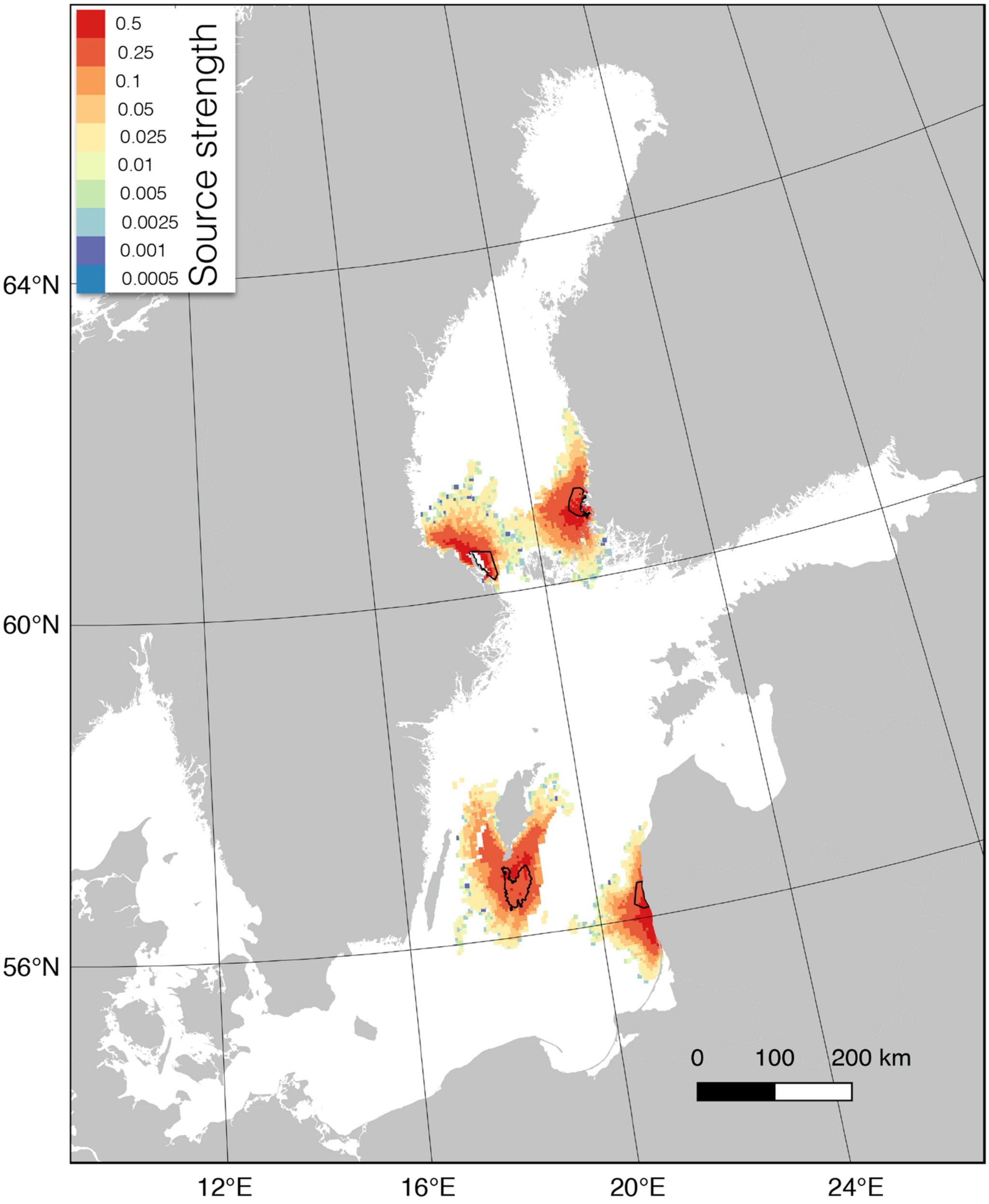

**FIGURE 3** Visualization of source areas surrounding four selected HELCOM Marine Protected Areas (MPAs; ID 105, 115, 142, and 309) where connectivity is modelled as water transport during 10 days in the surface layer (0–2 m). The colour code indicates the relative source strength on a geometric scale

explained by the ratio between MPA size and local mean dispersal distance (Figure 6), with a ratio above 2–4 indicating high local retention (>0.4). Note that the relatively low retention for trait combination 1, despite a short PLD of 5 days, depends on the more limited distribution of suitable habitat (0–10 m depth).

### 3.3 | Analysis of MPA connectivity – identification of the optimal *de novo* MPA network

The EPT framework was used to identify the optimally connected MPA network using model grid cells as building blocks. This can be done for an arbitrary target of MPA total area and Figure 7 shows an example for 8,200 km$^2$, indicating the most important areas for network connectivity. This network will maximize the growth rate of the global metapopulation that the MPAs aim to protect, assuming in this case the selected total MPA area, a defined habitat (here depths between 0 and 30 m), and that survival and reproductive rates are homogeneous in the domain. The geographic distribution of the predicted optimal network suggests that the present HELCOM MPA network is reasonably well connected since the two networks overlap in most areas. However, there are apparent gaps in the present HELCOM MPAs along the Swedish east coast and Finnish west coast, especially in the Finnish Archipelago Sea.

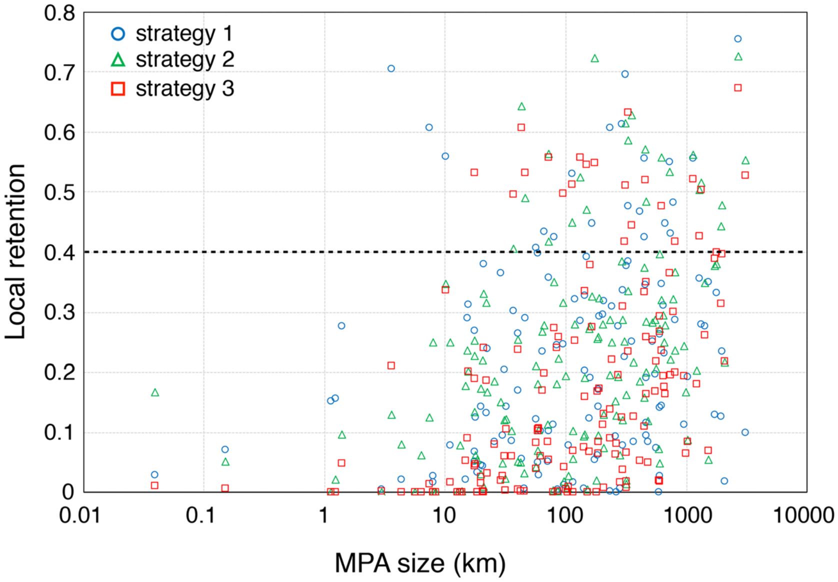

**FIGURE 4** Local retention for the three dispersal trait combinations (Table 1) as a function of the area of individual HELCOM Marine Protected Areas (MPAs). The dashed line indicates the local retention (40%), which has been suggested as necessary for persistence of local populations

### 3.4 | Analysis of MPA connectivity – identification of optimal extension of existing MPA network

A more realistic scenario than *de novo* design of MPA networks, as presented above, is the extension of an existing network to improve connectivity and enhance functionality. A new algorithm is presented here, based on EPT, to identify the optimal extension to an existing MPA network, again with respect to maximizing the global metapopulation growth rate. Figure 8 shows an example of an optimal extension of 1,400 km$^2$ (ca. 3%) for the HELCOM MPA network. Not surprisingly, given the result of the *de novo* network in Figure 7, many new MPAs are suggested along the Swedish and the Finnish coast of the Baltic Proper and the Gulf of Bothnia to enhance network connectivity and metapopulation growth in the existing MPA network.

### 3.5 | Identification of connectivity barriers

Patterns of dispersal and habitat distribution will determine connectivity between areas and regions. Using a recently developed barrier analysis based on the connectivity matrix (Nilsson Jacobi, André, Döös, & Jonsson, 2012) well-connected regions and barriers are identified for dispersal trait combinations 1 and 2 (Table 1) and with habitat restrictions based on depth (Figure 9). For each trait combination the geographic distribution of barriers is shown for two user-defined thresholds of allowable dispersal across barriers. The cases with few barriers (Figures 9A, C) represent processes that are sensitive to very low dispersal rates across barriers (here 0.1–0.3%), e.g. typical of genetic differentiation when selection is weak. When the allowed dispersal across barriers is increased, the domain is divided into more regions separated by weaker barriers (Figures 9B, D), which is characteristic of demographic independence, e.g. indicating separate fish stocks.

## 4 | DISCUSSION

MPAs are today recognized as a major management strategy to help conserve marine features such as species, ecosystem processes, habitats, and cultural heritage. About 6% of the marine area within the European Union is currently assigned as MPAs (EEA, 2015) and 3.5% world-wide (Lubchenco & Grorud-Colvert, 2015). The siting of MPAs has mainly considered the representation of biodiversity patterns and habitat types (Pressey, Cabeza, Watts, Cowling, & Wilson, 2007), within socio-economic constraints (Agardy, 2000). However, the performance of MPAs is generally poorly known, e.g. if they contribute to long-term persistence of biological features. Important functional aspects of MPAs are their size, or adequacy, and connectivity, e.g. through larval dispersal among MPAs and with surrounding unprotected areas (Gaines et al., 2003; Shanks et al., 2003). There is a growing ambition to design MPAs as ecologically coherent networks (Fenberg et al., 2012) where groups of MPAs deliver more benefits than unconnected, individual MPAs (HELCOM, 2016). Much of the success of MPAs also relies on management actions, type of restrictions and efficient enforcement, which is often insufficiently implemented (Edgar et al., 2014).

The set of tools described here to assess ecological coherence and applied to the HELCOM MPA network is based on biophysical modelling of larval dispersal and is mainly relevant for organisms with sedentary adults where connectivity largely depends on physical water transport of larvae or other propagules. However, it is important to emphasize that the net larval dispersal is also influenced by biological traits, mainly spawning time, pelagic larval duration, and behaviours affecting depth position (e.g. Corell et al., 2012; Paris, Chérubin, & Cowen, 2007), and also possible settling behaviour. The combination of oceanographic circulation models with individual-based particle tracking models including relevant biological traits is considered a valuable approach to estimate connectivity in the

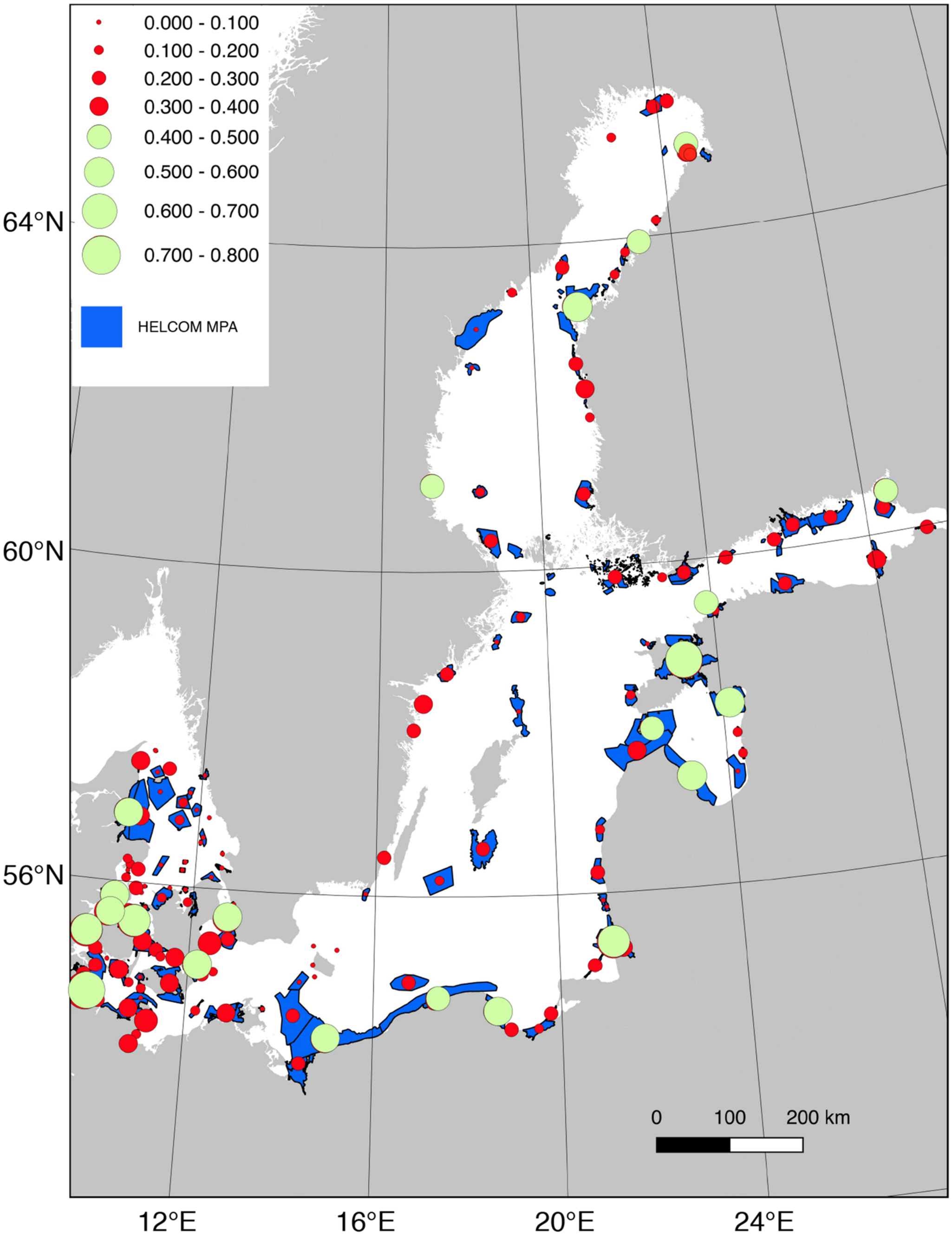

**FIGURE 5** Geographic differences in local retention for individual HELCOM Marine Protected Areas (MPAs; blue polygons). Green circles indicate where local retention of trait combination 2 (Table 1) is <40%, which has been suggested as necessary for persistence of local populations

seascape (Cowen & Sponaugle, 2009; Hufnagl et al., 2017; Paris, Chérubin, & Cowen, 2007). Several studies also show that connectivity estimated from biophysical models can explain significant variation in population structure revealed by genetic markers (Buonomo et al., 2017; Jahnke et al., 2018; Selkoe et al., 2010). Biophysical models are now also increasingly used to aid in MPA design (Engie & Klinger, 2007; Moksnes et al., 2014, 2015; Pujolar et al., 2013) and spatial management (Dubois et al., 2016). Some marine organisms, mainly fish and mammals, disperse as juveniles or adults through active migration, often between suitable biotope patches or sometimes shifting biotopes during development. The connectivity for actively migrating species is commonly estimated through marking-recapture, or classic landscape/seascape analyses of habitat distribution (e.g. Sundblad et al., 2011) although this requires adequate habitat mapping, which is still in its infancy in the marine environment. Note, that because the interface between the biophysical model and the tools described here is the connectivity matrix, these tools can be applied to any connectivity matrix estimated with other methods, e.g. tagging (Moland, Olsen, Andvord, Knutsen, & Stenseth, 2011) or genetic assignment (Manel, Gaggiotti, & Waples, 2005).

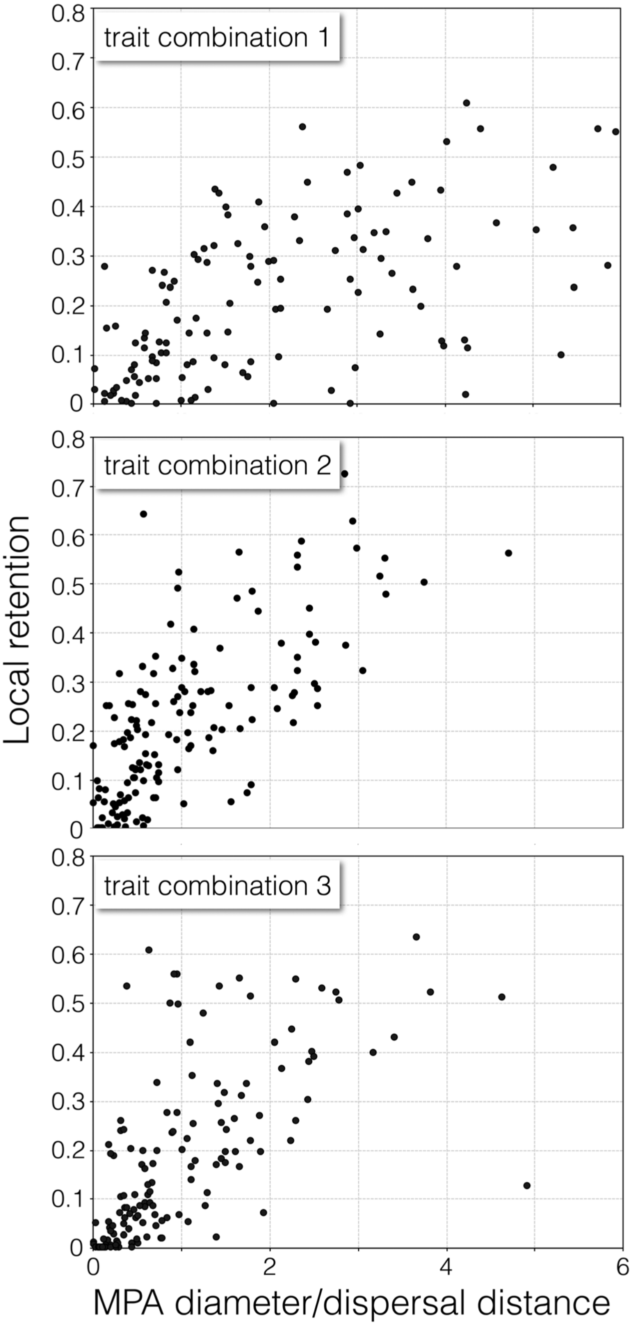

**FIGURE 6** Expected local retention as a function of the ratio between Marine Protected Area (MPA) size and mean local dispersal distance for three dispersal trait combinations (Table 1). The MPA size was calculated as the diameter of a circle with the same area as the MPA polygon

The overall target in spatial management is often to assign a total area of protected environment and there is a trade-off between number of areas and their size. This problem led to the classic debate whether the best design of protected areas is 'single large or several small (SLOSS)' (Soulé & Simberloff, 1986). There are several complex aspects of the SLOSS trade-off, e.g. species–area relationships and local extinction. However, this trade-off is largely resolved by adopting a metapopulation perspective with population dynamics among protected as well as unprotected areas including explicit consideration of dispersal probability and extinction risk (e.g. Hanski, 1999). In the marine environment where many organisms disperse with larvae for potentially long distances, local populations defined by habitat patchiness may be largely open (Caley et al., 1996; Pinsky et al., 2012). Thus, a metapopulation perspective is arguably a suitable framework although classic local extinctions may be rare (Kritzer & Sale, 2004).

In a metapopulation perspective MPAs can be considered as local populations enjoying some effect of protection (e.g. higher reproduction or survival rates) existing together with unprotected local populations. At extreme ends of a continuum, unprotected areas may perform as well as the MPAs or, as in a scorched-earth scenario, unprotected areas are devoid of protected features (Allison, Lubchenco, & Carr, 1998). The most common situation is that also unprotected areas harbour features that MPAs intend to protect. In that case one important question in MPA design is which areas to select to ensure persistence of the whole metapopulation, also including unprotected areas. This is the main view taken in the development of tools presented here. However, there may be cases closer to the scorched-earth scenario, e.g. when protecting very rare and threatened species where the MPAs represent the only viable habitat and the full metapopulation network.

A simple application of the connectivity matrix is to identify source areas for individual MPAs (Figure 3). Sources may here be areas that supply an MPA with recruits, but also areas causing environmental impact on protected areas, e.g. non-indigenous species, discharge of contaminants or deposition of dredge spoils. The main message is that also activities in a considerable area outside an MPA may affect the conditions within the boundaries of MPAs. However, the shape of this external area will depend on the local circulation pattern. The source area will be a function of residence time in the water, the depth of dispersal and seasonal variation in circulation. In a similar way it is easy to extract from the connectivity matrix the probability that fertilized eggs, larvae or other propagules released within an MPA also settle within that MPA. High local retention may lead to a largely self-recruited, closed local population, which may persist without immigration from other protected or unprotected local populations. Especially, for a scorched-earth scenario such self-persistence of individual MPAs may be important. However, sufficient local retention may require very large MPAs, especially for species with planktonic larvae (Figures 4, 5). The MPA size resulting in high local retention is approximately of the same order as the local mean dispersal distance (Figure 6). This is not surprising and has been suggested as a simple rule of thumb (Shanks et al., 2003), although local dispersal distance is rarely known and may need to be estimated, e.g. with a biophysical model. The level of local retention leading to sufficient recruitment to replace the local population is poorly known and is likely to differ between species and areas. Here we used 40% local retention to indicate a threshold for persistence of a local population (Corell et al., 2012; Kaplan, Botsford, O'Farrell, Gaines, & Jorgensen, 2009). The

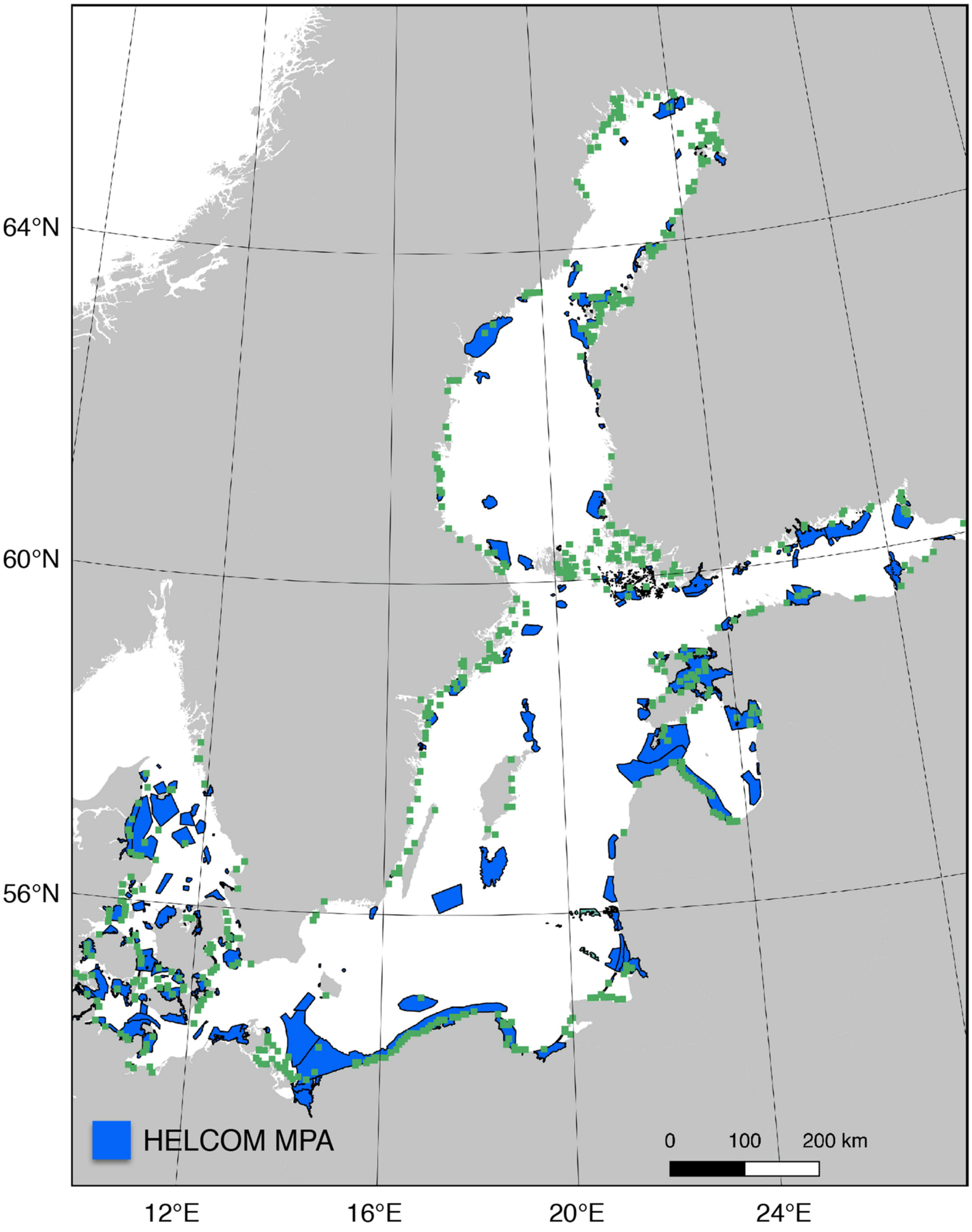

**FIGURE 7** Identification of an optimal multi-species consensus network (green squares based on the eigenvalue perturbation theory framework and the three dispersal trait combinations in Table 1. Also shown is the present HELCOM Marine Protected Area (MPA) network as blue polygons

application of this tool to assess the adequacy of individual HELCOM MPAs shows that only 15% of MPAs are sufficiently large to ensure 40% local retention of the three combinations of dispersal traits suggesting a minimum size of about twice the dispersal distance, which depends on the geographic location (Figure 2). The low local retention is a combined effect of dispersal distance and the distribution of suitable habitat (here only defined as depth intervals). There are also large geographic differences in adequacy with few sufficiently large MPAs along the Swedish coast. The result suggesting that most HELCOM MPAs are too small for local retention is consistent with earlier model assessments of MPA size in the Baltic Sea and North Sea area (Corell et al., 2012; Jonsson et al., 2016), indicating the importance of a functional network of MPAs.

In tune with the metapopulation perspective, MPAs are increasingly viewed as networks of interacting local populations (Botsford et al., 2009). Exchange of larvae between local populations including MPAs may result in persistence of the whole metapopulation despite many populations, or MPAs, being too small for sufficient local recruitment (Hastings & Botsford, 2006). Although connectivity has for some time been highlighted as important to provide such network persistence, a clear framework has been lacking about how to include information on connectivity in the design of MPAs.

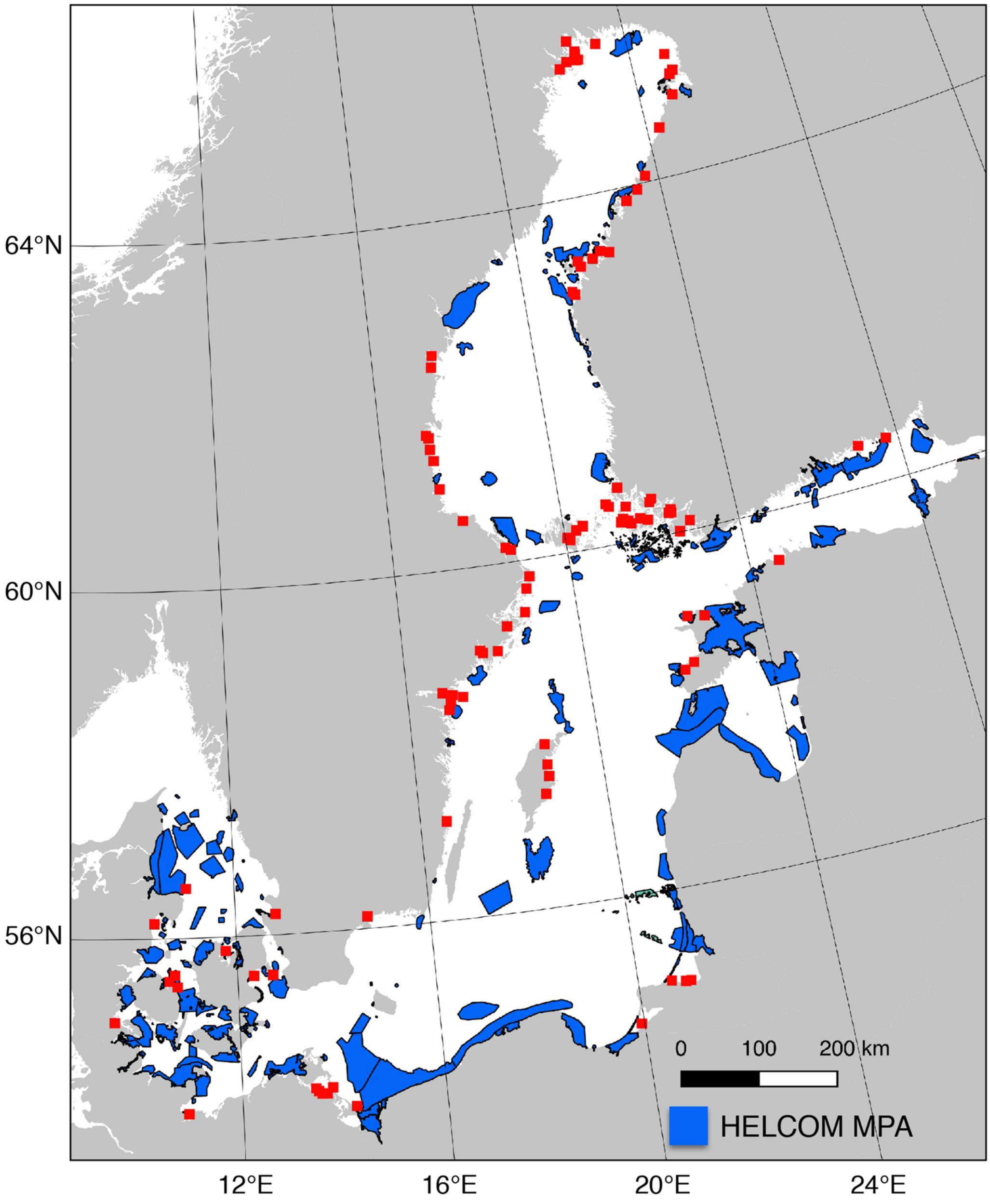

**FIGURE 8** Optimal extension (red squares) of the present HELCOM Marine Protected Area (MPA) network (blue polygons) based on a multi-species consensus solution for the three dispersal trait combinations (Table 1)

Suggested approaches to implement connectivity range from rules of thumb based on assumed dispersal distance (Shanks et al., 2003), GIS models of number of connections for set distances (HELCOM, 2016), advanced graph theory (Treml et al., 2008), source–sink analyses (Dubois et al., 2016), to weights in cost–benefit calculations in conservation prioritization tools (Beger et al., 2010; Virtanen et al., 2018). We have added another possibility. Based on work by Ovaskainen and Hanski (2003), connectivity is directly linked to metapopulation dynamics to identify optimal MPA networks (Nilsson Jacobi & Jonsson, 2011). By applying EPT to the connectivity matrix, it is possible to find the best network of MPAs that maximizes the growth rate of the global metapopulation (protected and unprotected areas) when the metapopulation is small, which is typical of threatened species. One advantage of this approach is that there is a unique network of MPAs for each connectivity matrix and the total protected area, and that this network is directly linked to persistence of the whole metapopulation. If habitat information is available, e.g. presence–absence or habitat quality (Virtanen et al., 2018), this can easily be incorporated (Berglund et al., 2012; Jahnke et al., 2018).

The EPT framework for single species, or dispersal strategies, can be extended to include multiple strategies where the resulting optimal MPA network can be seen as a consensus network offering sufficient protection for all targeted species (Jonsson et al., 2016). When including multiple species (multiple connectivity matrices) in the EPT framework the user has to specify some level of protection

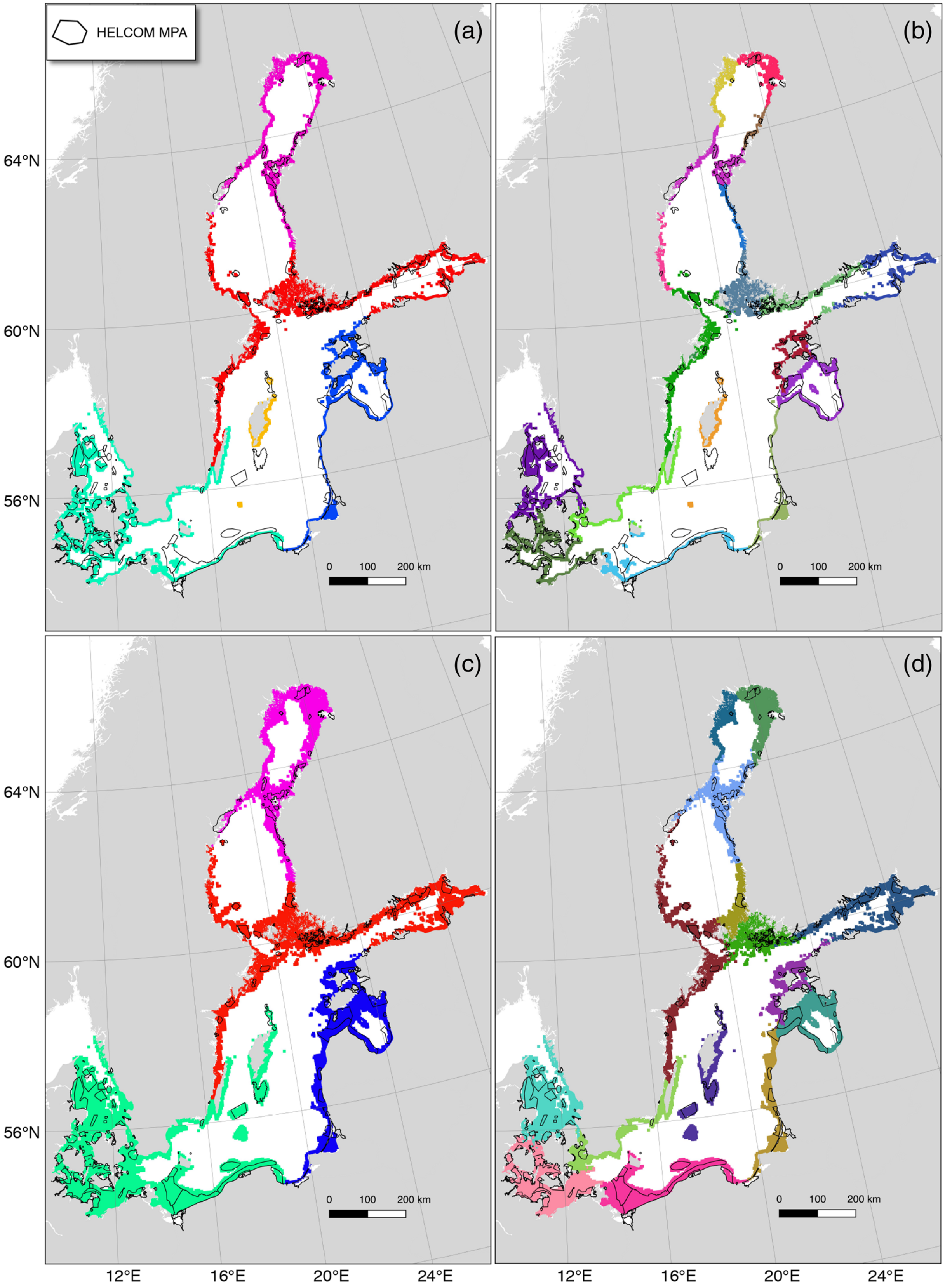

**FIGURE 9** Identification of dispersal barriers for the dispersal trait combinations 1 and 2 (Table 1). For trait combination 1, two selected thresholds of lowest allowable connectivity result in 6 and 20 clusters, respectively (panels a and b). For trait combination 2, the two selected thresholds result in 4 and 15 clusters, respectively (panels c and d). Colours are only chosen to make transitions at dispersal barriers clear. Also shown are outlines of HELCOM Marine Protected Area (MPA) polygons

for the least protected species (Jonsson et al., 2016). The existing HELCOM MPA network overlaps to a surprising extent with the optimal network, considering that connectivity was not an explicit criterion in the design of HELCOM MPA. This overlap suggests that connectivity of HELCOM MPAs is expected to be relatively satisfactory. There are some gaps mainly along the Swedish coast and in the Finnish Archipelago Sea (where new MPAs have recently been added).

It is generally unrealistic to completely re-design existing MPA networks, e.g. suggesting an optimal *de novo* network with respect to connectivity. The more realistic option is to extend existing networks with new MPAs in order to enhance connectivity within the whole network. An algorithm based on the EPT framework was developed to identify the optimal extension to an existing MPA network. Again, optimization is based on maximizing the growth rate of the whole metapopulation. When applied to the HELCOM MPAs an optimal extension of 3% of the total protected area (Figure 8), most of the suggested extension includes the Swedish coast and the Finnish coast along the Baltic Proper and Bothnian Bay, as well as in the Archipelago Sea. Interestingly, many of the new areas in an extended network (Figure 8) approximately coincide with a recently suggested extension of MPAs along the Finnish coast based on a prioritizing analysis of biodiversity and habitats (Virtanen et al., 2018). This overlap is probably fortuitous since the MPAs are based on different criteria (although high connectivity may be correlated to biodiversity), but together give strong support for a future extension. A recent EPT assessment of MPA connectivity in the Kattegat and Skagerrak Seas proposed an extended network to enhance connectivity (Moksnes et al., 2015), which now forms the basis for establishment of new MPAs within the OSPAR network.

Connectivity patterns in the seascape may reveal areas with high internal connectivity with partial dispersal barriers to other such areas. Such barriers may indicate demographically independent local populations (stocks) or genetically differentiated populations with local adaptations if barriers are sufficiently strong (Allendorf, Luikart, & Aitken, 2013). Based on the connectivity, well-connected clusters can be identified in a way to minimize the total dispersal (leakage) among such groups, subjected to some penalty of aggregating groups (Nilsson Jacobi et al., 2012). This tool aids to visualize the structure of the connectivity matrix projected onto a geographic map. Colour-coded areas indicate management units (Palsbøll, Bérubé, & Allendorf, 2007) separated by dispersal barriers (Figure 9). Dispersal barriers are generally partial and the number of dispersal barriers decrease as less dispersal is allowed across barriers (Figure 9). Genetically differentiated local populations are expected to be associated with fewer, strong barriers (Figure 9a, c; Jahnke et al., 2018), while a larger

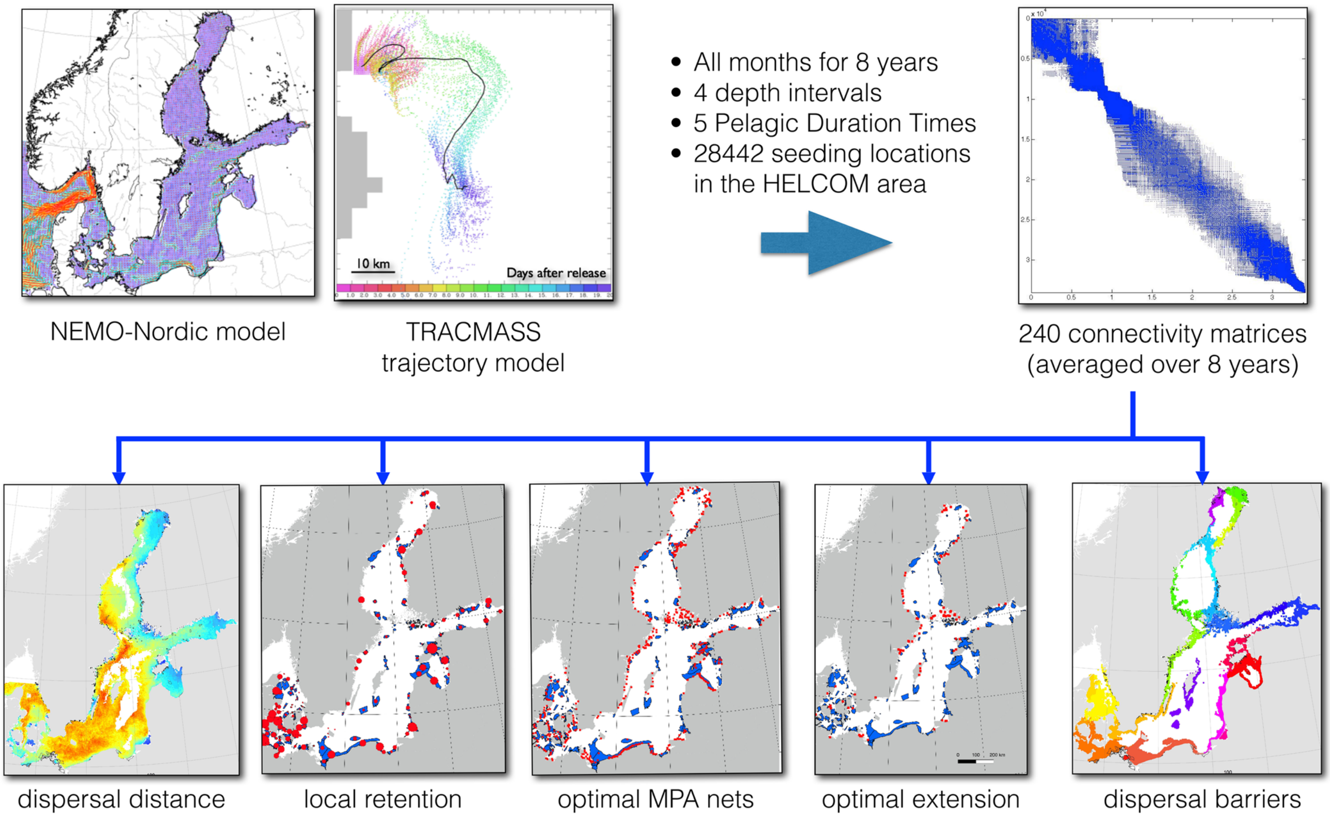

**FIGURE 10** An overview of the workflow using tools to assess ecological coherence of Marine Protected Areas (MPAs) based on biophysical modelling of dispersal patterns summarized in connectivity matrices for a range of dispersal trait combinations. From the connectivity matrices tools are applied to calculate dispersal distance and of local retention, to identify networks with optimal topology and optimal extension of existing MPA networks, and finally to identify partial dispersal barriers, which may indicate management units

number of more 'leaky' barriers may represent the distribution of demographically independent stocks (Nilsson Jacobi et al., 2012). Such local populations or stocks may require separate conservation and management actions, and siting of MPAs may be stratified across such management units. This cluster approach indicates that there are several partial dispersal barriers within the HELCOM area, and a few strong barriers may have evolutionary significance (Figures 9a, c). Examples of general barriers are between Kattegat/Belt Sea and the Baltic Sea, the Gdansk Bay, the Finnish Bothnian Bay coast, south of Öland, and the Swedish coast at the northern Quark. Two reviews (Johannesson & André, 2006; Wennerström et al., 2013) discuss the genetic structure and possible barriers to gene flow for several populations in the Baltic Sea and the bordering Kattegat/Skagerrak. Connectivity barriers may indicate the presence of unique local adaptations to different regions in the strong Baltic Sea environmental gradients. Barriers may also slow down recolonization and reduce resilience to regional disturbances, and may impede range shifts as a response to a changing climate (Jonsson et al., 2018). If regions between dispersal barriers are regarded as management units, it can be seen that the HELCOM MPAs are fairly well distributed between many of these units. Again, there are some exceptions where there are units where MPAs are more scarce, mainly along the Swedish coast in the Bothnia Sea and Bothnian Bay, as well as between Stockholm and Öland.

The assessment of the HELCOM MPA network with respect to ecological coherence showed that individual MPAs are generally too small for persistence based only on local recruitment. However, the overall connectivity among the MPAs and with surrounding unprotected areas seems satisfactory with respect to a positive effect on the whole metapopulation. An analysis of the optimal extension to enhance the effect of connectivity, however, indicates that there are some gaps, especially along the Swedish coast. A barrier analysis also suggests that HELCOM MPAs are adequately distributed among putative management units based on connectivity.

A summary of the tools and workflow to assess the ecological coherence of MPA networks is shown in Figure 10. Although biophysical modelling produces estimates with unrivalled coverage in space and time, there are limitations to this approach. To adequately model larval dispersal of a species, information is needed of critical larval traits such as pelagic duration and drift depth since they can strongly influence dispersal distance and direction (Corell et al., 2012; Moksnes & Jonsson, 2019). In the present study, we had access to a unique library of data on larval drifts depth and seasonal abundance in the HELCOM-area to improve the biophysical modelling (Moksnes et al., 2014), but such data are usually missing from most areas. Only organisms where dispersal is significantly influenced by the oceanographic circulation can be considered, excluding, e.g. migratory fish. Most regional biophysical models still lack the spatial resolution to accurately represent very complex coastlines and archipelagos, e.g. typical of some Baltic Sea areas. Low resolution of complex coastlines will be likely to lead to overestimated connectivity and underestimated self-recruitment close to the coast and for shallow-water species. However, recent studies comparing connectivity results of drifting seagrass shoots in the Kattegat–Skagerrak area using a similar biophysical modelling approach combined with population genetic analyses found very consistent results (Jahnke et al., 2018), suggesting that the model used here can also produce reliable results in topographically complex coastal environments. At present, some hydrodynamic processes are absent in most models, e.g. Stokes drift from surface waves, and future development will probably lead to an increasingly realistic representation of ocean transport. The present lack of habitat mapping or species distribution models for most marine areas is a further bottleneck in the assessment of connectivity, although some recent, mainly regional, mapping shows great promise (e.g. Virtanen et al., 2018). However, the tools presented here are all based on the connectivity matrix, which may be estimated using other methods, e.g. genetically based, or with more highly resolved biophysical models in the future.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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