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BIODIVERSITY RESEARCH

How to select networks of marine protected areas for multiple species with different dispersal strategies

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ABSTRACT

Aim To develop and test theory based on connectivity to identify optimal networks of marine protected areas (MPAs) that protect multiple species with a range of dispersal strategies.

Location The eastern North Sea in the Atlantic Ocean.

Methods Theory of finding optimal MPA network is based on eigenvalue perturbation theory applied to population connectivity. Previous theory is here extended to the persistence of multiple species by solving a maximization problem with constraints, which identifies an optimal consensus network of MPAs. The theory is applied to two test cases within a 120,000 km^2 area in the North Sea where connectivity was estimated with a biophysical model. In a realistic case, the theory is applied to the protection of rocky-reef habitats, where the biophysical model is parameterized with realistic dispersal traits for key species. Theoretical predictions of optimal networks were validated with a simple metapopulation model. Persistence of optimal consensus MPA networks is compared to randomly selected networks as well as to the existing MPA network.

Results Despite few overlapping MPA sites for the optimal networks based on single dispersal strategies, the consensus network for multiple dispersal strategies performed well for 3 of 4 contrasting strategies even without user-defined constraints. In the test with five realistic dispersal strategies, representing a community on threatened rocky reefs, the consensus network performed equally well compared to solutions for single species. Different dispersal strategies were also protected jointly across the MPA network (93% of sites), in contrast to simulations of the existing MPA network (2% of sites). Consensus networks based on connectivity were significantly more efficient compared to existing MPAs.

Main conclusions Our findings suggest that the new theoretic framework can identify a consensus MPA network that protects a whole community containing species with multiple dispersal strategies.

Keywords

connectivity, conservation biology, dispersal, eigenvalue perturbation, larval ecology, marine protected area.

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INTRODUCTION

Regulating human disturbance in the oceans through marine protected areas (MPA) is now recognized as a potentially effective management and conservation strategy to rebuild over-fished stocks and to maintain general biodiversity (e.g. Gaines *et al.*, 2010) as well as ecosystem functions (Micheli & Halpern, 2005). Several studies have documented increase in population density, body size and reproductive output after MPA implementations (Lester *et al.*, 2009; Fenberg *et al.*, 2012). Theoretical analyses further suggest that networks of MPAs can provide refuge that allows for persistent

populations in areas where harvest and disturbance rates otherwise would lead to population collapse (Kaplan *et al.*, 2006; White *et al.*, 2010; Pujolar *et al.*, 2013). However, population persistence within MPAs is expected to critically depend on the size and spatial arrangement of MPAs as well as the dispersal ability of target species (e.g. Shanks *et al.*, 2003; Kininmonth *et al.*, 2011; Moffitt *et al.*, 2011). Most marine invertebrates and fish produce free-swimming larvae that may be transported by ocean circulation for days to months (Thorson, 1950; Sale & Kritzer, 2003). Population replacement may thus depend on sufficient local retention within an MPA or subsidies through larval dispersal (or adult migration) from other MPAs within the network (Hastings & Botsford, 2006; Burgess *et al.*, 2014). An important aspect of population persistence within networks of MPAs is thus the connectivity among individual MPAs (and the surrounding environment), which is a function of ocean circulation, life-history traits of target species and the spatial arrangement of MPAs (Gaines *et al.*, 2003; Treml *et al.*, 2012; Thomas *et al.*, 2014).

The site selection of MPAs is often a compromise between many socio-economic political interests and there is growing concern about insufficient biological functionality of existing MPA networks (Fenberg *et al.*, 2012). However, there is an increasing ambition at the policymaking level to improve management and conservation efficiency of MPAs by assessing biologically relevant aspects to achieve ecologically coherent MPA networks (Abdulla *et al.*, 2008; Beger *et al.*, 2010; Fenberg *et al.*, 2012). One key aspect of functional MPA networks is the connectivity, which can strongly affect short-term population persistence (Hastings & Botsford, 2006; Figueira, 2009) as well as the long-term population-genetic structure and evolution of local adaptations (Hellberg, 2009).

With estimates of the connectivity structure within an area (e.g. a coast or a basin), it is possible to find the optimally connected MPA network for a given total target area with respect to meta-population persistence (Ovaskainen & Hanski, 2003; Nilsson Jacobi & Jonsson, 2011). The optimization of MPA networks with respect to connectivity is relatively straightforward when a single species is the target of protection, for example an over-fished or a red-listed species. However, finding an MPA network that offers sufficient connectivity for multiple species with different life-history traits, for example spawning season and pelagic larval duration, is more complex (White *et al.*, 2010; Moffitt *et al.*, 2011). With increasing emphasis on ecosystem-based management (e.g. Pikitch *et al.*, 2004) and sustainable ecosystem services (Roberts *et al.*, 2003), future protection will focus on whole assemblages of species forming interacting meta-communities (Guichard *et al.*, 2004; Baskett *et al.*, 2007). This aim is also evident within international conventions for the protection of the sea, for example HELCOM and OSPAR, which explicitly agree to protect multiple-species biodiversity (HELCOM, 2009; OSPAR, 2013). The challenge is then to design MPA networks that ensure the joint persistence of several populations within a community.

In this study, we extend the theoretical framework proposed in Nilsson Jacobi & Jonsson (2011) to find optimally connected MPA networks aimed to protect a community where species differ in dispersal abilities. We apply the theory to a community occupying deep rocky reefs that is considered a threatened habitat in coastal areas (Halpern *et al.*, 2007). First we demonstrate theoretically how a consensus network can be found for a test case with four contrasting dispersal strategies. The consensus network is identified using an optimization algorithm that considers the protection needs for each individual species but also includes possible protection strategies that use interspecies synergies by choosing MPAs that have positive effects on several species simultaneously. Secondly, we apply this technique to a realistic case of a rocky-reef community and also compare the performance of the consensus network with the existing network of MPAs using metapopulation modelling.

METHODS

Study area

The geographic domain where we apply our theoretical framework for MPA siting covers part of the southern Baltic Sea, the Kattegat, Skagerrak and part of the North Sea spanning 54–59° N and 7–15° E with a total area of 120,000 km^2 (Fig. 1). The dispersal of marine larvae is influenced by a complex oceanographic circulation in this area (Leppäranta & Myrberg, 2009). There is a gradient in tidal influence from the meso-tidal North Sea to the micro-tidal Kattegat and Baltic Sea. The Jutland coastal current transports water from the North Sea into Skagerrak and Kattegat. The Baltic surface current transports brackish water northward, and there is also a southward compensatory flow below the pycnocline.

The dispersal model

The connectivity due to dispersal of planktonic larvae was estimated with biophysical modelling based on the BaltiX oceanographic circulation model and an offline Lagrangian particle tracking model. BaltiX is a regional Baltic/North Sea configuration of the NEMO ocean model (Madec, 2010), with a horizontal resolution of about 3.7 km and a vertical resolution of 56 layers of variable depth (Hordoir *et al.*, 2013 for details).

Lagrangian dispersal simulations were performed with the trajectory model TRACMASS (De Vries & Döös, 2001) using interpolated velocity fields from the BaltiX model. Velocity fields were updated for all grid boxes in the model domain every 3 h, and the trajectory calculations were performed with a 15-min time step. Every month during the spawning season 49 (interspersed within each grid), virtual larvae were released in all 8992 grid cells in the target area (Fig. 1) with a bottom depth less than 100 m, and this was repeated for 8 years (1995–2002). For calculations of mean dispersal distance in the study area, we used dispersal data within the whole BaltiX model domain but only the subarea covering

Figure 1 Map of the geographic area considered in this study. The blue area marks the seafloor between 20 and 100 m depth.

the target area (8992 grid cells) is shown (Fig. 2). Biological traits considered in the Lagrangian simulations were spawning season, pelagic larval duration time (PLD) and the depth where each larval type is assumed to maintain their vertical position (Moksnes et al., 2014). Classes of theoretical (case 1) and empirical (case 2) traits were used to parameterize the Lagrangian trajectory simulations (Tables 1 & 2). In total, the study is based on more than 400 million virtual larval trajectories. Connectivity among all grid cells in the study region (8992 grid cells) was estimated by calculating the proportion of released particles from site i that ended up in site j. For all analyses, we averaged connectivity over the 8 years, which well sample the North Atlantic Oscillation (NAO) climate cycle in the area (Berglund et al., 2012). We assumed no mortality of larvae because we do not have any information about spatial and temporal patterns of mortality risk.

Finding an optimal consensus MPA network based on multiple-species connectivity

We used eigenvalue perturbation theory (EPT) applied to the connectivity matrices of single dispersal strategies to select

optimal MPA networks (for details, Nilsson Jacobi & Jonsson, 2011). Briefly, this method finds an optimal subset of MPAs of given total area that maximizes the growth rate of the whole metapopulation when it is 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 δ (here set to 20%). The increase in connectivity by δ 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 and/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. Nilsson Jacobi & Jonsson (2011) showed that these two cases lead to identical results when applying EPT (to first order) to select sites for an optimal MPA network.

We now extend the EPT method for single species to multiple species. Consider a connectivity matrix where the elements C_{ij} determine the probability for a juvenile born at
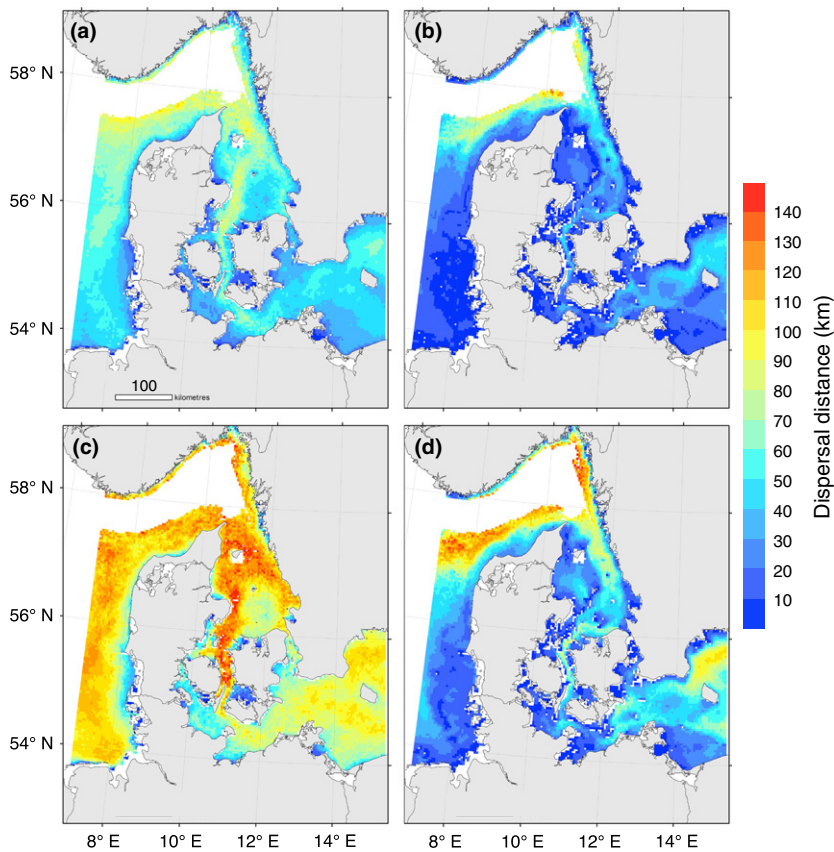
Figure 2 Maps showing the mean dispersal distance for the four dispersal strategies in the test case 1: (a) A1, (b) A2, (c) A3, (d) A4. Dispersal distances are calculated from each grid cell in the ocean circulation model and with the larval traits in Table 1.

Table 1 Larval traits used in the biophysical model generating connectivity matrices for the test case 1 with the contrasting dispersal strategies A1–A4. Traits include time of larval release, pelagic larval duration (PLD) and drift depth during dispersal.

Larval release	PLD (days)	Drift depth (m)	ID
January–December	10	0–2	A1
January–December	10	24–26	A2
January–December	30	0–2	A3
January–December	30	24–26	A4

location j to successfully establish at location i. We further define the habitat quality by a diagonal matrix H_{ii} that measures either a multiplicative factor on the reproduction rate at location i or the probability to survive and establish at location i. In the former case, the effective spreading process is determined by the matrix CH and in the latter case by HC. If we do not have any information about the habitat quality, the H matrix can be ignored (set to the identity matrix). In Nilsson Jacobi & Jonsson (2011), we show that a perturbation analysis of the eigenvalues of the matrix HC (or CH) can be used to determine how effective protection of a location is in terms of how much the overall population growth is expected to increase as a result of a certain degree of protection. The expected effect can be derived analytically as a product $u_{ki} * v_{ki}$, where u_{ki} is the ith element of the kth dominating right eigenvector of HC (or CH) and v_k is the

kth dominating left eigenvector. Using this idea, we can calculate a list of priority scores for each location. This method solves the problem of prioritizing protection areas for a *single* species, but it is also the starting point for our approach to *multispecies* protection. Assume now that we are considering the overall protection of a set of species (or groups of dispersal strategies), which we denote by an index $\alpha = 1, 2,\ldots$. We then have a set of connectivity matrices C_{ij}^α and habitat matrices H_{ii}^α. Let π_i^α denote the priority score of location i for species α. The subset of locations with the highest priority scores form the optimal MPA network where the size of the selected subset depends on the total area planned for protection. Based on the single species case, it is possible to define π_i^α as:

$\pi_i^\alpha = \max_k \cdot v_{ki} \cdot u_{ki}$, where k can be any of the N most dominating eigenvalues.

The goal is now to select a number of locations that optimize the protection of all species. The most straightforward approach would be to select the most important locations for each species individually. This would, however, ignore the possibility for synergies in terms of locations that are beneficial for multiple species simultaneously but may not be the most important location for any individual species. To define a more efficient scheme that can identify such synergies, we define the selection of protection areas as an optimization problem. Two variables are introduced:

p_i is an identifier variable, $p_i = 1$ if site i is protected and $p_i = 0$ otherwise; and f_i is the cost of protecting site i, for

Table 2 Larval traits used in the biophysical model generating connectivity matrices for the realistic test case 2 for deep rocky reefs. A number of dominating rocky-reef taxa are grouped into the dispersal strategies B1–B5, which include time of larval release, pelagic larval duration (PLD) and drift depth during dispersal. Examples of species that are represented by the different larval traits are from (Moksnes *et al.*, 2014).

Larval release	PLD (d)	Depth (m)	Rocky-reef taxa	ID
April–August	10	0% 0–2	Anthozoa	B1
		20% 10–12	Crinoidea	
		40% 24–26		
		40% 48–50		
April–August	30	0% 0–2 m	Ophiurida	B2
		20% 10–12	*Galathea* sp	
		40% 24–26	*Pisidia longicornis*	
		40% 48–50	*Zeugopterus punctatus*	
April–August	30	10% 0–2 m	Echinoida	B3
		40% 10–12	Mytilidae	
		40% 24–26	*Homarus gammarus*	
		10% 48–50	*Sabella* spp.	
April–August	60	10% 0–2	Gadidae	B4
		40% 10–12	Labridae	
		40% 24–26	*Cancer pagurus*	
		10% 48–50		
April–August	30	40% 0–2	Asteroidea	B5
		30% 10–12	*Liocarcinus* sp.	
		20% 24–26		
		10% 48–50		

example in terms of economic costs, for example missed opportunities for fishery estimated from catch statistics or from VMS positions (Gonzalez-Mirelis *et al.*, 2014).

The algorithm for deciding the protected areas can be formulated as a discrete linear programming problem in terms of a maximization problem with constraints:

$$\max_{p_i \epsilon \{0,1\}} \sum_{\alpha} \sum_i \pi_i^{\alpha} p_i \quad \text{maximizes total protection} \quad (1)$$

$$\sum_i \pi_i^{\alpha} p_i \geq K^{\alpha} \text{ constraint 1: minimal protection for each species}$$

$$\sum f_i p_i \leq F \text{ constraint 2: maximum total cost}$$

In some cases, setting $f_i = 1$ makes the solutions to the maximization (minimization) problem highly redundant and standard algorithms for solving linear programming problems may not converge. In these cases, a small random perturbation of the costs f_i typically gives better convergence. An advantage with using discrete linear programming is that such problems can be solved efficiently by standard mathematics software. The cost for protection of a site is an input variable in equation (1), but due to lack of information, we assume that all sites are equally expensive to protect, that is $f_i = 1$. The algorithm also includes two types of control parameters: K^{α} that sets the minimal accepted protection of

species α, and F that controls the maximal total cost. In the model scenarios, we use a parameter setting where $K^{\alpha} = 10$ and $F = 100$.

Validation of optimal MPA networks with a metapopulation model

To evaluate whether the sites identified by the EPT method really represented superior MPA networks, we carried out metapopulation modelling. The optimal EPT-based networks for single dispersal strategies were compared to randomly selected networks, and we also explored how well the consensus networks performed for each single dispersal strategy. The random networks were a random subset of model grid cells satisfying the criteria of depth (20–100 m) and presence of rocky reefs (test case 2) with the same total area as for the non-random networks. In addition, the performance of the optimal MPA networks was compared to present real-world MPA networks. The simplistic metapopulation model considered all sites (grid cells) within the study domain as local populations of an annual organism connected by dispersal through a connectivity matrix. Every grid cell was given the same growth rate except those grid cells included in MPA networks, which were assumed to grow 20% faster because of being protected. Growth of local populations was density-dependent, and carrying capacity was reached assuming a logistic growth function. To simulate stochastic reductions in population abundance, for example caused by regional hydrologic and climatic factors, the metapopulation was stochastically reduced by 95% (arbitrarily set as a reduction threatening persistence) with an expected interval of 8 years (covering extremes of the NAO index). Each model simulation was run for 100 years, and this was repeated 100 times. For each model simulation, the mean size of the metapopulation at low abundance (below 5% of carrying capacity) was recorded without and with protection (as a result of the MPA network). The rationale for only recording the metapopulation size at low abundances is that this is when protection is assumed to be most important. Mathematically the population model can be formulated as:

$$n_{t+1,i} = \chi(t) \sum_j E_{ii} C_{ij} \left[n_{t,j} + r n_{t,j} \left(1 - \frac{n_{t,j}}{K} \right) \right] \quad (2)$$

$$\chi(t) = \begin{cases} \varepsilon = 0.05 \text{ with probability } 0.125 \text{ at each time step} \\ \varepsilon = 1 \text{ otherwise} \end{cases}$$

where $n_{t,i}$ is the vector of the local population size in site i at time t, E is a diagonal matrix with the protection effect if within an MPA (20% higher reproduction rate) for each local population, C is the connectivity matrix specifying the dispersal of larvae between all local populations, r is the reproductive rate, K is the carrying capacity, and $\chi(t)$ is a stochastic variable specifying reductions of the metapopulation. The effect of protection was assessed as the population size within the MPA network as well as the effect on the

whole metapopulation. Note that the results from the metapopulation model should be interpreted mainly in a qualitative way because the metapopulation size is a function of the largely unknown population parameters: reproductive rate, carrying capacity and the effect of protection. However, the qualitative conclusions were rather insensitive to selected parameters as long as population size is assessed well below carrying capacity.

Test case 1: single and multispecies networks for theoretical larval traits

To demonstrate and explore the performance of the new theoretical framework, we first constructed a test case community occupying all habitats within a depth range of 20–100 m with four types of dispersal strategies with contrasting PLD and drift depths, and spawning all year round (Table 1). In the target geographic area (Fig. 1), PLD and drift depth have been suggested to dominate dispersal (Corell *et al.*, 2012), and larval traits were selected to maximize differences in dispersal patterns, although within the natural range of dominant larval traits in the study area. The two drift depths (0–2 and 22–24 m) placed the larvae above and below the pycnocline, respectively, and could therefore result in opposite dispersal directions. Apart from estimating connectivity, we also calculated mean dispersal distance (weighted mean with respect to the probability of dispersal) for each grid cell. Also mean dispersal direction was calculated for two connectivity matrices (A1 and A2) to illustrate differences in transport with drift depth. Using EPT, we first identified optimal networks for each single dispersal strategy and then, using equation (1), identified the consensus network for the whole community. We then explored the performance of this consensus network with the metapopulation model as described above.

Test case 2: consensus network for realistic rocky-reef communities

In a second test of a consensus network, we constructed a more ecologically realistic community inhabiting deep rocky reefs (20–100 m) using modelled data of habitat distribution and empirical data to select realistic larval traits. In this assessment, we considered dispersal only among grid cells with modelled presence of hard substrates.

Using a unique set of data of the larval depth distribution and spawning season of 45 fish and 80 invertebrate taxa, based on over 300 depth-specific plankton samples in the Kattegat–Skagerrak area (Moksnes *et al.*, 2014), five types of larval traits were selected that represent the dominant organisms found on deep rocky reefs in the study area (Table 2). Information on PLD was obtained from the literature (Moksnes *et al.*, 2014). In contrast to the fixed larval drift depths and PLDs, and continuous spawning season used in case 1, the five larval types included variation and overlap in larval traits, reflecting the empirical data.

To predict rocky-reef locations, we used the GIS resources within EUSeaMap (http://jncc.defra.gov.uk/) for the outer Skagerrak and eastern North Sea, and for the inner Skagerrak, Kattegat and the south-west Baltic Sea, we used the BALANCE marine landscape model available through HELCOM (http://maps.helcom.fi). Point samples (1 km resolution) from GIS maps of predicted rocky reefs were joined to the computational grid of the BaltiX ocean circulation model in order to combine rocky-reef locations with larval connectivity. If any sample point within a BaltiX grid cell predicted the presence of rocky reefs, this grid cell was classified as a suitable habitat. The area bounded by the depth interval 20–100 m consisted of 5133 BaltiX grid cells, and of these 983 grid cells were predicted to contain rocky-reef habitats. We acknowledge that there is considerable uncertainty in the predictions of rocky reefs, but at present, this represents the best data available.

As in test case 1, we first calculated the EPT-based optimal network for each of the five single dispersal strategies (Table 2) and then identified the consensus network for the whole community. We then compared model predictions of optimal MPA networks with random networks as well as the existing MPA network in the study area, including Natura 2000 MPAs (European Council, 1992), OSPAR MPAs (OSPAR, 2013) and national protected areas (Moksnes *et al.*, 2014 for a complete list of MPAs). Only the part of the existing MPA networks that satisfied the habitat prediction of rocky reefs was included in the analysis of test case 2, which in total consisted of 163 grid cells (2230 km^2). The size of the EPT-based optimal MPA networks for rocky reefs was chosen to be of the same size as this existing network to allow comparison of their performance. The comparison in performance was explored with the metapopulation model as described above.

RESULTS

Test case 1: single and multispecies networks for theoretical larval traits

As expected the longest dispersal distances for the four dispersal strategies in test case 1 are found for larvae with long PLD and drifting in surface waters, although there are large geographic differences (Fig. 2). Depending on dispersal strategy and release point, dispersal distance ranged from a few km to more than 150 km. In this coastal system, the dispersal direction was very dependent on drift depth where there is a marked northward surface current along the Danish west coast as well as along the Swedish Kattegat and Skagerrak coast (Fig. S1a in Supporting Information). This current pattern is partly reversed below the pycnocline where mainly southward flows dominate (Fig. S1b).

From the four connectivity matrices representing the dispersal probabilities of the larval dispersal strategies in case 1, we ranked all grid cells in the study area according to their expected contribution to metapopulation persistence based

on the EPT framework. For each dispersal strategy, Fig. 3(a–d) shows a subset of 200 grid cells (2730 km^2) of the highest ranked grid cells using EPT. The four EPT networks have many overlapping grid cells (see Venn diagram in Fig. S2). However, 18–62% of the grid cells are unique for a dispersal strategy and only 5% are shared among all. Strategies A2 and A4 shared 69% of grid cells indicating that the strategies sharing drift depths showed similar dispersal patterns.

From the four EPT-based optimal MPA networks in Figs 3(a–d), we used equation (1) to find an optimal consensus network for a whole community that included all the dispersal strategies in Table 1. The resulting consensus network is shown in Fig. 3(e). The metapopulation model showed that the EPT-based optimal MPA networks for each of the four dispersal strategies resulted in significantly larger metapopulation sizes than randomly selected networks of the same total size (Fig. 4a). While the effect of protection was 5–11% for random networks, the effect for the optimal networks was between 33% and 53% in terms of the size of the whole metapopulation (Fig. 4a). A critical question is how well the consensus network performs for the four larval dispersal strategies when compared with the within-strategy optimal networks. Figure 4(a) shows that the consensus network (Fig. 3e) performs almost as well as the individual EPT networks with the exception of strategy A1. However, if there is information about the relative priority of protection for the different target species, the user can increase the control parameter K^α in equation (1), for example for strategy A1. An example is shown in Fig. S3. As expected, the effect of protection is greater within the MPA networks than for the whole metapopulation and Fig. 4(b) shows that the consensus optimal network increased population size within the MPA network with 28–87%. The random MPA networks performed relatively better if only the local populations within the MPAs were considered compared to the whole metapopulation, which is expected because the EPT framework considers the global metapopulation effect.

Test case 2: consensus network for realistic rocky-reef communities

The individual optimal EPT networks for the five dispersal strategies (B1–B5) in the realistic case 2 were first calculated, and from these, a consensus optimal MPA network was identified (equation (1)) as shown in Fig. 3(f). Due to the fairly high overlap in dispersal characteristics for the five strategies (Table 2), there was also a substantial overlap of the sites selected for the EPT-based MPA networks. Only 10, 8, 5, 4 and 8 sites were exclusive for the dispersal strategies B1–B5, respectively, and 107 of a total of 163 sites were common to all five EPT optimal networks. Thus, the overlap of the optimal networks was much greater than for the test case 1 with more contrasting dispersal strategies. Due to the large overlap of sites, it is not surprising that the consensus optimal network performed as well as all the five individual optimal networks (Fig. 4c). All the optimal networks also

performed considerably better than randomly selected networks. The consensus optimal MPA network further resulted in a much larger metapopulation size compared with the existing MPA network (Fig. 4d). While the existing MPA network increased metapopulation size with slightly more than 20%, the consensus optimal network resulted in an almost 80% increase.

The consensus network worked well for all five dispersal strategies, but for the protection of the whole community, it is essential that all five taxonomic groups co-occur, at least at many of the selected MPA sites. Figure 5(a) shows that most of the 163 sites of the optimal consensus network indeed harbour all five taxonomic groups at relatively high densities, while a randomly selected network failed to protect mainly strategies B1 and B4 in most sites (Fig. 5b). For the consensus optimal network 93 ± 0.01% (mean ± SE) of the MPA sites harboured, all five groups at high densities but only 2.2 ± 0.005% of the randomly selected sites achieved this.

DISCUSSION

In this work, we show how the EPT framework (Nilsson Jacobi & Jonsson, 2011) can be extended to identify an optimal consensus MPA network for multiple species, which is called for with an increasing focus on ecosystem-based management (e.g. Pikitch *et al.*, 2004). Defined as a linear programming problem, it is possible to find consensus MPA networks, which will depend on both the degree of overlap between individual optimal networks, but also on user-defined constraints, such as the distribution of protected sites over different isolated subpopulations, minimal protection for each species and the site-specific cost, for example in terms of monitoring and loss of fishing opportunities. The user-defined parameters K^α and F can be used to explore the effect on the consensus MPA network for different scenarios of species-specific requirements for protection and estimated costs of implementation and management. In the first test case, we included four contrasting dispersal strategies. The optimal networks for each dispersal strategy performed considerably better than randomly selected networks as was also found in Nilsson Jacobi & Jonsson (2011) demonstrating the effectiveness of the EPT framework. The overlap between the individual EPT-based optimal networks was moderate with only 5% of the sites being common to all four dispersal strategies. Despite the low overlap, the validation with a metapopulation model showed that the optimal consensus network performed well for populations within the MPA networks and almost as well for the whole metapopulation. The consensus optimal network performed less well for the dispersal strategy A1 illustrating the optimization problem when searching for a consensus network. It is, however, easy to change the control parameter of the algorithm (equation (1)) to force a better protection strategy for the species with A1 dispersal pattern, by increasing K^α for this case. For clarity, we here choose to show the direct output of the algorithm without iterative tweaking of control parameters.
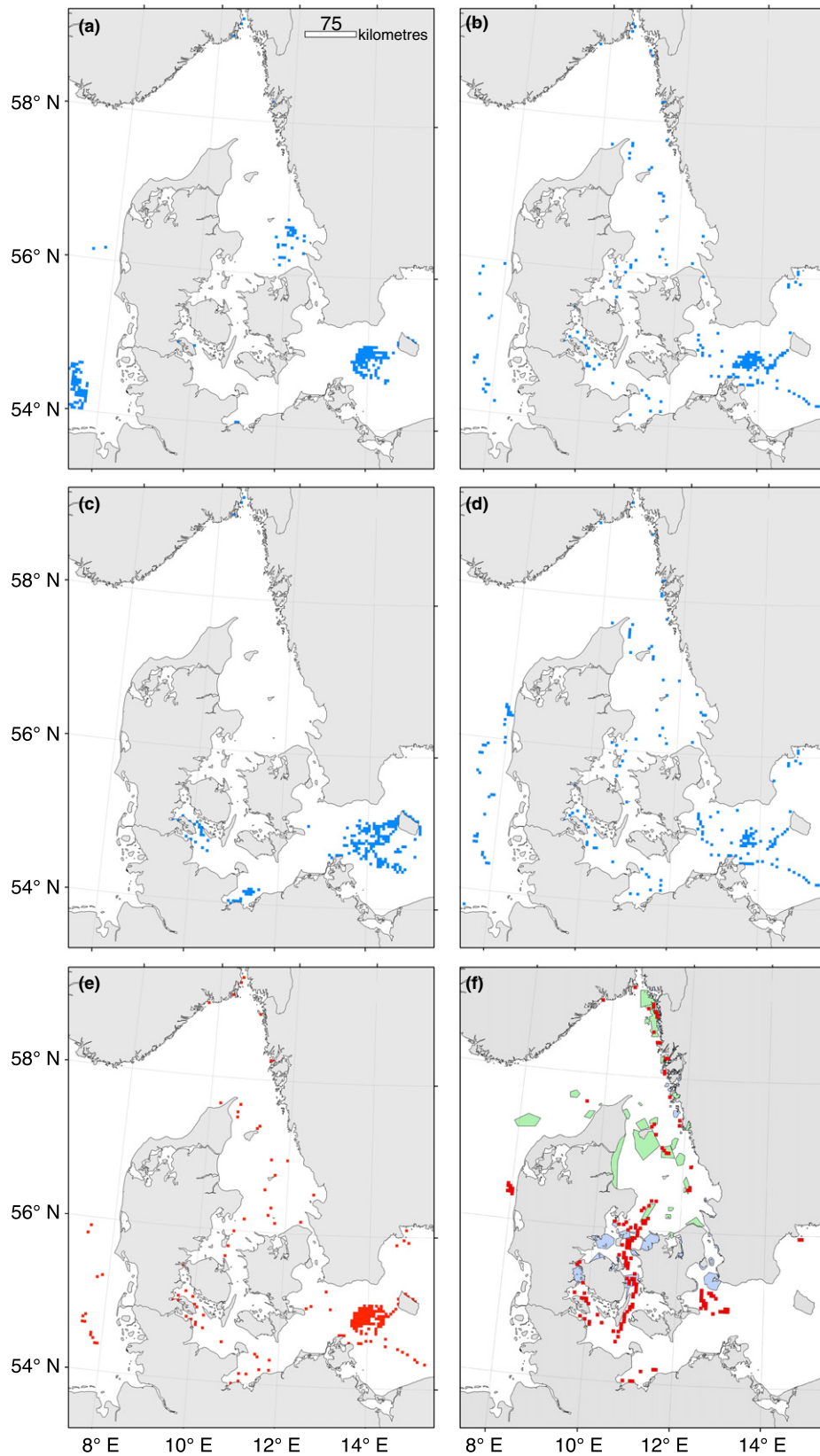
Figure 3 Maps showing the EPT-based optimal networks of MPAs for the four dispersal strategies A1–A4 in test case 1 (blue squares in panels a–d) and the consensus network for dispersal strategies in test case 1 (red squares in panel e). The panel f shows the consensus network (red squares) for the five dispersal strategies (B1–B5) in test case 2. Also shown is the present MPA network as blue (Natura 2000) or green (OSPAR MPAs) polygons.
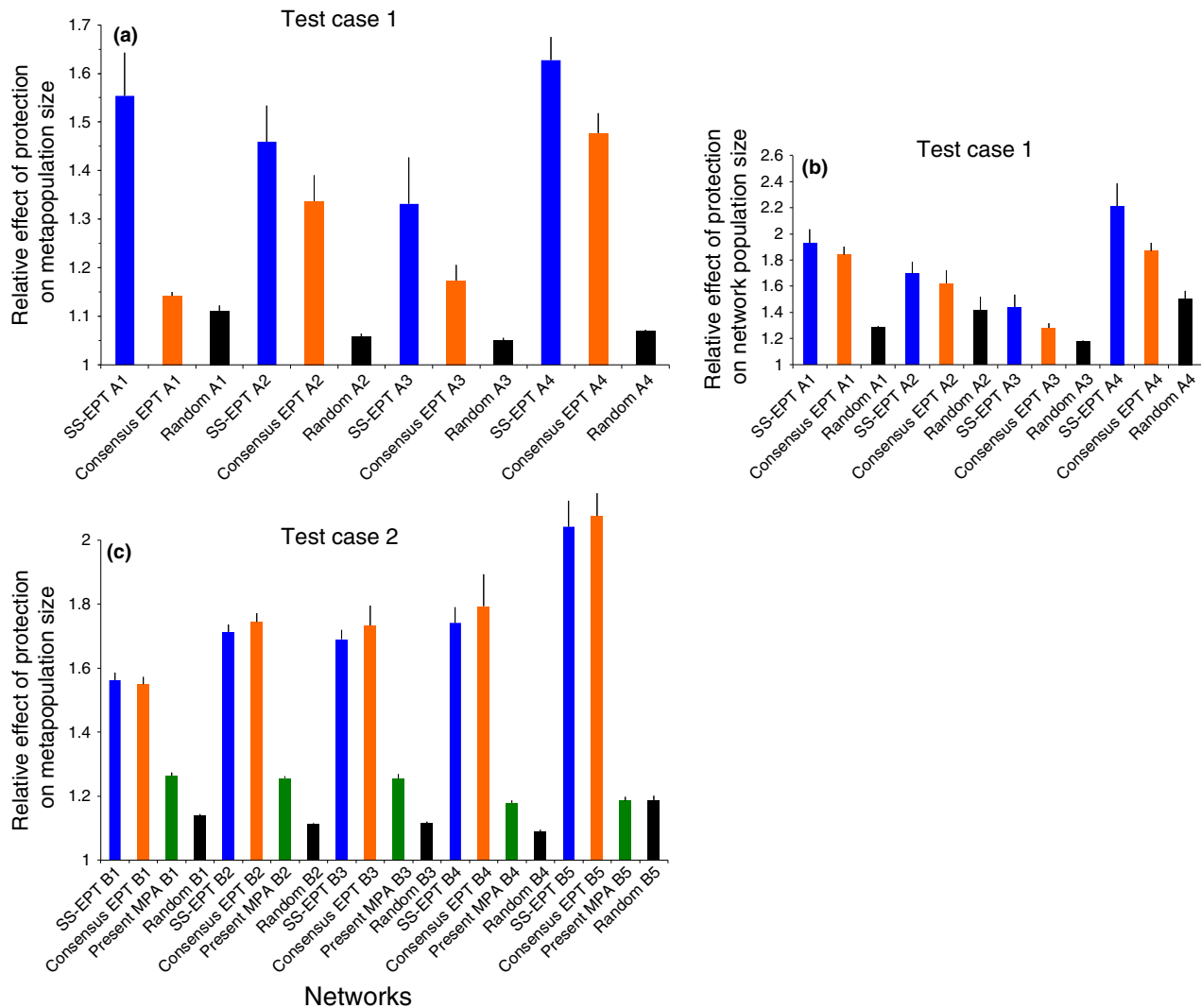
Figure 4 Validation of the performance of optimal networks with the metapopulation model (equation (2)) for the two test cases. (a) The effect of protecting dispersal strategies in test case 1 (A1–A4) on the global metapopulation by either single-strategy optimal EPT-based networks (SS-EPT) or the optimal consensus network (consensus EPT). Also shown are results for randomly selected networks. (b) Effect of protection in test case 1 on the population size within the protected network for the optimal SS-EPT, consensus EPT and randomly selected networks, respectively. (c) The effect of protecting dispersal strategies on realistic deep rocky reefs in test case 2 (B1–B5) on the global metapopulation by either optimal SS-EPT networks or the optimal consensus EPT network. Also shown are results for the effect of the present MPA network within the Natura 2000 (blue polygons in Fig. 3f) and the OSPAR (green polygons in Fig. 3f) systems. Finally, these results are compared with randomly selected networks. Note that only those parts of the Natura 2000 and OSPAR networks between 20 and 100 m depths and with predicted rocky reefs were included in the analysis. Performance is measured as the metapopulation size with protection through MPA networks relative to the metapopulation size without protection. Each column is the mean of 100 replicate simulations and the error bar represents the SE.

The application of the EPT framework and identification of a consensus MPA network proved even more successful in the realistic case where a deep rocky-reef community was targeted for protection. The consensus network of the five dispersal strategies performed almost as well as the individual optimal networks for each dispersal strategy. The overlap between the optimal networks for five dispersal strategies was here considerably greater than for the theoretical test case 1 because the dispersal strategies for the realistic case showed overlaps in PLD and dispersal depth reflecting available

information about variation in these traits. This points to the importance of intraspecific variation in larval dispersal traits in terms of bet-hedging for suitable settling sites. The variation in dispersal traits should also make selection of MPA sites for multiple dispersal strategies less critical since it will be easier to find a consensus network that ensures connectivity for all species.

A particular constraint when the goal is to protect communities, that is an assemblage of species that co-occur locally, is that successful conservation should maintain this
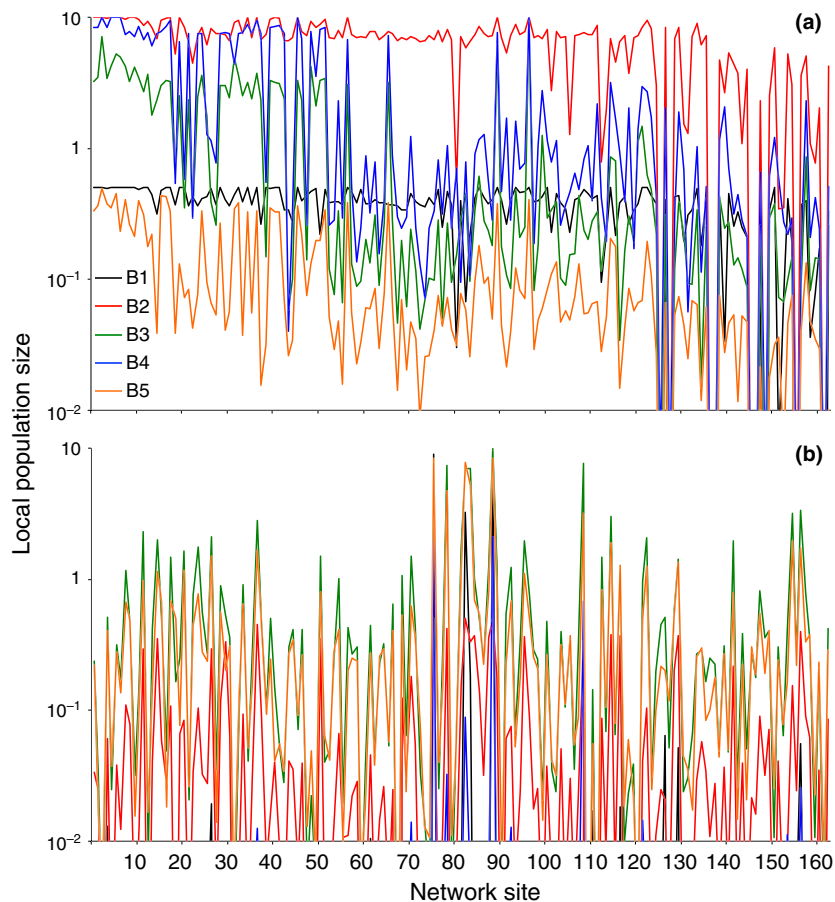
Figure 5 The degree of co-occurrence of populations within the MPA network of the dispersal strategies B1–B5 in the realistic case with a deep rocky-reef habitat. (a) Co-occurrence within the consensus network, (b) co-occurrence within a randomly selected network. Co-occurrence is arbitrarily evaluated above a local population size of 0.01. Each network consisted of 163 sites.

species assemblage within the MPA network. The realistic case for the deep rocky reefs shows that the optimal consensus network resulted in co-occurrence of all five dispersal strategies in over 90% of the MPA sites, while co-occurrence was much more erratic in a randomly selected network with an incomplete community in many sites.

The comparison with the existing MPA network showed that the consensus network performed better for all five dispersal strategies. In fact, the existing MPA network performed only marginally better than a completely random network, which is not surprising because connectivity was not part of the site selection criteria. The analysis indicates that present worries about existing MPA networks may be valid, that is that they are not biologically functional and lack ecological coherence (Abdulla *et al.*, 2008; HELCOM, 2009). The analysis of co-occurrence of taxa with different dispersal strategies also suggests that MPA networks selected without considering connectivity may fail in the protection of whole communities.

There are some limitations with the approach we here propose to identify optimal MPA networks or assess existing networks. First, connectivity is only one of many criteria for MPA site selection with respect to biological functionality (e.g. Agardy *et al.*, 2003; Kool *et al.*, 2013). Additional criteria may include habitat quality or other features and risk for disturbances (e.g. Roberts *et al.*, 2003). Second, detailed

information about connectivity is difficult to obtain. However, recent advances in biophysical modelling (e.g. Cowen & Sponaugle, 2009), as used here, together with high-resolution genotyping, for example using thousands of single nucleotide polymorphisms, (Allendorf *et al.*, 2010; Reitzel *et al.*, 2013) make this increasingly feasible (Kool *et al.*, 2013). A third obstacle is the currently poor mapping of the seafloor in most coastal areas. We used habitat predictions for rocky reefs, which is a coarse approximation of uncertain quality. A fourth limitation is that we do not consider any biological interactions. A community that is targeted for protection includes predators and prey as well as competing species, where each interacting species may show metapopulation dynamics. The persistence of such metacommunities (e.g. Guichard *et al.*, 2004) will be much more complex to predict and protection through MPAs may lead to counterintuitive effects (Baskett *et al.*, 2007; Kellner *et al.*, 2010) especially if non-equilibrium local dynamics, for example limit cycles, is considered (Gouhier *et al.*, 2013). The inclusion of species interactions in conservation planning is a future challenge.

The major strength with the present EPT approach is that design of MPA networks is dynamically linked to the dispersal probabilities allowing the identification of an optimal network with respect to population persistence. With the growing availability of detailed connectivity data from models or population genetics, EPT represents a practical method

to incorporate connectivity in a quantitative way to aid in spatial planning to propose MPA networks or assess existing networks, for example to identify suitable areas to add to the network. The extension to search for optimal consensus networks including multiple species or groups of dispersal strategies represents a first-order guideline to protect whole communities in the absence of detailed information on species interactions. Finally, it is desirable to combine the framework presented here with existing conservation-planning software to achieve more holistic predictions of sustainable MPA networks. Although existing planning tools do not explicitly analyse the effect of connectivity on site selection, it would be possible to implement EPT routines in existing grid-based software, for example Zonation (Lehtomäki & Moilanen, 2013).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Dispersal directions in the ocean circulation model.

Figure S2. Venn diagram showing spatial overlap of optimal networks.

Figure S3. Validation of the performance of optimal networks with the metapopulation model.

BIOSKETCHES

Per R. Jonsson is interested in how dispersal of marine organisms affects demography, evolution and strategies for management and conservation.

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