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Swedish Agency for Marine and Water Management

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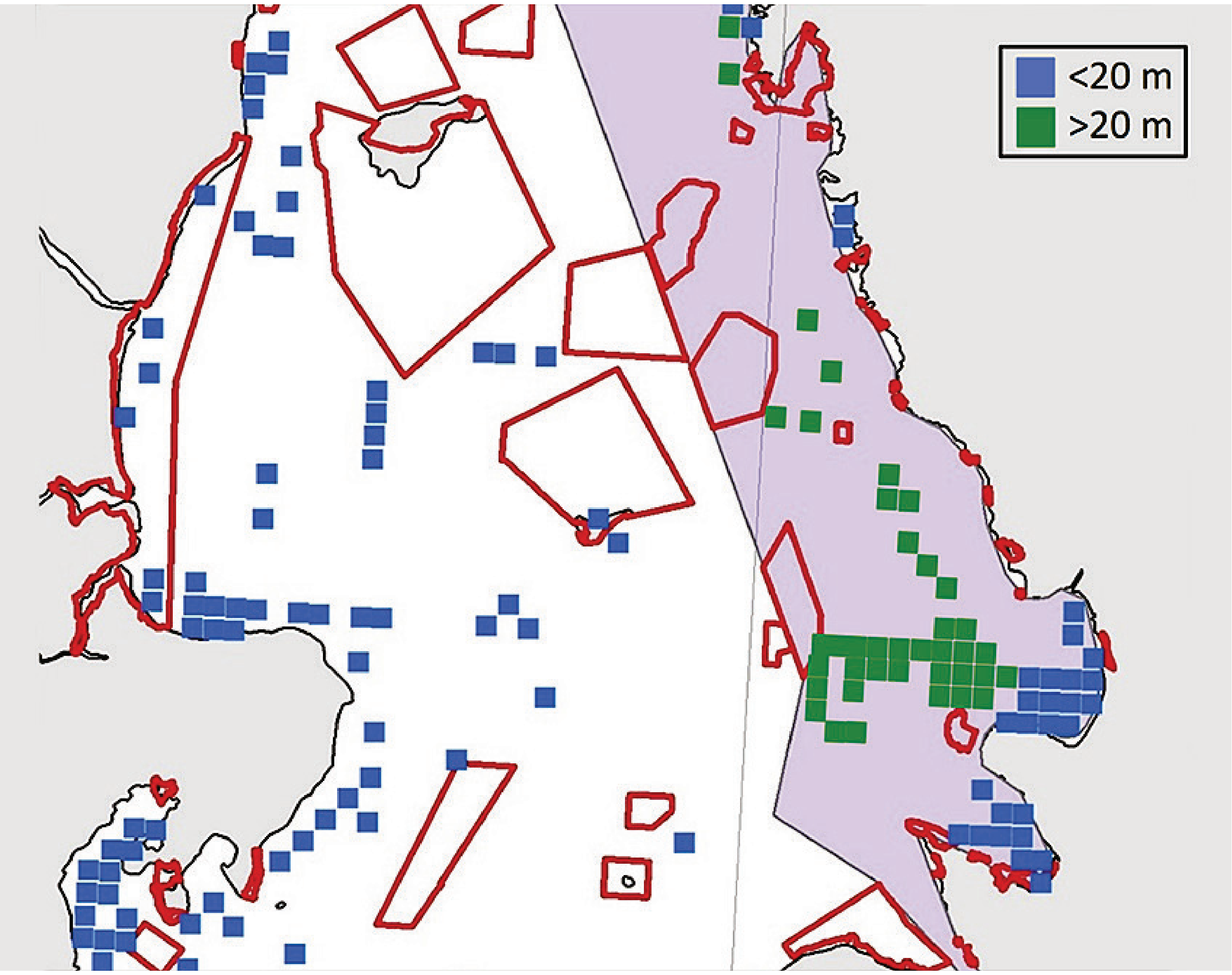

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Identifying new areas adding larval connectivity to existing networks of MPAs

The case of Kattegat and Skagerrak

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Preface

This study has been prepared by the Swedish Institute for the Marine Environment on request of the Swedish Agency for Water and Marine Management to provide managers of marine protected areas (MPAs) in the Kattegat-Skagerrak area with scientific information about larval dispersal and connectivity to improve the ecological coherence of the MPA-network in the region. The aim of the study was to use empirical data on larval traits and model tools to identify new areas that could be added to the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area that would best enhance larval connectivity in the network. A specific aim was to identify the best locations to place 1000 km^2 of new MPAs within Swedish waters in the Kattegat-Skagerrak area.

Förord

Inom ramen för Konventionen om biologisk mångfald har Sverige och 167 andra länder kommit överens om att 10 % av havet ska skyddas. Marint områdesskydd är en viktig del i arbetet med att nå flera miljömål, särskilt ”Hav i balans samt levande kust och skärgård” och ”Ett rikt växt och djurliv”. Detta har också tydliggjorts i etappmålet inom det svenska miljömålssystemet. Nätverk av marina områdesskydd är också en viktig del i förvaltningen av våra havsområden i Östersjön och Nordsjön där samarbete pågår inom Helcom respektive Ospar. Marint områdesskydd kopplar också till genomförandet av havsmiljödirektivet och är ett verktyg i havsplaneringen. På uppdrag av regeringen ska Havs- och vattenmyndigheten 2016 redovisa en analys av det befintliga nätverket av skyddade marina områden och bedöma om dessa är ekologiskt representativa och sammanhängande, samt analysera funktionaliteten av skyddet.

Ett rätt utformat nätverk av sammanhängande marina skyddsområden förväntas skydda mer än sina enskilda beståndsdelar. Det är dock ofta oklart hur nätverk av marina skyddsområden skall utformas på bästa sätt för att ta hänsyn till dynamiken i havet och passiv såväl som aktiv förflyttning av växter och djur mellan olika havsområden. Verktyg har saknats som inkluderar denna typ av samband vid utformning och utvärdering av nätverk av marina skyddsområden, speciellt när det gäller att hitta de bästa områden som kan adderas till existerande nätverk.

Denna rapport beskriver och tillämpar en metod för att studera hur populationer av växter och djur är sammanbundna via spridning i havet, dvs. populationernas konnektivitet.

Med hjälp av modellering av hur planktoniska larvstadier sprids försöker rapporten ge svar på frågan: vilka nya skyddsområden som bäst skulle förstärka konnektiviteten mellan existerande skyddade områden i Västerhavet?

Studien tillför ny kunskap och har samordnats av Havsmiljöinstitutet. Forskningsgruppen som genomfört studien är tvärvetenskaplig och förenar oceanografisk, matematisk, biologisk och ekologisk kunskap för att svara på en förvaltningsfråga. Det unika med studien är att frågorna har formulerats i samtal mellan forskare och förvaltare från HaV och länsstyrelser.

Antagandet att de skyddade områdena erbjuder bättre levnadsförhållanden än utanför områdena, är något som vi idag inte kan med säkerhet påstå. Liksom metoden i denna studie, måste det antagandet verifieras i fält.

Det är Havs- och vattenmyndighetens förhoppning att denna studie kan bidra till en framtida utveckling av ett väl fungerande nätverk av skyddade områden!

Björn Sjöberg
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Summary

Networks of marine protected areas (MPAs) are presently being developed in many countries with the aim to preserve biodiversity and restore overexploited stocks. However, one major challenge for the design and management of a functional MPA-network is the lack of information about how larval dispersal affects connectivity in the network and persistence of included species. Tools have been lacking that include larval connectivity into design and assessment of MPA-network, and in particular regarding finding the best new areas that will enhance larval connectivity in the existing networks.

In the present study we build on earlier model studies on larval dispersal and assessment of MPA-networks in the Kattegat-Skagerrak area (Moksnes et al. 2014), and use novel theoretical tools to identify new areas for the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area that would best enhance larval connectivity for benthic communities living shallower than 100 m. We also use new methods to identify areas with restricted larval dispersal and subpopulations within the study area, to assist in the selection of new MPAs. The assessment includes also benthic communities that are intolerant to low salinities and therefore have limited distribution in the Baltic Sea.

The study demonstrates that the connectivity and protection of benthic communities in the existing MPA-network could be substantially improved by a relatively small addition of carefully selected new MPAs. Adding approximately 1000 km^2 of model-selected areas to the existing network (representing an extension of the existing network area with 15–19 %) increased the simulated populations of benthic organism with on average 39–103 % in comparison with the existing network. In contrast, a random selection of new MPAs of the same size only increased the population sizes with 0–19 %.

The study identified several areas with restricted larval dispersal and isolated subpopulations within the study area, which may have important implications for management of both genetic and species diversity. The results suggest that it may be important to manage the western Baltic Sea, Kattegat, coastal Skagerrak (including both the Swedish and Norwegian coasts) and the area northwest of Jutland as separate management units since restricted larval dispersal may create genetically distinct subpopulations in these regions. The study also identified restricted larval dispersal within Kattegat and Skagerrak that may create areas with benthic communities that are demographically isolated from neighboring communities. For management of populations and local species diversity, it is important to ensure that there are MPAs within each demographically isolated area.

One such area was identified along the Swedish Kattegat coast, which presently has few large MPAs, in particular for shallow benthic communities (<20 m). The analysis identified shallow areas within the larger bays *Skälderviken* and the *Laholmsbukten,* and a deeper area located between the *Laholmsbukten* and *Stora Middelgrund* in southeastern Kattegatt as being key areas for larval connectivity and persistence of shallow and deep benthic communities, respectively, in Kattegat. The results suggest that these areas (covering approximately 700 km^2 in total) constitute the best additions, in respect of larval connectivity, to the existing MPA-network found within Swedish waters.

For management purposes, these results should only be viewed as guide for identifying general areas within the study region that are important for improving the connectivity of pelagic larvae within the existing MPA-network. Due to the limitation of the model they should not be viewed as a blue-print of the exact locations of an optimal extension, particularly not in the coastal zone. However, the study does represent the best available assessment to day of larval dispersal and connectivity in the study area, and the result could therefore provide manager with helpful information of one important aspect to include in the decision process when selecting new MPAs.

Sammanfattning

Nätverk av marina skyddsområden utgör en förvaltningsstrategi som ökar i användning för att skydda hotade marina arter och livsmiljöer. Det är dock ofta oklart hur nätverk av marina skyddsområden skall utformas på bästa sätt. Viktig information som saknas är hur planktoniska larvstadier sprids med havsströmmar och hur detta påverkar konnektiviteten i nätverket, dvs. hur bottensamhällen i olika områden är sammanlänkade via larvspridning. Verktyg har saknats som inkluderar denna typ av konnektivitet vid utformning och utvärdering av nätverk av marina skyddsområden, speciellt när det gäller att hitta de bästa områdena som kan adderas till existerande nätverk.

Denna studie bygger på tidigare modellstudier av larvspridning och utvärdering av ekologiskt uthålliga nätverk i Västerhavet (Moksnes m.fl. 2014). Här använder vi nya teoretiska verktyg för att identifiera nya skyddsområden inom Skagerack-Kattegatt-Bälthavet som på bästa sätt höjer konnektiviteten via larvspridning inom existerande nätverk för bottenlevande organismer som lever grundare än 100 m. Vi använder också nya metoder för att identifiera delområden som har begränsad larvspridning och konnektivitet till angränsande områden (d.v.s. partiella spridningsbarriärer), vilket utgör ett viktigt underlag vid val av nya skyddsområden. I studien har vi också inkluderat analys av marina organismer som är intoleranta för låga salthalter och därför har begränsad utbredning i Östersjön.

Resultaten från analysen visar att konnektiviteten och skyddet av marina bottensamhällen inom det existerande nätverket i Västerhavet skulle kunna förbättras avsevärt genom ett relativt litet tillskott av noga utvalda, nya skyddsområden. Ett tillskott på ca 1000 km^2 av nya skyddsområden som valts av modellverktyget (motsvarande 15–19 % av de existerade nätverken) skulle öka storleken på bottensamhällena i Västerhavet med 39–103 % i jämförelse med det existerande nätverket, enligt modellresultaten. Ett slumpvist valt tillskott av samma storlek skulle endast öka bottensamhällenas storlek med 0–19 %.

Studien identifierade flera delområden som har begränsad larvspridning och konnektivitet till angränsande områden, vilket ger viktig information vid förvaltning av biologisk mångfald. Exempelvis indikerar resultaten att det kan vara av vikt att behandla den västra delen av Östersjön, Kattegatt, svenska och norska Skagerackkusten samt området nordväst om Jylland som separata förvaltningsområden där genetiska skillnader kan hittas inom samma art. Studien identifierade också flera delområden inom Kattegatt och Skagerack med tillräckligt begränsad larvspridning till närliggande områden för att de skall kunna utgöra isolerade samhällen i fråga om ekologiska processer. Vid förvaltning av lokal artdiversitet är det viktigt att se till att det finns ett skyddsområde inom varje delområde där ett demografiskt isolerat bottensamhälle har identifierats.

I sydöstra Kattegatt, längs den svenska kusten identifierades ett sådant isolerat delområde som idag saknar större marina skyddsområden. Grundområden inom *Skälderviken* och *Laholmsbukten*, samt djupare områden mellan *Laholmsbukten* and *Stora Middelgrund* identifierades som nyckelområden för larvspridning och konnektivitet i Västerhavet. Studien föreslår att dessa områden (som täcker ca 700 km^2 totalt) utgör de bästa tillskotten inom svenska

vatten för att höja konnektiviteten i det existerande nätverket av marina skyddsområden i Västerhavet.

Då de använda modellerna har begränsningar bör studiens resultat endast användas vid förvaltningssammanhang för att identifiera generella områden som är viktiga för konnektivitet av larver längs Sveriges kuster, och inte ses som en karta för exakt positionering av nya skyddsområden. Detta gäller speciellt nära kusten där modellens grova upplösning ger mer osäkra resultat. Studien utgör dock den bästa tillgängliga analysen av larvspridningens effekter på marina skyddsområden i Västerhavet idag, och kan därför bidra men hjälpsam information för en viktig aspekt att inkludera när nya skyddsområden skall väljas.

1. Introduction

1.1. Marine protected areas – Importance of larval dispersal and connectivity

Marine protected areas (MPAs) are considered effective instruments to mitigate the loss of biodiversity and to restore overexploited stocks. In the Northeast Atlantic and the Baltic Sea, a network of MPAs have established through the EU-habitat directive, OSPAR and the Helsinki Commission with the aim to preserve biodiversity (HELCOM 2010, OSPAR 2011). However, the management of MPA-networks is challenged by a lack of information of how populations are connected between MPAs through larval dispersal. Most marine organisms have pelagic larvae or spores that spend weeks or months drifting in the water column, potentially dispersing large distances (10s to 100s of km). The transport of larvae among populations is a complex function of ocean circulation, duration of the pelagic stage and the drift depth of the larvae, which could result in large differences in dispersal between species and areas. However, our understanding of larval dispersal and connectivity among local marine populations is extremely poor (Cowen & Sponaugle 2009). It is therefore unclear whether a single MPA is large enough to allow settlement and recruitment within the MPA, or whether the distances between MPAs in a network are short enough to connect populations of targeted organisms. This lack of understanding creates problems both for the design and evaluation of functional MPA-networks (Nilsson Jacobi & Jonsson 2011). Moreover, since most MPA-networks aim to protect a large number of different organisms with very different dispersal potentials, the challenge is great to design a network that allows all organisms to persist, if at all possible. Realistic estimates of connectivity between habitats or MPAs that take into account local oceanographic circulation have not been available for any species in the HELCOM-OSPAR region (but see Moksnes et al. 2014). This lack of information was identified as an obstacle for evaluating the function of the MPA-networks in Northern Europe (HELCOM 2010, OSPAR 2011).

1.2. Assessing larval dispersal and connectivity with biophysical models

One of the most promising alternative methods to assess larval connectivity is numerical modeling of larval dispersal using 3D-hydrodynamic models of oceanographic flow coupled with models of biological traits (e.g. spawning season, larval duration and swimming depth). Assessments of such biophysical models have shown that they can successfully predict larval dispersal and connectivities in e.g. fish (Cowen et al. 2006, van der Molen et al. 2007). This approach has the advantage that it can generate a very high number of dispersal trajectories with high coverage in space and time resulting in detailed connectivity matrices for a range of dispersal strategies. Recently biophysical models have also been applied in a few studies to assess how dispersal and connectivity affect the designs of MPA-networks (White et al. 2010, Moffitt et al. 2011, Corell et al. 2012).

Although biophysical models can produce detailed connectivity matrices between sites, methods have been lacking of how to use the resulting connectivity matrices, which describe dispersal probabilities among sites, in a process to select an optimal network of MPAs in relation to larval connectivty. However, in a recent theoretical study, Nilsson Jacobi and Jonsson (2011) applied *eigenvalue perturbation theory* (EPT) on a connectivity matrix to identify the most valuable local populations for a metapopulation, and demonstrated that the EPT-method could be used as a tool to find optimal MPA networks. This method was subsequently developed to find the optimal network for a whole community of organisms with different dispersal capacities using multiple EPT ranking lists of diffierent larval types to identify a consensus network (Jonsson et al. *in press*).

In a recent model study, that used a unique set of empirical data of the larval traits, these methods were applied to identify the optimal MPA-networks with respect to the larval connectivity for shallow and deep benthic communities in the Kattegat-Skagerrak of the North Sea area (Moksnes et al. 2014). This study differed from previous assessments of the coherence of MPA-works (e.g. HELCOM 2010, OSPAR 2011, OSPAR 2013) in several important ways: (1) by not only assessing connectivity between MPAs, but including all areas that may harbor the type of benthic community being assessed, (2) by including some information on habitat distribution, (3) by including information on larval traits based on empirical studies, and (4) by using modeled connectivity matrices and the EPT-method to identify the optimum network of MPAs. The results of the model study demonstrated that in comparison to the existing MPA-network in the area, the EPT-selected consensus network of the same size resulted in 200–500 % larger population size of the benthic communities (Moksnes et al. 2014). This study suggests that the present MPA network in the Kattegat and Skagerrak area does not have the best design with regards to larval connectivity, and that the network could be improved substantially by carefully selecting the locations that enhance larval connectivity in the network.

1.3. Aims of study

In the present study we build on earlier model studies in the Kattegat-Skagerrak area (Moksnes et al. 2014), using the same model domain, larval traits, and EPT-methods, but with the aim to identify new areas to add to the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area that would best enhance larval connectivity in the network. As a complement to finding the optimal extensions to the network, we also assessed the degree of isolation between subpopulations within the study area as a result of restricted larval dispersal, which could influence the selection of new areas for the MPA-network. To address one of the limitations of the earlier study, we also assessed benthic communities that are intolerant to low salinities and therefore have limited distribution in the Danish Straits and the Baltic Sea. An additional aim of the study was to identify the best locations, with respect to the larval connectivity, for placing 1000 km^2 of new MPA area within Swedish waters in the Kattegat-Skagerrak area, to provide Swedish authorities with information that could support the decision process when selecting new MPAs for the planned extension of the Swedish MPA-network.

2. Methods

To identify the optimal areas based on larval connectivity that could be added to existing networks of MPAs in the Kattegat-Skagerrak area of the North Sea, we simulated larval dispersal of benthic organisms using a 3-D ocean circulation model coupled with a particle-tracking model. Optimal areas here refer to those areas where protection should contribute most to the persistence of the whole metapopulation (i.e. all subpopulations connected via larval dispersal) in the target area. Based on the resulting larval connectivity, we used *eigenvalue perturbation theory* (EPT) to develop a new mathematical tool to identify new MPAs that would best complement the existing network to maximize metapopulation persistence of benthic species both within and outside MPAs. Using metapopulation modeling, we finally examined if the new network with additional areas provided better protection to the benthic populations than a network with randomly chosen new areas. We also used modelled dispersal probabilities and a novel approach based on a minimization algorithm to identify invisible barriers to larval dispersal and subpopulations within the study area.

2.1. Oceanography of the study region

The biophysical model-study was focused on the Kattegat-Skagerrak area, but included also the eastern part of the North Sea along the west coast of Jutland, the Danish Straits and the western part of the Baltic Sea (fig. 1). The Skagerrak-Kattegat area borders the Baltic Sea and is strongly influenced by the outflow of brackish water through the Danish straits (The Sound (*Öresund*), Great Belt and Little Belt) into the Kattegat, resulting in a strong halocline at approximately 10–15 m depth, and a gradient of surface salinity from approximately 10 (practical salinity units) in the Danish straits and southern part of the Kattegat to 34 in northern Skagerrak. The Baltic current, which brings low saline surface waters from the Baltic Sea northward along the Swedish west coast, is the main residual component of the flow through Kattegat, but can be temporarily reversed on occasions with strong westerly winds. The Baltic current continues out in Skagerrak where the strong and permanent Norwegian coastal current, with velocities ranging up to 150 cm s^{-1}, continues the transport of the Baltic Sea outflow to the Norwegian Sea. The dominant coastal current in the southeastern North Sea is the Jutland current, which transports North Sea water along the west coast of Jutland and into Skagerrak and Kattegat, where it meets the Baltic current and turns north. Tides in Skagerrak and Kattegat do not play an important role for the water circulation, which is determined mainly by baroclinic flow of Baltic water and wind forced currents (Andersson and Rydberg 1993, Rodhe 1998).

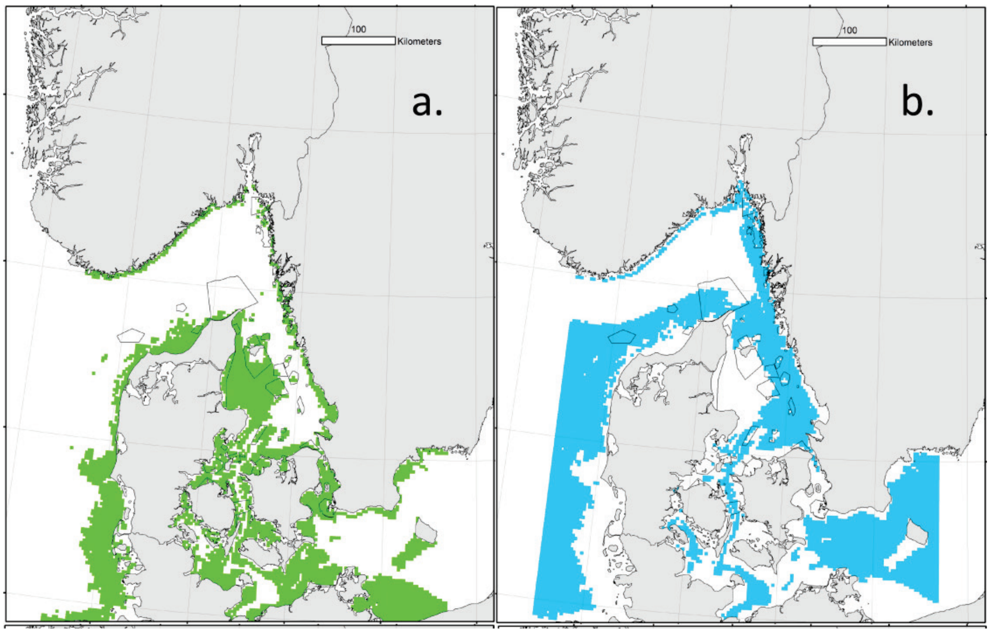


Figure 1. Maps showing the model domain and the distribution of (a) shallow (1–20 m) and (b) deep (21–100 m) areas. The marked areas are MPAs in the study region. Since bottoms deeper than 100 m was not included in the assessment of larval dispersal, the connectivity of the deeper central part of Skagerrak was not assessed (white area in Skagerrak in panel b).

2.2. Biophysical model

To simulate the dispersal of planktonic larvae in the model experiment, two different computer models were used. First a 3-D ocean circulation model produced fields of velocity, salinity and temperature to describe the environment in all parts of the model domain for the modeled time period. Secondly, a particle-tracking Lagrangian trajectory model calculated the displacement of individual virtual larvae (trajectories) in the flow field. Based on empirical data on larval traits (see Moksnes et al. 2014), we assessed the dispersal and connectivity of virtual larvae representing 4 benthic community types found in the area (see below for details).

2.2.1. Oceanographic model

The ocean flow data used for the model study were produced with the BaltiX model, which is a regional Baltic/North Sea configuration of the NEMO ocean model (Madec 2010; http://www.nemoocean.eu/). The spatial resolution is 2 nautical miles (3.7 km) in the horizontal, and 56 levels in the vertical, ranging from 3 m intervals at the surface to 23 m in the deepest parts. The model has a free surface and allows the grid boxes to stretch and shrink vertically to accurately model the tides without generating empty grid cells at low tide. The computational domain of BaltiX covers the entire Baltic Sea, the North Sea and English Channel, with open boundary conditions between Cornwall and Brittany, and between the Hebrides Islands and Norway. A regional atmospheric model (Rossby Centre regional atmospheric model) with a resolution of 50 km is used for the atmospheric forcing. The model has been validated and shown to provide realistic sea surface height (SSH), sea surface temperature (SST), ice cover, and deep-water salinity (Hordoir et al. 2013a, Moksnes et al.

2014b). The water exchange between the Baltic and the Kattegat in the BaltiX model is analyzed in Hordoir et al. (2013b).

2.2.2. Particle tracking model

The dispersal of virtual larvae was calculated with the Lagrangian trajectory model TRACMASS (Döös 1995, De Vries and Döös 2001). It is an off-line particle-tracking model that calculates transport of particles using flow field data from a 3-D circulation model. Velocity fields were updated for all grid boxes in the model domain every three hours in this study, and the trajectory calculations were done with a 15-minute time step. To get the trajectory of a given particle the velocities are interpolated from the sides of the grid box and the successive transportation of the particle within the box is calculated analytically. To mimic larval traits, the vertical position of the trajectories was locked at predetermined depths. For a technical /mathematical description of the algorithms used in TRACMASS see for example the appendix in Döös (1995), and de Vries and Döös (2001).

2.2.3. Study domain and larval types

Study domain

In the model experiment, larval trajectories were released and monitored for settlement in all 3.7x3.7 km model grid cells from 1–100 m depth in an area starting in the German Wadden Sea in the west to the western part of the Baltic Sea in the east (fig. 1). The study area consisted of 8992 grid cells. Although the main focus of this study was on the Kattegat-Skagerrak area, a larger region was included in the model to avoid boundary effects and to allow a natural exchange of larvae also from nearby regions. Since bottoms deeper than 100 m was not included in the assessment of larval dispersal, the connectivity of the deeper central part of Skagerrak was not assessed (fig. 1). The dispersal experiments were repeated for 8 years (1995–2002) to cover extremes in the North-Atlantic Oscillation cycle (Hurrell and Deser 2009).

Included MPA-network

To be able to identify the optimal areas in respect of larval connectivity that could be added to the existing MPA-network in the study area, the spatial distribution of existing MPAs that provided protection to benthic communities in the Skagerrak-Kattegat area and the Danish Straits (i.e. OSPAR-MPAs, Natura 2000 and marine reserves) were included in the model. Data on the location of MPAs within the study area (i.e. Kattegat and Skagerrak) were obtained in GIS-format from the County Administrative Board of Västra Götaland, Sweden. Since the BaltiX-model has a spatial resolution of 3.7 x 3.7 km^2 and a simplified coast line with poor resolution of small fjords and coastal archipelagoes, all MPAs smaller than 1 km^2 were excluded from the analyses, and larger MPAs located inside the coastal topography not resolved by the model were placed in the closest grid cell in the model. Because of this size-limitation, few Norwegian MPAs were included in the study. The large OSPAR-MPA *Bratten* (O-S-0520189) in the center of Skagerrak was not included in the analyses since it is located deeper than 100 m and is not included in the model domain where larvae were seeded. In addition, the study did not include areas were commercial fishing is restricted, e.g. the Swedish trawling boundary restricting trawling to 4 nm off the coast. In total, 134 MPAs ranging in size from 1.2 to 2 711 km^2 covering a total area of approximately 12 000 km^2, and including in total 824 grid cells, were included in the study (see Moksnes et al. 2014 for a detailed description of the MPAs).

Simulated benthic communities

The model experiment assessed larval dispersal of 4 types of benthic *communities (1) shallow benthic organisms tolerant to low salinities, (2) shallow benthic organisms intolerant to low salinities, (3) deep benthic organisms tolerant to low salinities, and (2) deep benthic organisms intolerant to low salinities*. The organisms that were tolerant or intolerant to low salinities used the same larval dispersal types within each depth habitat, but the intolerant larvae were not started within the low salinity areas and excluded if they settled within a low salinity area.

Organisms with salinity restriction include plants and animals that are intolerant to low salinities during at least some part of the life cycle (e.g. most echinoderms, certain crustaceans, molluscs, polychaetes, fish, etc.), and that could therefore not survive or reproduce in the Baltic Sea. To approximate the southern distribution of these organisms in the Kattegat and the Danish Straits, we used ICES data of salinity measurements below 20 m depth in the study area (ICES 2014), and an annual mean salinity value of approximately 25 in the bottom water to represent a minimum salinity. Using this value as a guide, as well as literature on the distribution of benthic species in the study area (Ojaveer et al. 2010), we set the southern border for organisms intolerant to low salinities from the northern part of The Sound to the middle of the Great and Little Belt (fig. 2).

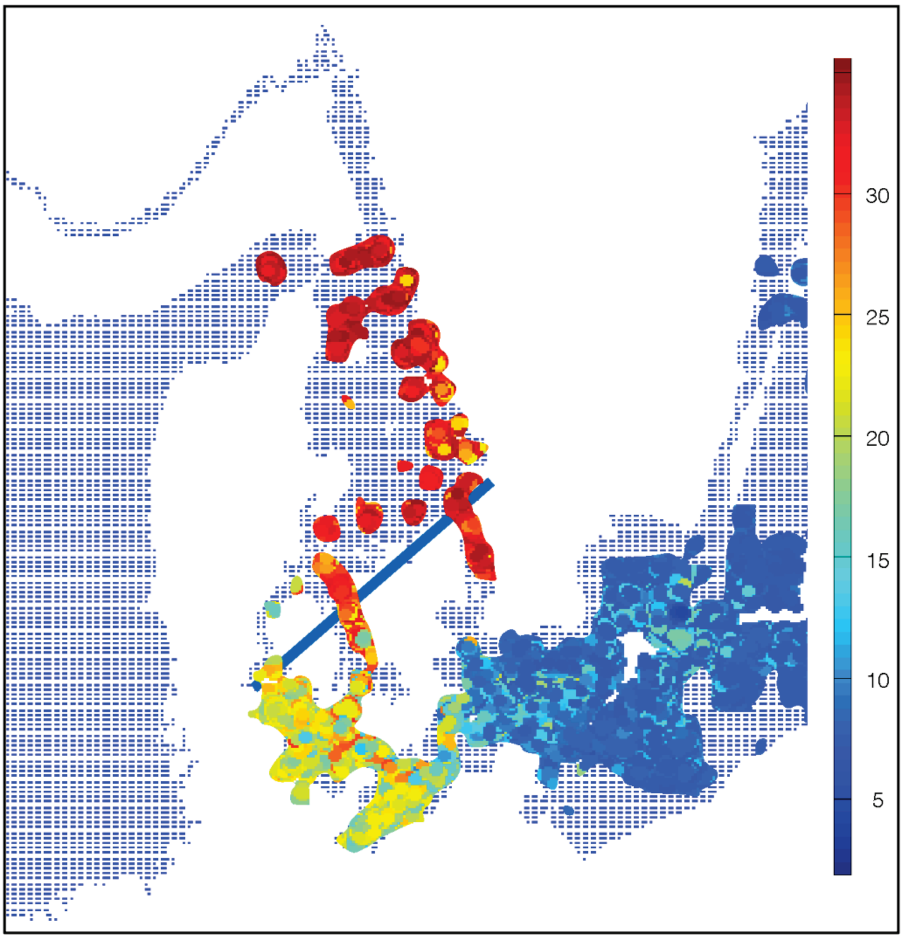
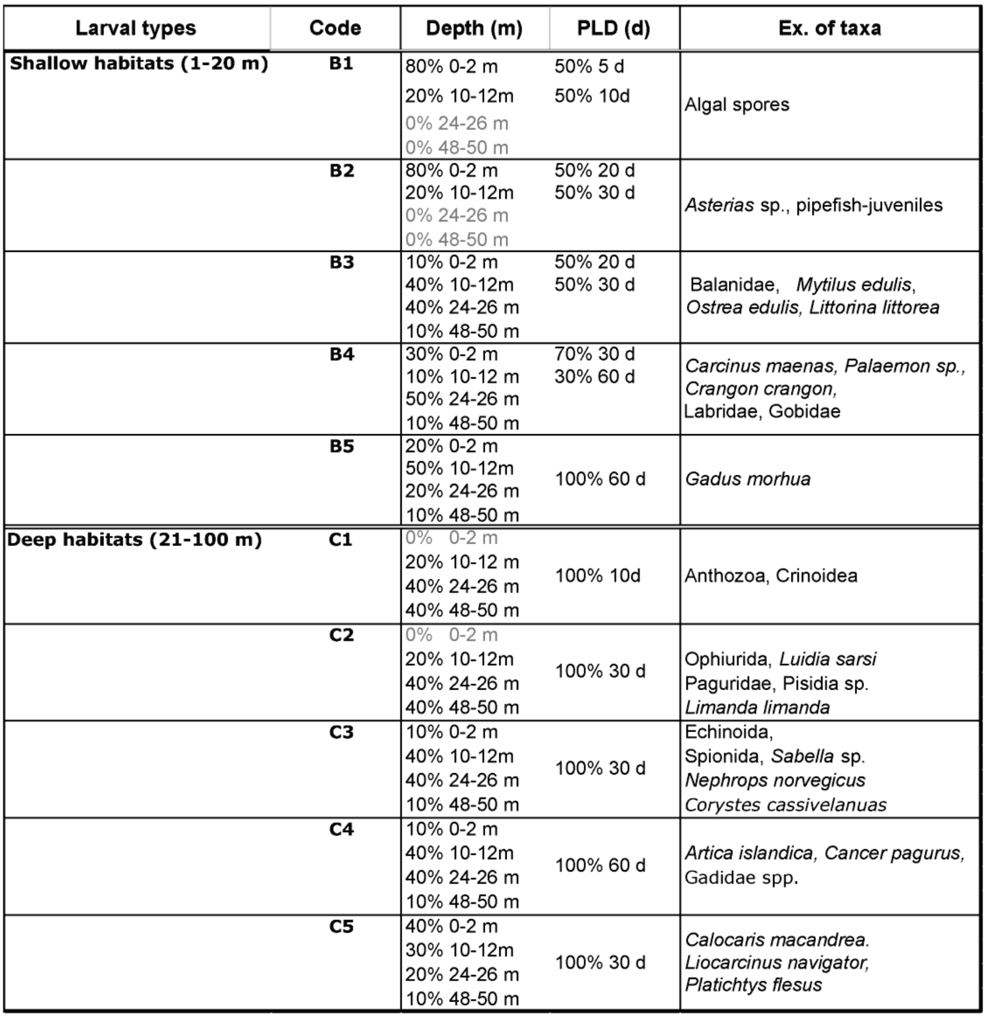


Figure 2. *Salinity restrictions*. Annual average salinity values at >20 m in the study area (ICES 2014) and the selected southern border in Kattegat for organisms intolerant to low salinities during some part of development.

The modeled organisms were separated into benthic communities living above and below 20 m (fig. 1). This separation was based on the higher salinity fluctuation above this depth affecting the composition and diversity of the benthic communities in the Kattegat-Skagerrak area. Moreover, the maximum depth for macroalgae is around 20 m along the Swedish west coast (Naturvårdsverket 2007), and thus 20 m also approximately separates the photic and the aphotic zone in this area. Because of lack of accurate data, we did not try to separate between hard and soft bottom communities (see Moksnes et al. 2014 for details).

The shallow and deep benthic communities hosted 5 larval types each, carefully chosen to represent selected groups of benthic plants and animals found above or below 20 m depth on both hard substrate and soft sediment habitats. The assessed drift depths and pelagic larval duration (PLD) varied between 0 to 50 m, and 5 to 60 days, respectively, whereas most larvae were released from April to August each year (Table 1). The chosen drift depths, PLDs and larval release dates were based on the results from a plankton survey and literature search, and when designing the larval types the goal was to include the dominant taxa from shallow and deep benthic habitats in the study area, as well as including as many as possible of the organisms from OSPAR's list of threatened and/or declining species (OSPAR 2008:6; see Moksnes et al. 2014 for details). For each larval type, 49 trajectories were released on the 15th of each month during the stated larval release periods, during 8 years (1995–2008). Shallow benthic virtual larvae were only released from and allowed to settle on grid cells with a depth between 1–20 m, and deep benthic larvae only on grid cells with a depth between 21–100. In total 335 million trajectories were modeled in the study.

Table 1. Summary of 5 larval types included in the shallow and deep benthic community types assessed in the study, and examples of species that are represented by the different larval traits. See Moksnes et al. 2014 for detailed description of the included larval types.



Larval types	Code	Depth (m)	PLD (d)	Ex. of taxa
Shallow habitats (1-20 m)	**B1**	80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 5 d 50% 10d	Algal spores
	B2	80% 0-2 m 20% 10-12m 0% 24-26 m 0% 48-50 m	50% 20 d 50% 30 d	*Asterias* sp., pipefish-juveniles
	B3	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	50% 20 d 50% 30 d	Balanidae, *Mytilus edulis*, *Ostrea edulis, Littorina littorea*
	B4	30% 0-2 m 10% 10-12 m 50% 24-26 m 10% 48-50 m	70% 30 d 30% 60 d	*Carcinus maenas, Palaemon sp.*, *Crangon crangon,* Labridae, Gobidae
	B5	20% 0-2 m 50% 10-12m 20% 24-26 m 10% 48-50 m	100% 60 d	*Gadus morhua*
Deep habitats (21-100 m)	**C1**	0% 0-2 m 20% 10-12 m 40% 24-26 m 40% 48-50 m	100% 10d	Anthozoa, Crinoidea
	C2	0% 0-2 m 20% 10-12m 40% 24-26 m 40% 48-50 m	100% 30 d	Ophiurida, *Luidia sarsi* Paguridae, Pisidia sp. *Limanda limanda*
	C3	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 30 d	Echinoida, Spionida, *Sabella* sp. *Nephrops norvegicus* *Corystes cassivelanuas*
	C4	10% 0-2 m 40% 10-12m 40% 24-26 m 10% 48-50 m	100% 60 d	*Artica islandica, Cancer pagurus,* Gadidae spp.
	C5	40% 0-2 m 30% 10-12m 20% 24-26 m 10% 48-50 m	100% 30 d	*Calocaris macandrea.* *Liocarcinus navigator,* *Platichtys flesus*

2.3. Connectivity analyses

At the end of the simulated pelagic larval period, only trajectories that were located above the same depth and salinity type as from where it was released was considered to have settled successfully and was included to estimate the connectivity between any two grid cells. If a trajectory ended up above a different depth or salinity class it was scored as lost, and it was not included in the connectivity matrices. We constructed 4 separate classes of connectivity matrices for the 4 types of benthic communities tested.

2.3.1. EPT-analyses

To identify the optimal areas to add to the existing network of MPAs with respect to the larval connectivity between sites we applied the new method using *eigenvalue perturbation theory* (EPT; Nilsson Jacobi and Jonsson 2011). An optimum network is here defined as the network of a given size that maximizes the growth rate of the whole metapopulation in the model domain when its abundance is low (far from carrying capacity), which is the typical case for threatened populations. A simplistic explanation of the EPT method is that the method estimates how good each grid cell is at both receiving settling larvae (source-strength) and at supplying settling larvae to other grid cells (sink-strength) and ranks all grid-cells after their combined source-sink-strength. The highest ranked grid cells thus represent the most valuable areas and local populations in the metapopulation for that particular larval type. We carried out EPT-analyses on the matrices for each of the 4 types of benthic communities separately. To be able to find the consensus network that would protect all 5 larval types in each community, we used a newly developed theory that can find networks for multiple species based on multiple EPT ranking lists (see Jonsson et al. *in press* for details).

In earlier studies we have used EPT-methods to find the optimal areas for a coherent MPA-network in the study area, without respect to the existing network (Moksnes et al. 2014). In this study we develop the EPT-method further, by including the existing MPA-network and use EPT to find the optimal areas to add to the existing network. The new metod ranks areas not yet included in the existing MPA network by using the multi-species EPT method to calculate the marginal effect of protecting each area given the existing MPA network (Nilsson Jacobi et al. *in prep*.)

2.3.2. Metapopulation models

To evaluate if the added grid cells identified by the EPT-method really improved the performance of the existing MPA network, we carried out metapopulation modeling where we explored the effect of protection when implementing different networks according to 4 scenarios: (1) the existing MPA networks, (2) randomly selected network, (3) the existing MPA-network with an additional 1000 km^2 of MPA-area selected with the EPT-method, and (4) the existing MPA-network with 1000 km^2 of randomly selected additional MPA-area. These analyses were carried out separately for the 4 types of benthic communities.

The simplistic metapopulation model considered all grid cells within the study domain as local populations of an annual organism connected by dispersal through the connectivity matrix. Every grid cell was given the same growth rate (inverted dominant eigenvalue of the connectivity matrix) except those grid cells included in MPA networks, which was assumed to grow 20 % faster because of being protected. Growth of local populations was density-dependent approaching carrying capacity according to a logistic function. To simulate stochastic reductions in population abundance, e.g. caused by hydrologic and climatic factors, the metapopulation was stochastically reduced by 95 % with an expected interval of 8 years. 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 an 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 (see Moksnes et al. 2014 for details).

To compare the protective effect of the different MPA-networks, the relative effect of protection was estimated by dividing the total size of the metapopulations (i.e. metacommunities) with and without protection for each of the 4 scenarios. This comparison was done for all 4 types of benthic communities.

2.3.3. Identification of dispersal barriers and subpopulations

Understanding spatial population structure and identifying areas with restricted larval connectivity to neighboring areas due to oceanographic dispersal barriers is essential in management of marine organism since dispersal barriers may create genetically or demographically isolated subpopulations. However, this constitutes a challenge for species with pelagic larvae that can disperse large differences. For the design of MPA-networks it is important to ensure that there are MPAs located in all supopulations of the metapopulation (Nilsson Jacobi et al. 2012).

Depending on the conservation goal of a species or community, different degrees of isolation between subpopulation may be of interest to identify. For management of commercial species and conservation of species diversity in an area, identification of demographically independent population or management units (MU) may be of interest (Moritz 1994, Palsböll et al. 2007). Since a low level of connectivity between subpopulations has little impact on the population parameters of the subpopulations, a certain degree of larval exchange can occur between demographically independent populations. The level of connectivity that leads to demographical independence is not well understood, and is likely to vary between species and populations, but below 10 % has been suggested as a critical boundary (Hastings 1993).

If the conservation goal is to protect genetic diversity and isolated genetically distinct subpopulations, the relevant population subdivision must be more isolated with very low connectivity between subpopulations. These management units have been termed *evolutionary significant units* (ESU; Ryder 1986, Allendorf & Luikart 2007). The critical boundary in connectivity that separates ESUs is not well understood, and also depends on the effective population size (Lowe & Allendorf 2010), which in general is poorly known for marine species. Connectivities below 1 % is probably required for genetic differentiation but depends greatly also on the strength of selection (Nilsson Jacobi et al. 2012).

In this study we assessed barriers to larval dispersal for populations within multispecies benthic communities, and the existence of areas with different degrees of isolation within the study area. We applied a novel approach based on a minimization algorithm that used the modeled dispersal probabilities generated in the connectivity analyses (Nilsson Jacobi et al. 2012). The basic idea in the algorithm is to split a metapopulation into subpopulations with maximal internal connectivity and minimal “leakage” between subpopulations.

In this study we assess dispersal barriers of communities consisting of several species with different larval types, and the described barriers and “sub-communities” are therefore dominated by the larval type with the largest dispersal distance. The identified subcommunities should thus be seen as a conservative estimate of the number of isolated areas in the region. For species with lower dispersal capacity the number subpopulation could be underestimated. In the analysis we used different degrees of leakage of larvae between subdivided communities, measured as the mean connectivity (Q) between the subcommunities (Nilsson Jacobi et al. 2012), so that 3–5, 14–16 and 30–32 subcommunities were obtain for each of the 4 types of benthic communities. The used range of mean connectivities with neighboring subcommunities (1–10 %) likely include both demographically independent and evolutionary significant units. Since the a smaller region was included for the benthic communities intolerant to low salinities, the mean connectivities used for these communities were slightly larger than the one used for the communities that were tolerant to low salinities.

3. Results

3.1. Identification of dispersal barriers and management units

The minimization algorithm identified several distinct dispersal barriers and areas with isolated benthic communities within the study area, which varied between community types. Independent of the mean connectivity used, a dispersal barrier was found between Kattegat and the Baltic Sea in the northern part of the Danish Straits, and Kattegat, Skagerrak and the west coast of Jutland were often identified as separate subcommunities, but more so for the shallow communities (fig. 3 and 4; see appendix 1 for more detailed figures from all analyses).

Using a low mean connectivity of larvae between subdivided areas (1–2 %), which may more identify evolutionary significant units, resulted in 3 to 5 subcommunities within the study area for the 4 types of benthic communities and showed different dispersal barriers depending on depth and salinity tolerance (fig. 3). For both the shallow and deep communities tolerant to low salinities, a dispersal barrier was found between Kattegat and the Danish Straits located in the northern part of The Sound and in the middle of the Danish belts, whereas no dispersal barrier was found within the Kattegat-Skagerrak area (fig. 3a,c). For the shallow community, a dispersal barrier was also found between the shallow North Sea areas along the west coast of Jutland and Kattegat-Skagerrak area, whereas this barrier was not present for the deep community. For the shallow community intolerant to low salinity, Kattegat, coastal Skagerrak, and the northwestern and southwestern coasts of Jutland were identified as 4 separate subcommunities, whereas for the deep community intolerant to low salinity, the North Sea, Skagerrak and northern part of Kattegat formed one isolated community separate from the remaining part of Kattegat (fig. 3b,d). The higher number of subdivided communities in the Kattegat-Skagerrak area for the species intolerant to low salinity was in part explained by a higher mean connectivity used in the analyses compared to the tolerant communities.

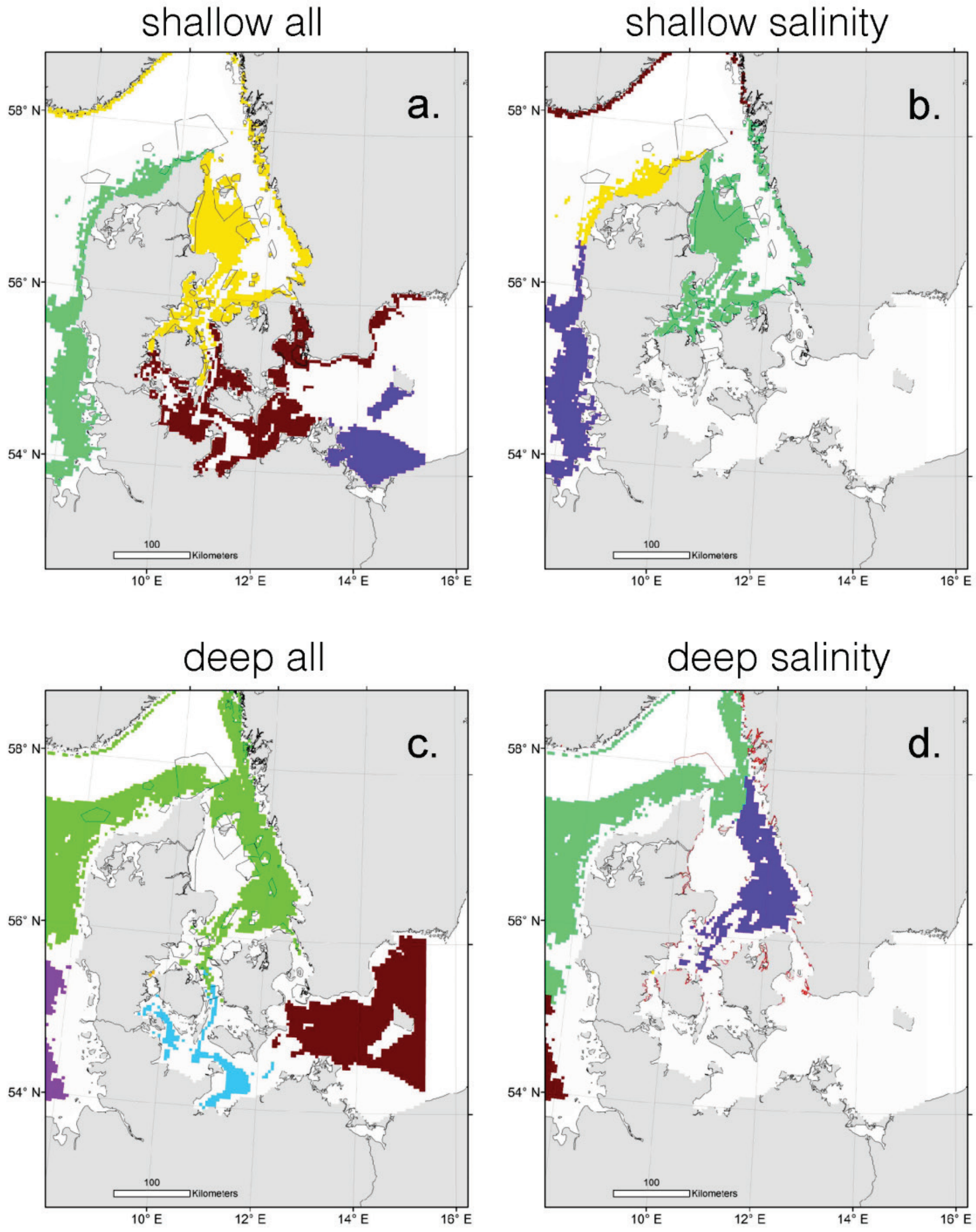


Figure 3. *Identification of evolutionary important management units*. Illustration of the resulting spatial structure of subpopulations within the benthic communities when assessing relatively strong dispersal barriers with a mean connectivity of 1–2 % of larvae between subdivided areas for the 4 benthic communities: (a) *shallow benthic organisms tolerant to low salinities* (shallow all), (b) *shallow benthic organisms intolerant to low salinities* (shallow salinity), (c) *deep benthic organisms tolerant to low salinities* (deep all), and (d) *deep benthic organisms intolerant to low salinities* (deep salinity). Black lines marks the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area.

Using a mean connectivity of around 10 % between subdivided communities, which may identify demographically independent units, resulted in finer separation of 14 to 16 subcommunities within the study area for the 4 types of benthic communities (fig. 4). For the shallow community tolerant to low salinities, the Danish Straits separated into 1–3 subcommunities per sound, and Kattegat into 3 subcommunities: a smaller in the southwestern corner north of the island Funen, a larger covering southern Kattegat and the Swedish coast up to Gothenburg, and a third subcommunity covering both the northwestern part of Kattegat and the Swedish Skagerrak coast up to Havstensund, south of the Koster archipelago (fig. 4a). Another subcommunity covered the rest of the Swedish coast and the whole Norwegian Skagerrak coast. The west coast of Jutland and the Wadden Sea consisted of 3 separate subcommunities (fig. 4a).

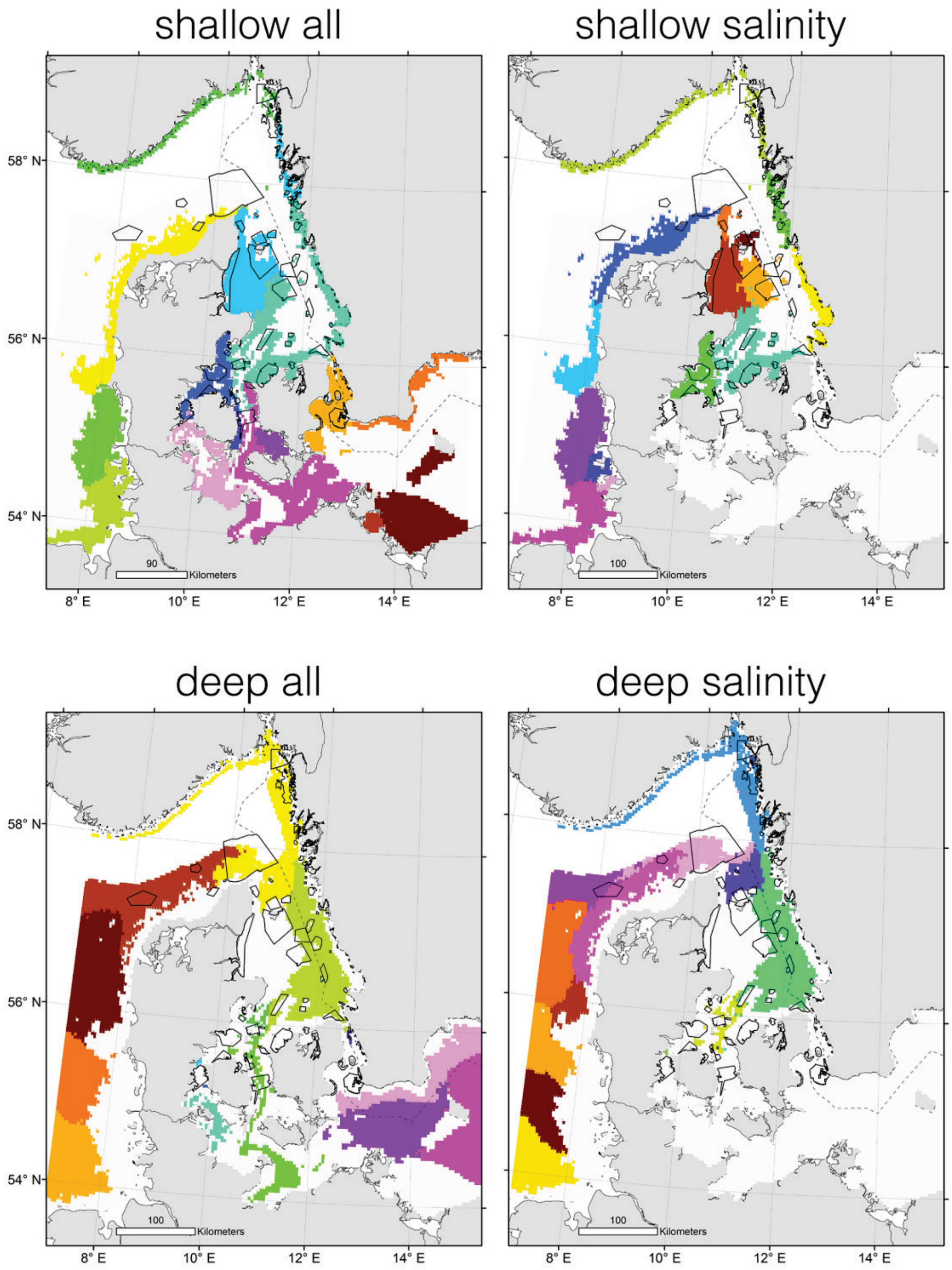


Figure 4. *Identification of demographically important management units*. Illustration of the resulting spatial structure of subpopulations within the benthic communities when assessing relatively weak dispersal barriers with a mean connectivity around 10% of larvae between subdivided areas for the 4 benthic communities (a) *shallow benthic organisms tolerant to low salinities* (shallow all), (b) *shallow benthic organisms intolerant to low salinities* (Shallow salinity), (c) *deep benthic organisms tolerant to low salinities* (Deep all), and (d) *deep benthic organisms intolerant to low salinities* (Deep salinity). Black lines marks the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area.

The shallow benthic community intolerant to low salinities showed similar dispersal barriers, but included more subcommunities, partly due to a higher mean connectivity used in the analysis. A new dispersal barrier was detected at the northern entrance to The Sound, splitting the southern subcommunity in Kattegat in two. A new subcommunity was also found along the Swedish west coast from the Kungsbacka fjord in the south to the island of Orust in the north, which was now separated from the western Kattegat. The rest of the Skagerrak coast in Sweden and Norway belonged to the same community. The north area of northwestern Kattegat and the west coast of Jutland was now also split into smaller subcommunities (fig. 4b).

The deep community tolerant to low salinities showed a partly different pattern with a large subcommunity stretching from northwestern Kattegat and the northeastern coast of Jutland over to the Swedish coast at the island of Tjörn and continuing all around the Norwegian Skagerrak coast. The remaining Kattegat consisted of a large subcommunity covering the eastern and southern part, and a small in the southwestern corner. In the Danish straits, one subcommunity was found in the deeper part of each sound, where the one in the Great Belt continued south into the Baltic Sea (fig. 4c). The deep community intolerant to low salinities showed almost identical dispersal barriers, with the exception in northern Kattegat where two new barriers were detected, splitting the Skagerrak subcommunity into three smaller parts (fig. 4b).

Assessing an even higher mean connectivity between subdivided communites (around 30 %), resulted in around 30 subcommunities within the study area, but with few new dispersal barriers within the target area in Kattegat and Skagerrak. For the shallow community intolerant to low salinities, a new dispersal barrier was detected at *Bjärehalvön* in southeastern Kattegat, and the subcommunities in western Kattegat were now split into several smaller parts. In Skagerrak, the Swedish and Norwegian coasts were now also split in two subcommunities (see fig 3 in appendix 1). For the deep community intolerant to low salinities, the subcommunity in southeastern Kattegat was now split into 4 new areas, with barriers located around *Lilla Middelgrund*, separating the northern and southern communities, and east of *Stora Middelgrund*, separating the eastern and western communities (fig 3, appendix 1).

3.2. Optimal new areas adding larval connectivity to existing MPA-networks

The identification of optimal areas that could be added to the existing MPA network, based on connectivity matrices from the model simulation and the EPT-method, resulted in different patterns for the 4 simulated communities. However, a higher concentration of selected areas were consistently found along the Danish and German coasts (83–89 %), and very few of the 400 highest ranked model grid cells were selected in coastal Skagerrak (3–7 %; fig. 5). The proportion of grid cells selected within the Swedish economic zone (including also the Baltic Sea area) varied between 9 and 13 % in the analyses of the 4 benthic communities.

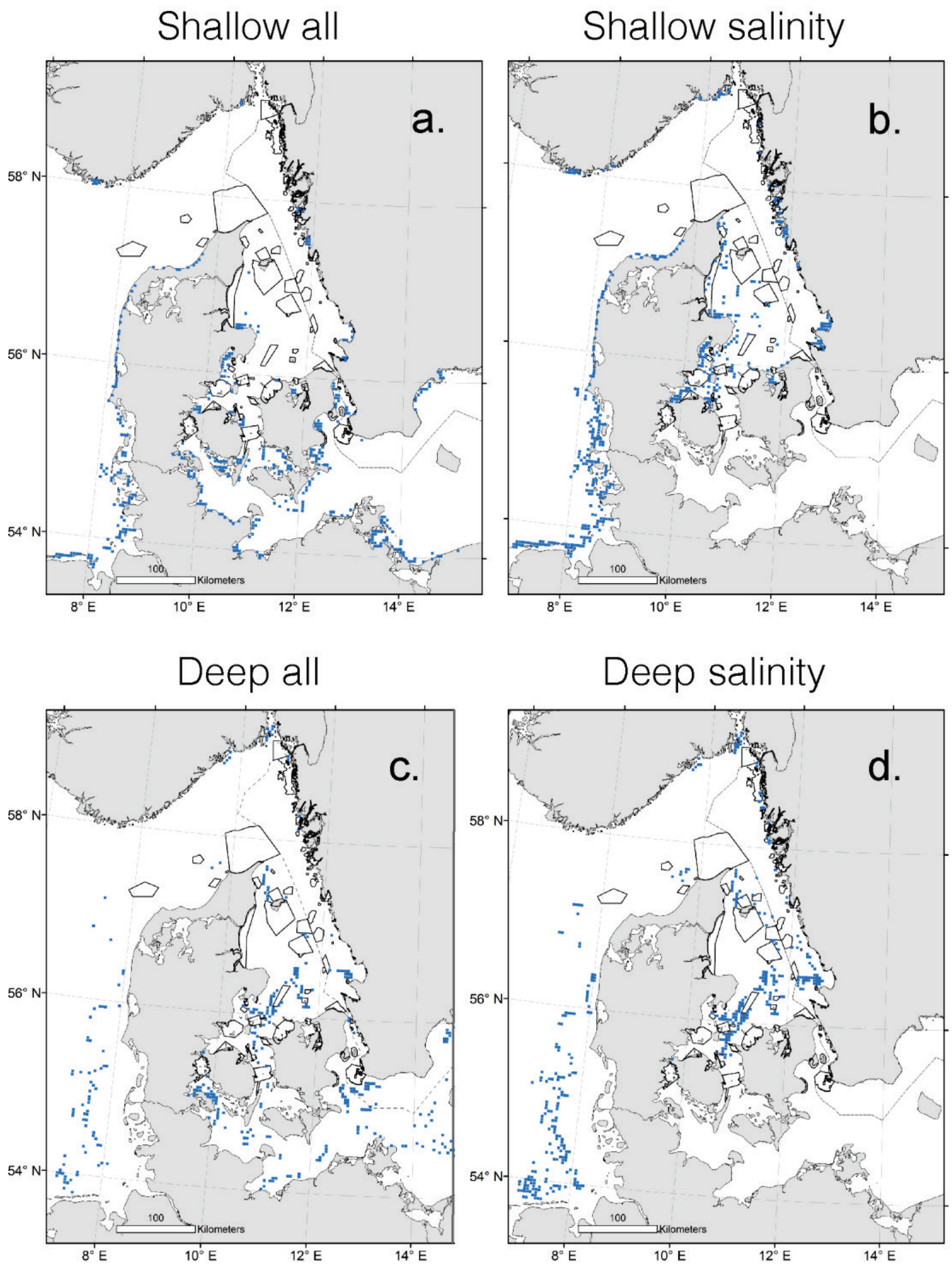


Figure 5. *Optimal areas that could be added to the existing MPA-network*. The blue squares mark the 400 highest ranked model grid cell in the EPT-analysis for the 4 benthic communities (a) *shallow benthic organisms tolerant to low salinities* (Shallow all), (b) *shallow benthic organisms intolerant to low salinities* (Shallow salinity), (c) *deep benthic organisms tolerant to low salinities* (Deep all), and (d) *deep benthic organisms intolerant to low salinities* (Deep salinity). Black solid lines marks the existing MPA-network included in the analysis. Dotted lines mark the Swedish economic zone.

The analysis of shallow benthic organisms tolerant to low salinities showed a high number of selected areas in the German and Danish Wadden Sea, around the Danish Straits, and along the German Baltic coast. A concentration of cells was also found in the Hanö Bay, on the Swedish Baltic coast (fig. 5a). In contrast, only a few grid cells were found along the west coast of Sweden, with a smaller concentration of cells found in the areas of *Skälderviken*, *Laholms-*

bukten, south of Gothenburg and inside Marstrand island. In Norway, only a few cells were selected outside the cities of Larvik and Kristiansand (fig. 5a). Restricting the shallow benthic communities to areas of higher salinities excluded areas in the Baltic Sea and the Danish Straits, and increased the number of cells in the other areas, but did not change distribution markedly. A higher number of grid cells were found along the Danish coast of western Kattegat, and also in the *Skälderviken*, *Laholmsbukten*, and around Gothenburg of the Swedish Kattegat coast. A few new grid cells were also found along the Swedish Skagerrak coast. In Norway the number of grid cells more than doubled, but around the same areas as for the communities tolerant to low salinities (fig. 5b).

The optimal new areas for deep benthic organisms showed a slightly different distribution than for the shallow communities, with a more scattered off-shore distribution in the southeastern North Sea, a concentration of selected areas in the deeper areas of southwestern Kattegat, west of *Laholmsbukten* in southeastern Kattegat. A smaller concentration of grid cells were also found between Skagen and the island Läsö in northwestern Kattegat. In Norway, the small number of grid cells were now found south of the Oslo fjord and the Langesund Bay (fig. 5cd). For the deep benthic organisms tolerant to low salinities, a concentration of selected grid cells were also found south of The Sound and Little Belt (fig. 5c). Similar to the shallow communities, restricting the larval dispersal to areas of high salinities did not change the general pattern of selected areas in Kattegat and Skagerrak, but increased the extent of the selected areas, in particular in the southern part of Kattegat. Along the Swedish Skagerrak coast a few selected grid cells were now found from the island of Orust in the south to the Koster archipelago in the north (fig. 5d).

3.3. Assessing the results with metapopulation models

To evaluate if the added grid cells identified by the EPT-method really represented a significant improvement to the existing MPA-network with respect to larval connectivity, we carried out metapopulation modeling assessing the protection effects of the different MPA-networks during periods of low population densities. Initial comparison between the existing MPA-network and a randomly selected network showed that the existing MPA-network provided slightly better protection for all benthic communities, resulting in 13 to 21 % larger metapopulation size than the random network for the 4 communities (fig. 6).

Adding 73 randomly selected grid cells (approximately 1000 km^2) to the existing MPA-networks of shallow habitats, increased the total area of the MPA-networks with 15 and 19 %, and increased the metapopulation sizes with on average 10 and 19 % in communities tolerant and intolerant to low salinities, respectively. However, adding the same number of grid cells selected with the EPT-method increased the metapopulation sizes with on average 101 and 105 % in communities tolerant and intolerant to low salinities, respectively (fig. 6ab). Thus, the EPT-method selected areas that provided 5 to 10 times better protection than a random selection of areas to add to the existing network of shallow habitats.

Adding 1000 km² of MPA-area to the existing MPA-networks of deep habitats showed a similar pattern, but with lower overall effects of MPA-extensions. An addition of 73 randomly selected grid increased the total area of the MPA-networks with 21 and 22 % in the deep communities tolerant and intolerant to low salinities, respectively, but showed no clear increase in metapopulation size in either community (0–1 % increase). However, adding 73 grid cells selected with the EPT-method increased the metapopulation sizes with on average 38 and 40 % in deep communities tolerant and intolerant to low salinities, respectively (fig. 6ab).

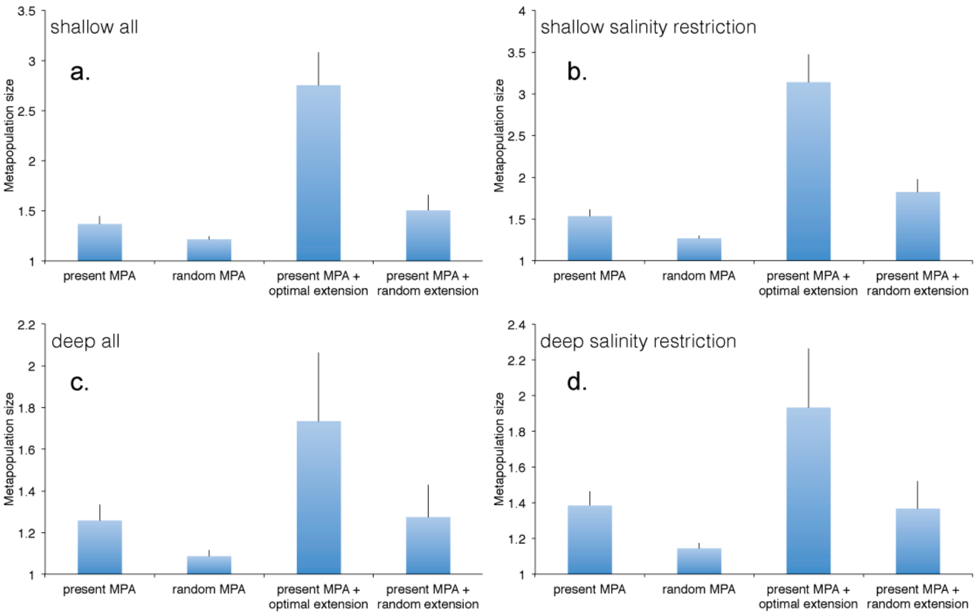


Figure 6. *Results from metapopulation modeling*. Comparison of the relative protective effects of different MPA-networks for the 4 benthic communities (a) *shallow benthic organisms tolerant to low salinities* (shallow all), (b) *shallow benthic organisms intolerant to low salinities* (shallow salinity restriction), (c) *deep benthic organisms tolerant to low salinities* (deep all), and (d) *deep benthic organisms intolerant to low salinities* (deep salinity restriction). Each panel show average size of the metapopulation (+SE) relative a metapopulation without any protection for 4 different networks: (1) the existing MPA-network (present MPA), (2) a randomly selected network (random MPA), (3) existing MPA-network with an EPT-selected addition of new areas (present MPA + optimal extention), and (4) existing MPA-network with a random addition of new areas (present MPA + random extention). The number of grid cells included in the MPA-network varied between benthic communities and was 472, 390, 352 and 336 in the *shallow all, shallow salnity, deep all* and *deep salinity* communities, respectively. The addition of MPA-areas were always 73 grid cells (constituting 15–22 % of the existing network).

4. Discussion

4.1. Limitations of the study

As in all model studies, this study has limitations and the result should therefore be viewed and used more as a guide of identifying the general areas within the study region that are important for improving the connectivity of pelagic larvae within the existing MPA-network, and less as a blue-print of the exact location of the optimal extension. One of the limitations of the study is the large spatial scale of the oceanographic model with poor resolution of the topographically complex coastal zone with fjords and smaller islands and which may therefore underestimate the retention of larvae and connectivity within the coastal zone. Because of the large scale of the model, all MPAs smaller than 1 km^2 were excluded from the study, and MPAs within fjord systems were placed by the closest available grid cell in the model. These MPAs may be locally important through self-recruitment, but at present little is known about circulation and retention of larvae within the coastal zone. For these reasons the results may have a higher degree of uncertainty for shallow habitats, in particular for areas with a topographically complex coast, such as the Swedish Skagerrak coast. At present, new studies using high-resolution oceanographic models of this area are being carried out to improve the understanding of circulation and retention of larvae within fjords and archipelagoes (Jonsson and Moksnes unpubl. data).

One improvement from earlier work with the same model (Moksnes et al. 2014) is that this study assessed physiological barriers to dispersal and survival by including also benthic organisms that are intolerant to the low salinities in the Danish Straits and the Baltic Sea, comprising many benthic species on e.g. OSPARs list of threatened and/or declining species. Although the tolerance to low salinity varies greatly between species (Ojaveer et al. 2010) and we used a rough boundary based on average salinity measures and distribution of species, the results from the analyses using the physiological barrier should still be more relevant for this group of species.

It is important to point out that the study only assessed the importance of larval connectivity for the MPA-network, and did not include migration of adult stages, or any aspects of habitat quality or distribution of species (information that is presently not available). Thus, if other criteria had been included, a different selection of areas could have been found.

Although there are limitations with the study, the oceanographic model used is state-of-the-art, and the larval traits simulations are based on a unique set of empirical data providing the best possible assessment today of larval dispersal and connectivity in the study area. The large-scale dispersal patterns between deeper areas away from the coast do not suffer from the mentioned scale-limitations and therefore provides a better description of the true larval connectivity. Thus, the results of dispersal barriers and subpopulation structure, and the identification of general areas that would enhance larval connectivity in the existing MPA-network should be of direct value for managers in the study area.

4.2. Management units

The study identified several distinct dispersal barriers to larvae and subpopulations within the study area, which have important implications for management of marine organisms. For management of genetic diversity and isolated genetically distinct subpopulations it is important to identify strong dispersal barriers that isolate subpopulations (Nilsson Jacobi et al. 2012). Using an average larval connectivity between subdivided communities of around 1 %, which may include evolutionary significant units (ESU; Allendorf & Luikart 2007) showed a clear separation between Kattegat and the Baltic Sea in the northern part of the Danish Straits for both shallow and deep benthic communities. For shallow communities, a barrier was also found at the tip of Jutland separating the Kattegat and costal Skagerrak populations from the North Sea. However, for deeper communities this barrier was not detected. A weaker dispersal barrier was also identified between Kattegat and Skagerrak around the island of Tjörn along the Swedish west coast for both shallow and deep benthic communities (fig. 3).

These results suggest that for benthic communities living shallower than 100 m, it may be important to manage the western Baltic Sea, Kattegat, coastal Skagerrak (including both the Swedish and Norwegian coasts) and the area northwest of Jutland as separate management units since barriers to larval dispersal may create genetically distinct subpopulations in these regions. This potential population structure may be important to take into account when assessing the environmental status of e.g. the marine biodiversity for the Marine Strategy Framework Directive. Since we assessed dispersal barriers for whole communities consisting of several species with different larval types, the size of the subcommunities are likely influenced by the species with the largest dispersal distance, making the number of identified management units conservative. For species with lower dispersal capacities, the size of management units may be smaller and the number larger. For the design of MPA-networks it is important to ensure that there are smaller MPA-networks within each of these regions. On this scale, there are several MPAs that include both shallow and deep benthic communities in each of theses regions in the Skagerrak-Kattegat-Danish Strait area, although there are presently few larger MPAs along the southern part of the Swedish Kattegat coast.

Higher migration rates between subpopulations that preclude genetic differentiation may still allow demographically independent subpopulation. Identification of this type of population structure is important for management of commercial populations and conservation of species diversity (Nilsson Jacobi et al. 2012). To assess the population structure with weaker dispersal barriers we used an average larval connectivity between subpopulations of around 10 %, which may be around the critical boundary for demographical independence (Hastings 1993). This analysis identified a number of potentially important demographic management units within the previous identified ESUs (fig. 4). For both shallow and deep communities, Kattegat and Skagerrak were identified as demographically isolated from each other, although the dispersal barrier was weaker between northwestern Kattegat and the southern part of the Swedish Skagerrak coast (fig. 4a,c), indicating an interesting source-sink dynamic across the sea basin. For most communities, southwestern, northwestern and eastern Kattegat were identified as one or more separate areas with partly isolated communities. For shallow communities, the Skagerrak coast was separated into two subcommunities with a dispersal barrier south of the Koster archipelago, whereas for the deeper communities it consisted of a single community.

Since the level of connectivity that leads to demographical independence is not well understood (Nilsson Jacobi et al. 2012), it is unclear which of the subpopulations identified in the different assessments that represent true demographic subpopulations for different species. However, the more general results may still be useful in identifying management areas for benthic species with pelagic larval stages in the area, that could guide e.g. the design of MPA-networks.

4.3. Identifying new areas adding connectivity to existing MPA-network

4.3.1. Method evaluation and the impact of adding new areas

In the study we used the modeled larval connectivies for multispecies benthic communities, and a new development of the EPT-method (Jonsson et al. *in press*) to identify the best areas within the model domain that could be added to the existing MPA-network present in the Danish Straits-Kattegat-Skagerrak region. Using independent metapopulation models to test these results, we found that the EPT-method selected areas that provided 5 to 10 times better protection to the metapopulation of the benthic communities compared to a random selection of new areas to the existing network. These analyses suggested that adding approximately 1000 km^2 of new MPAs to the existing network (representing an addition of 15–19 % in area extension of the existing networks) based on the EPT-method could increase the metapopulation sizes during periods with low populations sizes with on average 103 and 39 % for the shallow and deep benthic communities, respectively. In comparison, the existing MPA-networks (without the extension) would increase the metapopulation sizes with on average 45 and 32 % for shallow and deep communities, respectively, in comparison to having no MPA-protection at all (fig. 6). Although the absolute values of these effects are dependent on the assumption of the metapopulation model, the results still demonstrate that the function of the existing MPA-network can be substantially improved by a relatively small addition of new areas, and that the EPT-method is very efficient in identifying the areas that improve the larval connectivity of the network.

4.3.2. Identifying new MPA-areas in the Kattegat-Skagerrak region

The EPT-method identified the optimal areas that could be added to the existing MPA-network within the whole model domain, and many selected areas were found along the west coast of Jutland and in the Baltic Sea, outside the target area of Kattegat and Skagerrak. However, by identifying the 400 highest ranked new model grid cell areas to add to the existing MPA-network, enough selected sites are included within the target area to be able to identify the optimal additions also within this region. By combining the identified larval dispersal barriers and subpopulations, the distribution of the existing MPA-network, and the selected optimal additions to the existing network (fig. 7), subpopulation without or with a low number of existing MPAs could be identified as high priority areas.

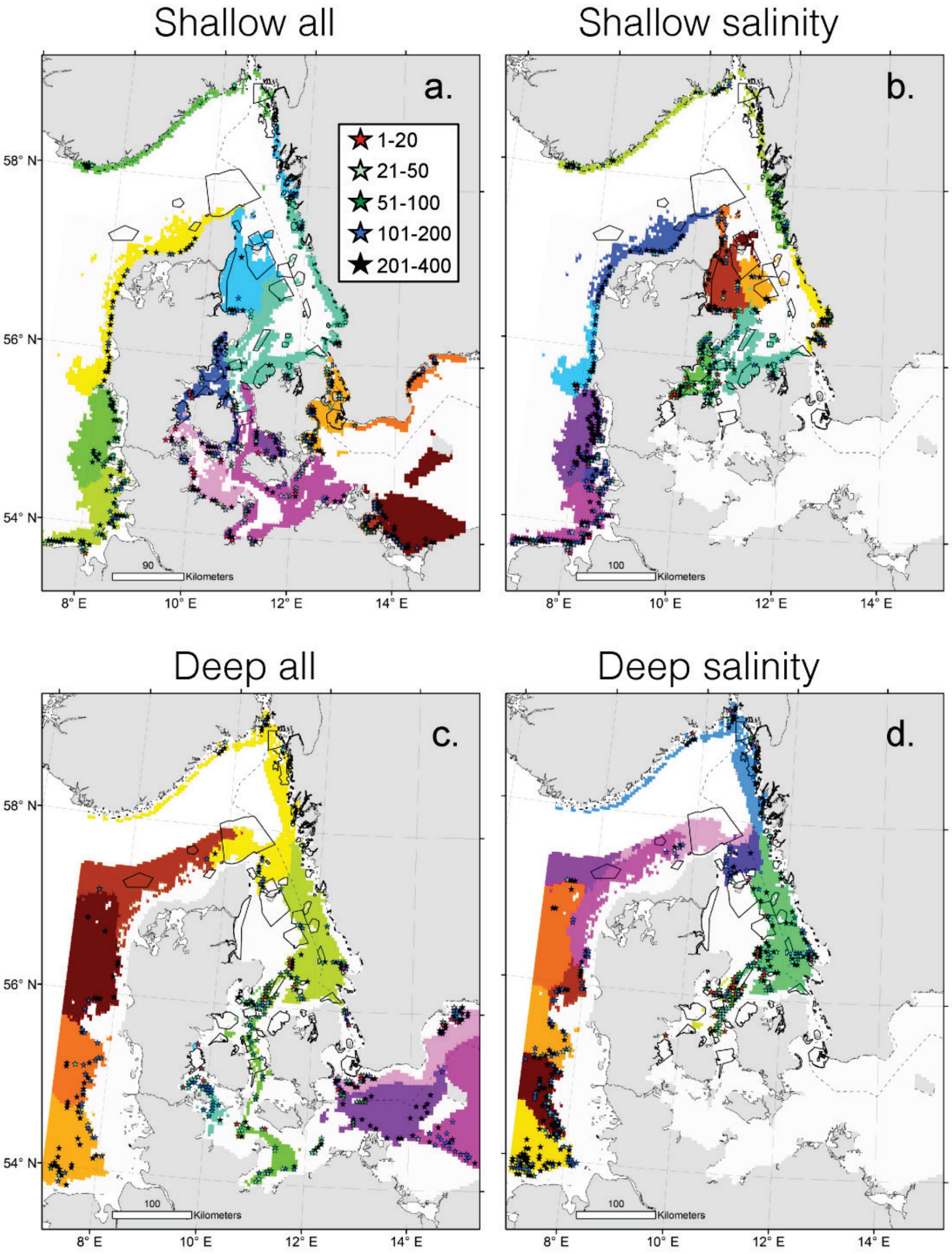


Figure 7. *Subpopulations and optimal areas for MPA-additions.* The figure show a combination of figure 4 and 5 depicting both the 14-16 identified subpopulations and the 400 highest ranked model grid cell in the EPT-analysis (stars) for the 4 benthic communities. The stars are color-coded where the red marks the 20 highest ranked cells, light green the next highest, etc. (see legend in panel a). Black solid lines marks the existing MPA-network included in the analysis. Dotted lines mark the Swedish economic zone.

The Sound

For benthic organisms tolerant to low salinities, the EPT-analysis identified several high ranked areas in The Sound that could be added to the existing network. For deep benthic communities a smaller area was identified just west of the existing Swedish nature reserve *Knähaken* in the northern part of the sound, and also just south of the island *Ven*, constituting approximately 41 km² in total (fig. 5c, 7c). For shallow communities, a large number areas were selected along the Danish side of the Sound, but also just east of the Danish Natura 2000 reserve *Saltholm* towards Malmö on the Swedish coast, constituting approximately 34 km² in Swedish waters (fig. 5a, 7a).

Swedish Kattegat and Skagerrak

One area within the Kattegat-Skagerrak region with relatively few and small MPAs is the shallow area (<20 m) along the Swedish coast in southeastern Kattegat, from *Bjärehalvön* in the south to the southern part of the Kungsbacka fjord in the North. At present there are only smaller MPAs around *Skälderviken* in the southern part (*Kullaberg-Skälderviken* and *Hallands Väderö*). In this study we identified this area as a potential subpopulation for shallow benthic communities that may be relevant for the management of local populations (fig. 7b). It would therefore be important to increase the number of MPAs in this area. The EPT-analysis of shallow benthic communities identified a high number of optimal MPA-areas to add to the existing MPA-network within the *Skälderviken* and the *Laholmsbukten* within this subpopulation. Several of the selected grid cells were among the 50 highest ranked cells within the whole study domain suggesting that these two large bays play key roles for the larval connectivity in southern Kattegat (fig. 7ab). Including all selected areas would constitute approximately 137 and 205 km² of new MPA area in the *Skälderviken* and the *Laholmsbukten*, respectively. Further north in Kattegat, still within the same subpopulation, a smaller area was selected north of city of Varberg (27 km²). In the northern part of Swedish Kattegat and Swedish Skagerrak, there exist a higher number of MPA today, why it may be less critical to add MPAs there. The largest area selected here was north of the Onsala peninsula, east of the existing marine reserve *Vrångöskärgården* (110 km²). Smaller areas were also selected outside the river mouths of *Göta älv* and *Nordre älv*, and inside the island of Marstrand (fig. 5 and 7). Altogether the identified shallow areas of Swedish Kattegat and Kattegat constituted approximately 643 km².

For deep benthic communities a larger subpopulation was identified in southeastern Kattegat. Within the Swedish economic zone (fig. 7c,d), three relatively large MPAs exist today (*Fladen*, *Lilla Middelgrund* and *Stora Middelgrund och Röde bank*). The EPT-analysis of deep benthic communities identified a high number of optimal MPA-sites to add to the existing MPA-network covering a large area (approximately 370 km²) from the border of the Swedish economic zone, south of *Stora Middelgrund* all the way to the shallow area of the *Laholmsbukten* (fig. 7d). Many of the selected grid cells were among the 50 highest ranked cells within the whole study domain suggesting that this is a key area for larval connectivity of the deep benthic community in this subpopulation. A smaller number of sites (in total 82 km²) were also identified just north of this area following the 20 m depth contour north along the Swedish coast, east of the MPA *Lilla Middelgrund* (55 km²) and west of the Onsala pensinsula (27 km²). Altogether 584 km² of new MPAs were identified within the Swedish waters that could be added to this subpopulation in Kattegat. In Swedish Skagerrak, there are a number of MPAs that include deep habitats (20–100 m); the largest one being the Koster national park close to the Norwegian border. However, most other MPAs are located close to the shore and few are found in off-shore water (not counting the large MPA *Bratten* in the middle of Skagerrak at depth >100 m, which was not included in this study). However, the EPT analysis did not identify any off-shore area in Swedish Skagerrak to add to the existing MPA-network for deep communities, only smaller sites at various location along the coast, constituting approximately 150 km^2 (fig. 7c,d).

Danish Kattegat

Several subpopulations were identified in western Kattegat for shallow benthic communities; one in the southwestern corner north of the island of Funen, and several in northwestern Kattegat, north of Grenaa. Although several large MPAs are already found within these subpopulations, the EPT-analysis of shallow benthic communities identified a high number of MPA-sites to add to the existing MPA-network, in particular at the north part of Little Belt, north of Odense fjord, in Aalborg Bay, and north of Grenaa in *Treå Møllebugt* (fig. 7ab).

For the deep benthic communities, a smaller subpopulation was found in southwestern Kattegat stretching from northern to the southern side of the Great Belt into the western Baltic Sea. On the Kattegat side, a very large number of sites were selected from around the MPA *Schultz og Hasten grund* in the north to the entrance of the Great Belt (fig. 7c,d). This is the same concentration of sites selected in an earlier study as being part of an optimal MPA-network when the existing network was not considered (see fig. 14 in Moksnes et al. 2014). A high number of selected sites were also found in the center of southern Kattegat, belonging to the same subpopulation of south-eastern Kattegat as the selected Swedish sites described above (fig. 7c,d).

Norwegian Skagerrak

Few sites were selected along the Norwegian Skagerrak coast to be included in the existing MPA-network. For shallow communities a concentration of sites were found outside the cities of Larvik and Kristiansand, and for deep communities outside the Oslo fjord and the Langesund Bay (fig. 7). The low number of optimal MPA-areas selected along the Skagerrak coasts is consistent with earlier model studies, and is likely explained by asymmetric circulation in Skagerrak area with the strong north going transport of surface water with the Baltic current along the Swedish Skagerrak coast, and the strong westward going Norwegian coastal current along the Norwegian coast, decreasing the connectivity from the Skagerrak coast to Kattegat (Moksnes et al. 2014).

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Appendix

Illustration of dispersal barriers

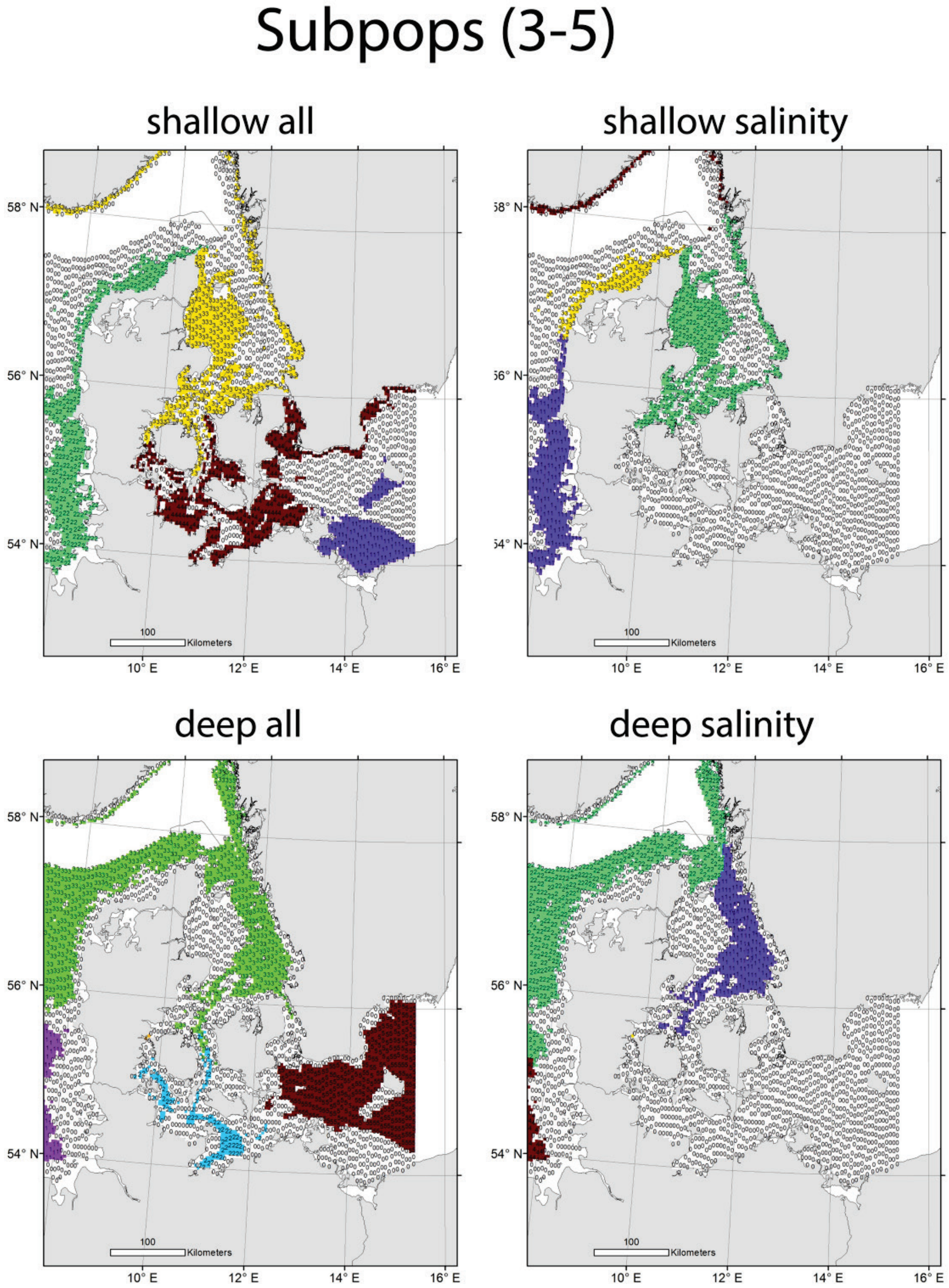

Figure A1. *3–4 Subcommunities*. Illustration of the dispersal barriers and subcommunities using a mean connectivity of 1–2 % between subdivided areas for the 4 benthic communities: (a) *shallow benthic organisms tolerant to low salinities* (shallow all), (b) *shallow benthic organisms intolerant to low salinities* (shallow salinity), (c) *deep benthic organisms tolerant to low salinities* (deep all), and (d) *deep benthic organisms intolerant to low salinities* (deep salinity). Black lines mark the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area. The same color and number marks the same subcommunity. Zero marks outside the model domain for the illustrated benthic community.

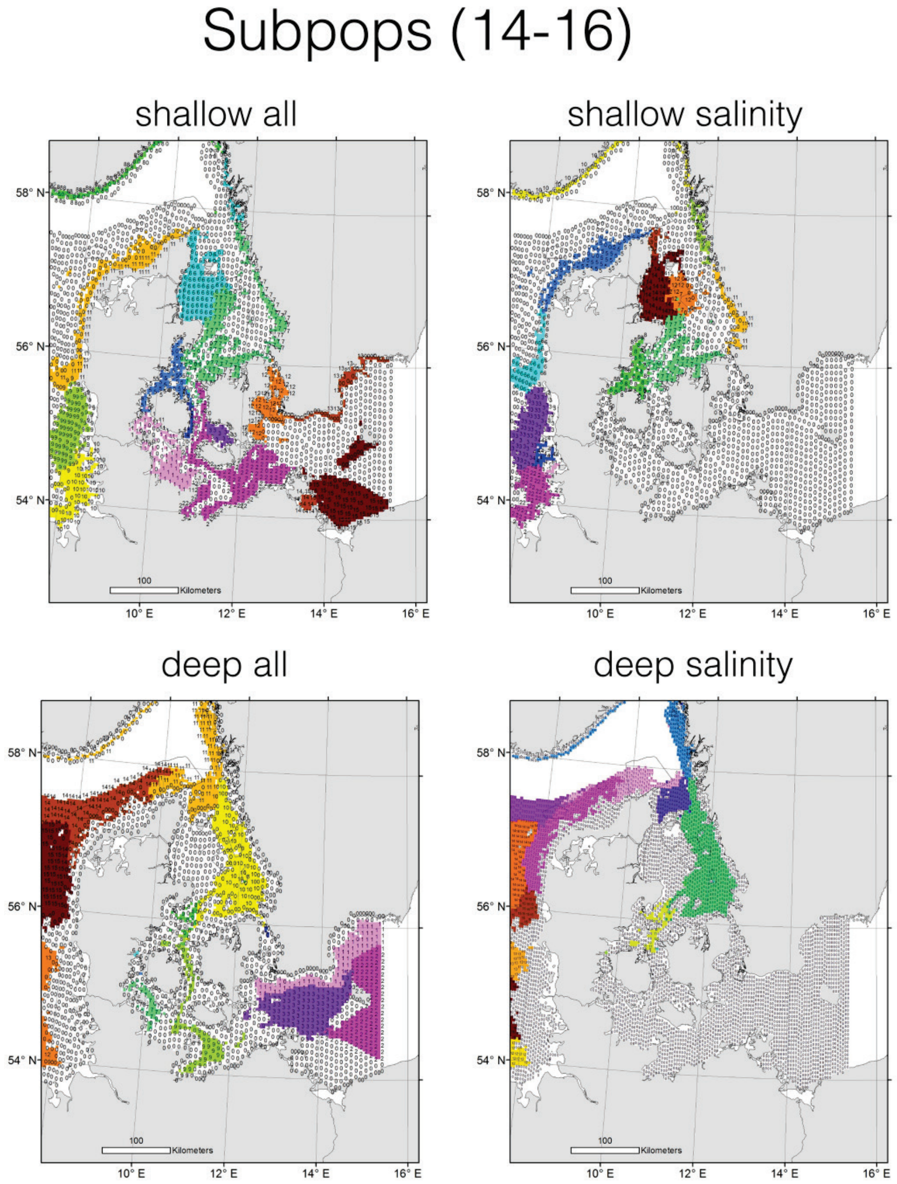

Figure A2. *14–16 Subcommunities*. Illustration of the dispersal barriers and subcommunities using a mean connectivity around 10 % between subdivided areas for the 4 benthic communities: (a) *shallow benthic organisms tolerant to low salinities* (shallow all), (b) *shallow benthic organisms intolerant to low salinities* (shallow salinity), (c) *deep benthic organisms tolerant to low salinities* (deep all), and (d) *deep benthic organisms intolerant to low salinities* (deep salinity). Black lines mark the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area. The same color and number marks the same subcommunity. Zero marks outside the model domain for the illustrated benthic community.

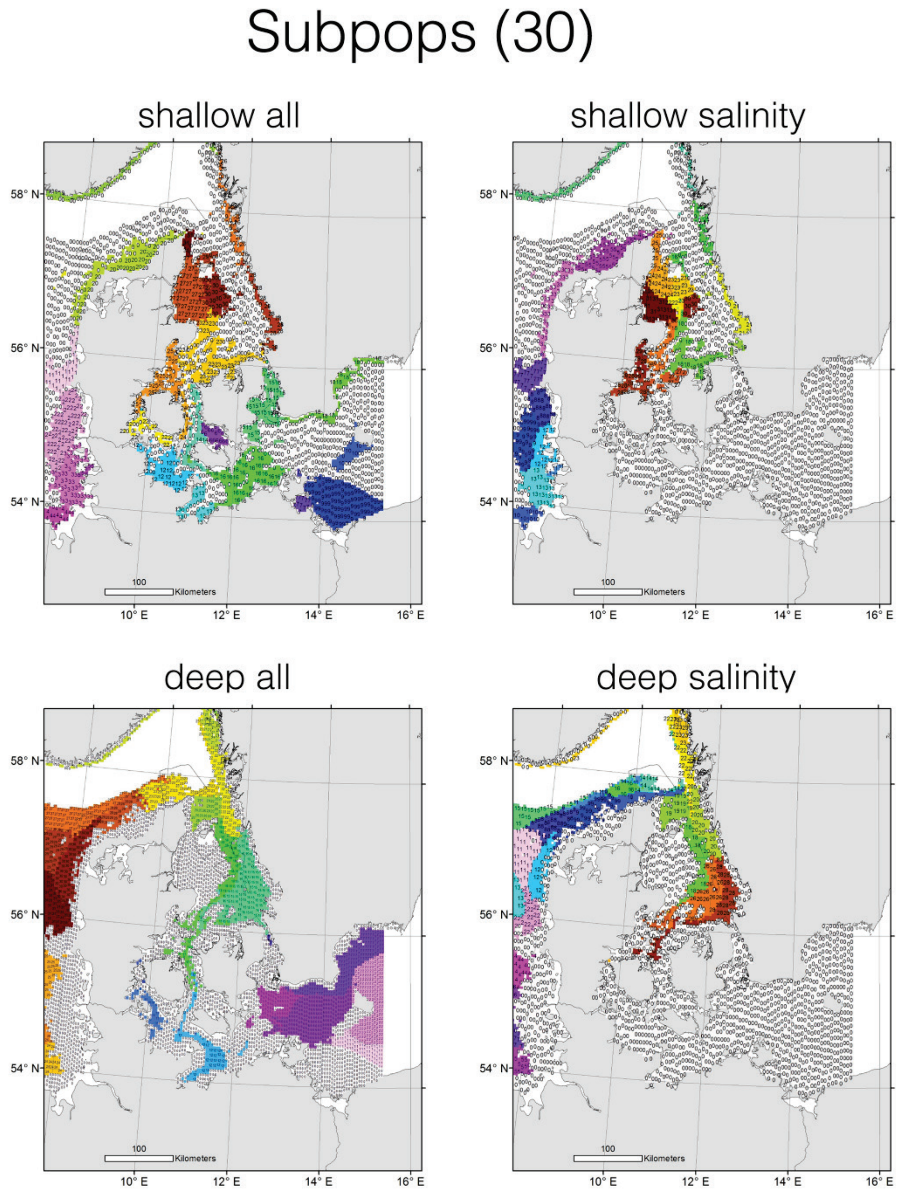

Figure A3. *30 Subcommunities*. Illustration of the dispersal barriers and subcommunities using a mean connectivity of around 30 % between subdivided areas for the 4 benthic communities: (a) *shallow benthic organisms tolerant to low salinities* (shallow all), (b) *shallow benthic organisms intolerant to low salinities* (shallow salinity), (c) *deep benthic organisms tolerant to low salinities* (deep all), and (d) *deep benthic organisms intolerant to low salinities* (deep salinity). Black lines mark the existing MPA-network in the Skagerrak-Kattegat-Danish Strait area. The same color and number marks the same subcommunity. Zero marks outside the model domain for the illustrated benthic community.

Identifying new areas adding larval connectivity to existing networks of MPAs

The case of Kattegat and Skagerrak

Sweden is committed to the Conventionon on Biological Diversity (CBD), Aichi target 11. It requests that 10 % of Sweden's seas are protected. A strategic designed network of marine protected areas should hopefully protect more than individual components. It is often unclear how the network of marine protected areas should be designed to add connectivity. This report presents a study that tries to answer the question of what new protected areas enhance the connectivity of the existing network in the Skagerrak-Kattegat-Danish Strait. The study uses empirical data on larval traits and model tools and the modeling of larval connectivity to identify the best locations to place new MPAs within Swedish waters in the Kattegat-Skagerrak area.

The Swedish Agency for Marine and Water Management hope that the report can contribute to a future development of the existing network in an optimal way.

Sverige ska leva upp till Konventionen om biologisk mångfald (CBD), Aichi mål 11. Den begär att 10 % av Sveriges hav ska skyddas. Ett strategiskt utformat nätverk av sammanhängande marina skyddsområden ska förhoppningsvis skydda mer än sina enskilda beståndsdelar. Det är dock ofta oklart hur nätverk av marina skyddsområden skall utformas på bästa sätt. Denna rapport presenterar en studie som försöker ge svar på frågan vilka nya skyddsområden som bäst skulle förhöja konnektiviteten i existerande nätverk i Västerhavet. Med hjälp av modellering av hur planktoniska larvstadier sprids för studien kunskapen framåt.

Det är Havs- och vattenmyndighetens förhoppning att rapporten kan bidra vid en framtida utveckling av existerande nätverk på ett optimalt sätt.

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