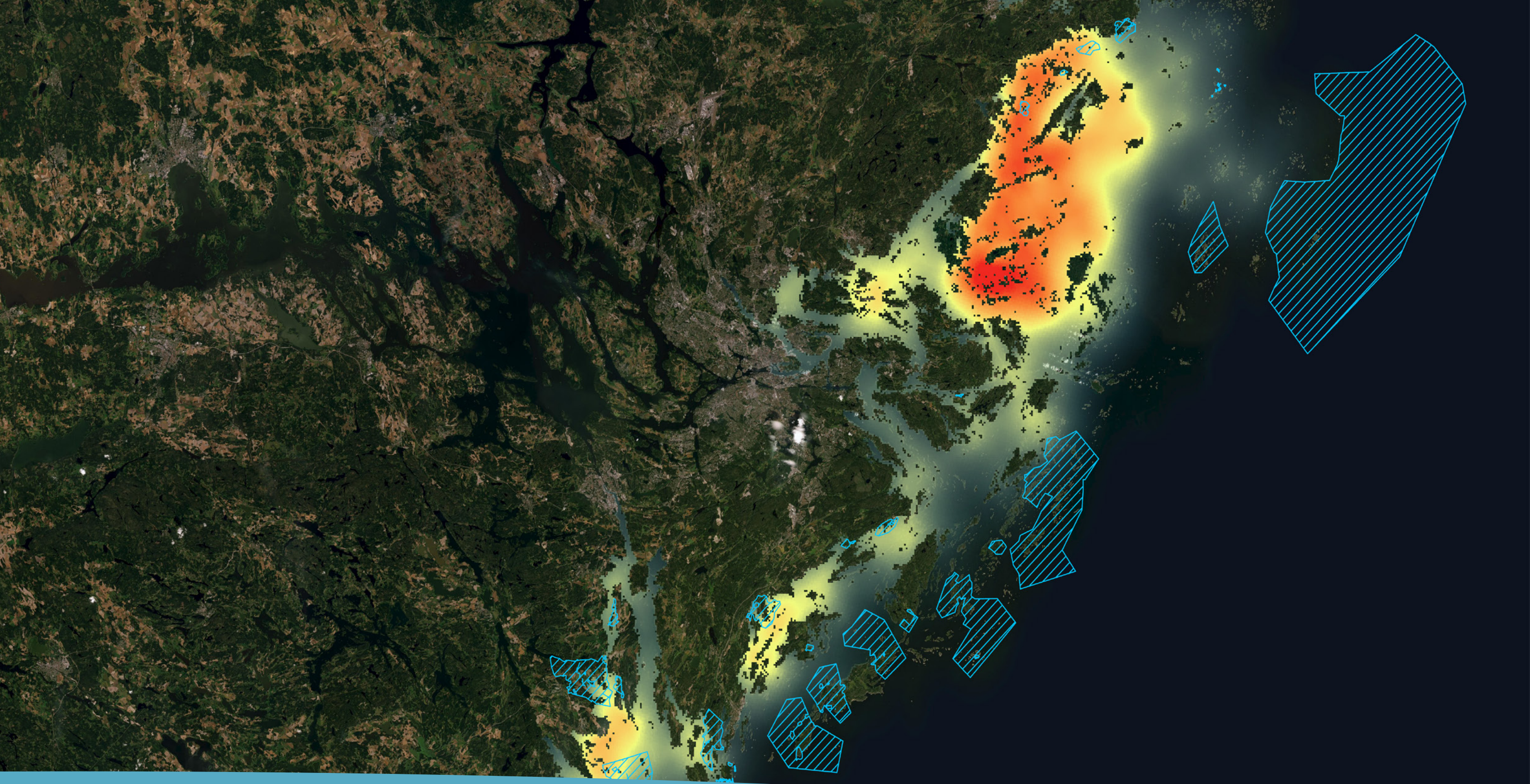

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## A coherence assessment


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Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

**Institutionen för akvatiska resurser**

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## Abstract

The Department of Aquatic Resources at the Swedish University of Agricultural Sciences (SLU Aqua) was commissioned by the Swedish Agency for Marine and Water Management to assess the ecological coherence of the marine protected area (MPA) network along the Swedish Baltic Sea coast, focusing on ecological connectivity and representativity, and species performing active migrations. The study also aimed to test the influence of anthropogenic pressures on connectivity and identify areas for expansion of the existing MPA network to maximise connectivity in the region. This report is the first to assess large-scale connectivity and ecological coherence of the MPA network in the Baltic Sea with a focus on coastal habitat-forming vegetation and fish species with active dispersal. Information on dispersal/migration distances was combined with species distribution models to produce connectivity maps. To align the coherence analyses with the conservation targets specified by responsible authorities, we included the nested targets for specific species ("preciserade bevarandevärden" in Swedish) listed within the Swedish framework for MPAs. Fish species like eel, salmon and trout, as well as birds and seals, which are also listed as nested targets, were not included in our analyses, since connectivity models of these long-distance migrants would be redundant as they do not affect the more small-scale connectivity patterns that are in focus in this study.

Hotspot areas for connectivity were identified, and these were generally concentrated in a few, relatively small areas. These hotspot areas are, however, highly susceptible to coastal development and human activities, as they are often situated in bays, inlets and topographically complex archipelagos. Anthropogenic pressures, in this case physical disturbance, had a relatively large predicted impact on connectivity, particularly on certain species. The majority of these species are of freshwater origin and have shorter migration distances (e.g. crucian carp, roach, common rudd, common bream/silver bream, and common bleak) than marine species like cod, flounder and herring, which perform long-distance migrations between open sea and coastal areas as part of their life cycle. Also large predatory fish like pike, pike-perch and perch, as well as habitat-forming submerged aquatic vegetation (SAV), showed a pronounced decrease in connectivity when incorporating physical disturbance into the models. This may be explained by most human pressures being concentrated along the coastline, often in shallow sheltered bays and inlets where human development coincides with sensitive vegetated habitats and important breeding, spawning, nursery and feeding grounds for fish. Connectivity is reduced when habitats become fragmented or diminished and populations become smaller and more isolated. This may in turn have consequences on genetic diversity, viability of populations and ultimately ecosystem functioning.

Representativity of habitats; i.e. amount of habitat protected, was below what is generally scientifically recommended and the new target of 30% protection by 2030 in the EU Biodiversity Strategy for all but three species (of 30 in total). Representativity was very poor regarding strict MPAs, an average of 2% across species. The target according to the EU Biodiversity Strategy is 10% strict protection. Similar results were found for connectivity where the amount connected habitat within MPAs was low. MPAs in the study area were sufficiently spaced (distance apart), but dominated by MPAs of small size. Priority areas with high connectivity (identified by the spatial prioritization software prioritizr) were insufficiently protected and the connectivity of the network could be greatly improved with targeted protection in just a few important locations. Areas that are well connected locally, but are isolated from other priority areas, are especially important to protect as they are critical to connectivity of the network. Regulations within the MPA network in Swedish Baltic Sea coastal waters are generally weak, particularly in the priority areas. Applying an ecosystem-based management approach and including stronger regulations of fisheries and of activities causing local physical disturbance in parts of the MPA network is encouraged in order to reach conservation goals. The results from this study can

be used to improve planning and management of the Baltic Sea MPA network, marine spatial planning in the region and improving the green infrastructure, securing important ecosystem services for future generations.

## Svensk sammanfattning

Institutionen för akvatiska resurser vid Sveriges Lantbruksuniversitet (SLU Aqua) har på uppdrag av Havs- och vattenmyndigheten (HaV) undersökt ekologisk konnektivitet och koherens för det svenska nätverket av marina skyddade områden med avseende på organismers spridningsförmåga och fokus på aktiv migration. I studien ingår även en analys av effekterna av lokal fysisk miljöpåverkan på konnektiviteten och en identifierande kartläggning av områden där konnektiviteten är svag och ytterligare skydd behövs. Rapporten är den första att göra en storskalig analys av konnektivitet och koherens av nätverket av skyddade områden i Östersjön med fokus på habitatbildande vegetation och fisk. Information om arters spridnings- och migrationsavstånd användes tillsammans med artutbredningskartor för att skapa konnektivitetsmodeller för olika arter i kustzonen i Bottniska viken och Egentliga Östersjön. I analyserna inkluderas även de preciserade bevarandevärden som identifierats inom Sveriges arbete med marina skyddade områden. Vissa långmigrerande arter som ingår bland de preciserade bevarandevärdena exkluderades från analyserna, eftersom dessa inte skulle påverka de mer finskaliga konnektivitetsmönster som undersöks i denna studie. Utifrån detta underlag gjordes en analys om fysisk påverkan på konnektiviteten för ett antal arter. I ett sista steg identifierades områden där nätverket av skyddade områden kan förstärkas för att förbättra den ekologiska konnektiviteten och bidra till ett mer sammanhängande nätverk.

Kärnområden med hög konnektivitet identifierades längs svenska östersjökusten. Dessa var generellt koncentrerade till ett fåtal relativt små områden i kustnära vikar och topografiskt komplex skärgårdsmiljö med hög mänsklig påverkan. Fysisk störning från exempelvis muddringar, byggnation och båttrafik påverkade konnektiviteten i modellerna för ett flertal arter. Framförallt habitatbildande vegetation och mer stationära fiskarter av sötvattensursprung såsom ruda, mört, sarv, braxen, björkna, och löja, men även större rovfiskar som gädda, abborre och gös påverkades i hög grad. Arter av marint ursprung och som vanligtvis migrerar längre sträckor, tex. torsk, plattfisk och strömming, påverkades betydligt mindre. Detta mönster kan förklaras av att den största mänskliga påverkan sker i grunda, skyddade vikar där de sammanfaller med känsliga vegetationsklädda bottnar och viktiga lek-, uppväxt- och födoområden för fisk. När dessa grunda habitat fragmenteras och försvinner minskar konnektiviteten och populationer krymper och blir mer isolerade. Detta kan i längden påverka den genetiska och biologiska mångfalden med effekter på hela ekosystemet.

Representativiteten av olika vegetationsbottnar, uppväxthabitat för fisk, samt områden med hög konnektivitet var lägre än de 30% (av havsytan) som förespråkas i bevarandesyfte i vetenskaplig litteratur, och samtidigt utgör mål för EUs Biodiversitetsstrategi till 2030 för alla arter utom tre (av totalt 30). Representativiteten i områden med strikt skydd var ännu lägre, knappt 2 % i medel bland alla arter. Här är målet enligt EUs biodiversitetsstrategi 10% strikt skydd. Resultatet var liknande för konnektivitet, där andelen sammanhängande habitat som omfattades av områdesskydd var låg. Avstånden mellan skyddade områden inom nätverket var tillräckliga, men storleken på de skyddade områdena var generellt väldigt små. Prioriterade områden med hög konnektivitet, identifierade med analysverktyget prioritizr, hade otillräcklig täckning inom nätverket av skyddade områden. Genom att utvidga nätverket i några få väl utvalda områden kan konnektiviteten öka betydligt. Områden med hög lokal konnektivitet som är isolerade från resten av nätverket längs östersjökusten kan vara extra viktiga att skydda. Regleringen av verksamheter som påverkar naturvärden och konnektivitet inom nätverket är generellt svag. En ekosystembaserad förvaltning där även fiske och verksamheter som ger lokal fysisk påverkan på arter och habitat regleras inom de skyddade områdena är viktig för att uppnå bevarandemålen. Vi hoppas att resultaten i denna rapport kan stötta utvecklingen av ett mer ekologiskt representativt och sammanhängande nätverk av effektivt förvaltade marina skyddade områden i Sverige. Dessa

analyser är viktiga för framtida arbete med grön infrastruktur, för fysisk planering av verksamheter i kustzonen och för att rikta områdesskydd och habitatrestaureringsåtgärder till områden som på ett effektivt sätt kan stärka nätverket.

# Preface

In 2015, the Government of Sweden commissioned the Swedish Agency for Marine and Water Management (SwAM) to analyse the existing marine protected area (MPA) network and develop an action plan, ensuring an effectively managed, ecologically representative, well-connected, and functional network of formal MPAs. These should cover at least 10% of Swedish marine waters by 2020. Recently, this goal was increased when the EU Commission committed to protect 30% of European waters by 2030 with specific objectives for a connected and ecologically coherent MPA network. To facilitate this process the Department of Aquatic Resources at the Swedish University of Agricultural Sciences (SLU Aqua) was assigned by SwAM to assess the ecological coherence of the MPA network along the Swedish Baltic Sea coast, with focus on ecological connectivity, including effects of anthropogenic pressures and suggestions for MPA network expansion in order to maximise connectivity. This report summarizes the findings of these coherence and spatial prioritization analyses, and is intended to guide responsible authorities in the work of expanding the MPA network towards the 30% target.

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# 1. Introduction

## 1.1. Marine protected areas (MPAs)

Climate change and anthropogenic disturbances cause major losses in biodiversity and threaten important ecosystem services in aquatic systems (Worm et al., 2006; Halpern et al., 2015; Korpinen et al., 2021). In many parts of the world, including the Baltic Sea, marine protected areas (MPAs) have been established to safeguard and restore species and habitats threatened by human activities (Duarte et al., 2020; Sala et al., 2021). MPAs can vary in their level of protection, from having no extraction or pressures allowed to only protecting certain features (Grorud-Colvert et al., 2021), resulting in variable outcomes (Lester and Halpern, 2008; Motta et al., 2021; Smallhorn-West et al., 2022). The size, age, shape, and distance between MPAs in a network also affect outcomes, with older and larger MPAs close to each other generally being more effective (Claudet et al., 2008; Vandeperre et al., 2011; Olds et al., 2016). Besides being of sufficient size and distance from each other, MPAs also need to be placed in the right areas and have necessary levels of regulations to provide efficient protection. They also need to be enforced, to ensure that the regulations are followed. At the same time, MPAs may have negative effects on the income and livelihoods of some users (Smallhorn-West et al., 2022). There are, however, tools available for finding useful trade-offs in these situations. By using ecological modelling and spatial optimisation tools in the planning of MPA networks, it may be possible to find solutions how to expand MPA networks in order to provide best possible protection at lowest possible cost.

The EU Commission has recently committed to protect 30% of European waters by 2030, with specific objectives for a connected and ecologically coherent MPA network (O'Leary et al., 2016; European Commission, 2020; Jones et al., 2020). To facilitate this process in Sweden, the Swedish Agency for Marine and Water Management (SwAM) together with the Foundation of Success (FOS), developed a framework for designing and effectively managing networks of MPAs (SwAM, 2021). The main goal is to design a representative, coherent and functional network of MPAs in Swedish waters. The framework contains definitions, guiding principles, and a methodology for MPA network design and management. The framework and methods are not yet complete, and setting goals for connectivity needs further development. The understanding of Baltic Sea habitats, species distributions, and patterns of connectivity is generally not sufficient. Moreover, knowledge on areas with high ecological value, such as connectivity hotspots is lacking, yet essential to optimize the expansion of the MPA network (Berkström et al., 2021).

These new, ambitious area targets for MPA coverage, in combination with ongoing environmental change, require sophisticated spatial planning to achieve ecologically coherent MPA networks. However, there is a substantial knowledge gap in spatial planning concerning how to design MPA networks that account for the distribution and connectivity of habitats. Moreover, knowledge on the effects of anthropogenic pressures and future climate scenarios on connectivity is lacking (Berkström et al., 2021).

## 1.2. Nested targets (preciserade bevarandevärden)

When planning and establishing MPAs, an important step is to define the ecological systems and habitats of conservation value. These are referred to as *conservation targets* (Swedish: bevarandevärden), while the species listed as being of significant ecological importance are referred to as more detailed *nested targets* (Swedish: preciserade bevarandevärden) in the Swedish framework for MPAs (SwAM, 2021). These nested targets are given extra attention in the current report. This information will be used by the county administrative boards, the authorities responsible for MPA establishment and governance, in future marine spatial planning and in the development of the Swedish MPA network. The list of nested targets was discussed and formalised during several workshops with numerous stakeholders, including SwAM and the county administrative boards. The list includes species and habitats that are threatened, or of key importance for ecosystem functioning, and that Sweden has committed to protect (Länsstyrelserna i Norrbottens, Västerbottens, Västernorrlands, Gävleborgs och Uppsala län, 2021).

## 1.3. Anthropogenic pressures

In the Baltic Sea and worldwide, shallow coastal waters are hotspots for biodiversity and ecosystem services, but are highly subjected to anthropogenic pressures (Bulleri and Chapman, 2010; Korpinen et al., 2021; Reckermann et al., 2022). These areas contain important habitat-forming species like macrophytes, macroalgae, and mussels that provide nursery and feeding areas for a number of aquatic species, of which many are of commercial or recreational importance (Staveley et al., 2016; Kraufvelin et al., 2018). These habitats and species are among the nested targets mentioned above. However, physical disturbance from boat traffic, jetties and dredging can have negative effects on these important habitats and nursery areas (Sundblad and Bergström, 2014; Macura et al., 2019). As much as 40 – 80% less vegetation is found in shallow protected bays with a high density of jetties and intense boat traffic compared to bays with fewer jetties in the

Baltic Sea (Hansen et al., 2018). Jetties and boat traffic also have a negative effect on the diversity of macrophytes, with sensitive species often disappearing (Eriksson et al., 2004; Sandström et al., 2005). These rare, shallow nursery areas are critical for the survival of many commercially important fish species and a strong positive relationship between the amount of benthic vegetation and species like pike, perch and cyprinid larvae has been found (Sundblad and Bergström, 2014; Hansen et al., 2018). Negative effects of jetties on eelgrass meadows have also been reported (Eriander et al., 2017) and can impact recruitment and fish production, as they function as important nursery grounds (Staveley et al. 2016, Perry et al. 2018).

Restoration attempts of coastal wetlands and eelgrass beds have been made in an effort to decrease fragmentation and increase connectivity (Nilsson et al., 2014; Eriander et al., 2017; Jahnke et al., 2018; Hansen et al., 2020; Jahnke et al., 2020). These restoration attempts, together with the protection of habitats and species within the MPA network, facilitate the preservation of *green infrastructure*. Green infrastructure can be described as a network of natural and semi-natural areas that are strategically managed to contribute to ecosystem functioning and deliver a wide range of ecosystem services (Chatzimentor et al., 2020). The preservation of green infrastructure focuses particularly on three elements: environmental protection, ecosystem multifunctionality and ecological connectivity (Lai et al., 2018; Nyström Sandman et al., 2020).

## 1.4. Ecological connectivity

Ecological connectivity refers to the movement and dispersal of organisms and material across populations, communities and ecosystems (Carr et al., 2017). It promotes persistence and recovery of flora and fauna by the dispersal and movement of spores, eggs, larvae and individuals among spatially distinct entities (Balbar and Metaxas, 2019). Connectivity in the marine environment can either be maintained by passive dispersal of organisms and material via water movement (e.g. currents, waves etc.) or by active movement of migrating individuals (Berkström et al., 2021). Some macroalgae and invertebrates can disperse by being attached to floating objects (Winston, 2012) and macrophytes and algae have been found to disperse by hitchhiking with fish or birds (Boedeltje et al., 2015; Hattermann et al., 2019). Bird-mediated dispersal of live embryos has also been recorded (Lovas-Kiss et al., 2020). Connectivity may, however, also promote spread and range shifts of invasive species to new areas with negative effects on native ecosystems (Holopainen et al. 2016).

Passive dispersal of pelagic fish and invertebrate larvae is more common in species of marine origin, while active dispersal by adult or sub adult individuals dominates in species of freshwater origin. Therefore, active dispersal is more common and prominent in coastal waters of the Baltic Sea, which has brackish conditions, than the Swedish west coast where salinity levels are close to marine conditions (Berkström et al., 2021). Previous studies in the Baltic Sea on ecological connectivity and the coherence of the MPA network have focused on passive larval dispersal using hydrodynamic models (Corell et al., 2012; Nilsson Jacobi et al., 2012; Jonsson et al., 2020). These models are best suited for modelling dispersal in the open sea, while they are of less value for understanding connectivity in heterogeneous coastal and archipelago regions. Information on ecological connectivity maintained by active dispersal is lacking overall (Berkström et al., 2021).

Many fish and invertebrates in the Baltic Sea migrate between shallow coastal areas and offshore areas during different stages of their life cycle, or among coastal habitats to feed or spawn (Aro, 1989; Candolin and Voigt, 2003; Tibblin et al., 2016). The productive shallow coastal shallow areas are used for reproduction by many species, as they provide optimum conditions for egg and larval development, as well as food and shelter for young individuals. Many commercially and recreationally important species depend on these shallow coastal areas during some parts of their life cycle, making them critical for fish production (Seitz et al., 2014). Loss and fragmentation of habitat can therefore have a large impact on population dynamics and productivity, potentially leading to reductions in the provisioning of ecosystem services as well as in ecosystem resilience. Thus, considering connectivity in MPA design and management is crucial.

## 1.5. Ecological coherence of MPA networks

Connectivity is highlighted as an important element in the design of ecologically coherent networks of MPAs and is one of four criteria used when assessing the ecological coherence of an MPA network (Ardron, 2008; Balbar and Metaxas, 2019). The other three criteria are adequacy, representativity and replication (Ardron, 2008). *Adequacy* refers to the MPAs being of appropriate size and shape and that they are placed in the right locations to ensure the persistence of conservation features (e.g. habitats and species) over time (Kukkala and Moilanen, 2013). *Representativity* reflects the proportion of each conservation feature being protected, while *replication* refers to the number of each conservation feature being protected. *Connectivity*, on the other hand, refers to the spatial configuration of the MPA network (structural connectivity) and the ability of organisms and material to move and disperse between individual MPAs (functional connectivity), as well as between individual MPAs and other suitable areas outside the MPA network, in order to maintain functioning populations (Kindlmann and Burel, 2008). Connectivity is closely related to the other three criteria since dispersal and migration of organisms and material also affect what appropriate size and shape an MPA needs to be in order to insure adequate protection and where MPAs should be located.

In some connectivity analyses, only areas within the MPA network are considered, i.e. a scorched-earth-scenario, but viable habitats outside the network may exist and act as stepping-stones for movement and dispersal where the MPA network is only a part of the wider meta-population (Allison et al., 1998; Jonsson et al., 2020). A *meta-population* at sea is defined by Kritzer and Sale (2004) as "a system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals". In other words, a meta-population is a group of spatially separated populations of the same species, which interact at some level. MPAs can in this perspective be considered to protect local populations (resulting in higher survival and reproduction rates) among other unprotected local populations (Jonsson et al., 2020). In the present study, connectivity is assessed in the whole study region and not only within the MPA network to capture the true extent of connectivity between habitats and facilitate the process of identifying areas for expanding the MPA network.

## 1.6. Conservation prioritisation and expansion of the MPA network

One of the major challenges when establishing MPAs is to place them in areas where they provide the highest conservation benefit in an efficient manner that minimises the required area and the associated costs of implementing a protected area (Pressey et al., 1993; Margules and Pressey, 2000; Virtanen et al., 2018). Because marine areas have a variety of uses (e.g. conservation, fisheries, shipping, energy, and recreation), it is infeasible to totally protect a given region and all aspects of biodiversity within it. Instead, networks of strategically placed MPAs must be designed that efficiently maximise biodiversity and ensure the maintenance of ecological functions for important species and ecosystems in the region. This can be achieved using spatial prioritisation to ensure adequate amounts of species and habitats are included in the network, and that MPAs are of sufficient size and spatial arrangement to maintain connectivity and ecological functions. However, MPAs are often designated based on *ad hoc* decisions, with little knowledge of the species and habitats included, and without consideration of the conservation objectives and targets of the broader MPA network (Agardy et al., 2016). This can lead to failures for individual MPAs in meeting their management objectives (Jameson et al., 2002; Edgar et al., 2014), and to sub-optimal MPA networks that fail to reach national objectives and which tend to be biased towards low-impact areas (Devillers et al., 2015).

To overcome these issues, priority areas for establishing new MPAs and expanding an MPA network can be developed, incorporating spatially explicit data on the spatial distribution species, habitats, connectivity, and various other important ecological features and processes. There are several widely used tools available for the development of spatial prioritisations, such as Marxan, Zonation and prioritizr (Ball et al., 2009; Lehtomäki and Moilanen, 2013; Hanson et al., 2021). Conservation prioritization analyses including connectivity, which is a major focus of this report, have been performed in the Baltic Sea (Virtanen et al., 2018), the

Mediterranean (Magris et al., 2018), and in the tropics (Makino et al., 2013; Krueck et al., 2017; Weeks, 2017), with most studies focusing on connectivity by passive larval dispersal using Marxan. More recently, tools like "prioritizr" have become available, which allow users to utilize algorithms that can determine optimal solutions to conservation planning problems, which provide enormous utility for developing maximally efficient spatial prioritisations based on the data available (Hanson et al., 2021).

## 1.7. Aim of the study

The aim of the present study was to assess the ecological coherence of the MPA network in Swedish Baltic Sea coastal waters, focusing on ecological connectivity and species performing active migrations. The study also aimed to spatially analyse the influence of anthropogenic pressures on connectivity, as well as to identify areas for expansion of the existing MPA network to maximise connectivity in the region.

# 2. Methods

The analysis for this report is divided into five sections: (1) Collating species distribution maps and dispersal information; (2) Connectivity modelling; (3) Analysis of the effects of anthropogenic pressures on connectivity; (4) Coherence assessment; and (5) Spatial prioritisation for expansion and strengthening of the MPA network. The full workflow is depicted in Figure 1, and the methods for each section are described below.

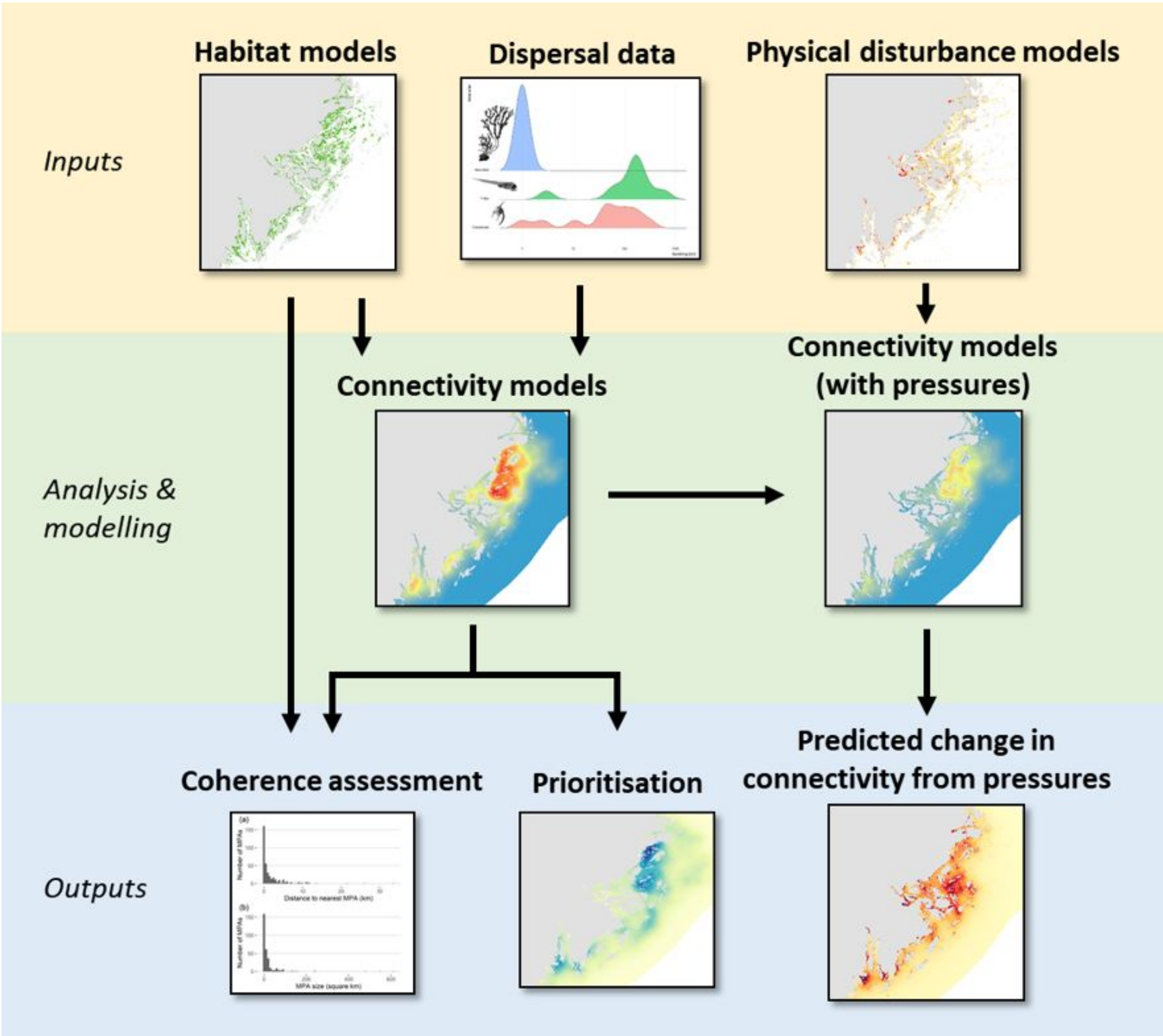


**Figure 1.** Methodological workflow for the analyses in this report.

## 2.1. Species distribution maps and dispersal distances

The focal species of this study were fishes and vegetation in the coastal zone of the Swedish Baltic Sea (Figure 2.). The coastal zone was defined as all sea areas within a 15 km buffer of the Swedish baseline (connecting the outmost islands of the archipelago). The analysis included 22 species of fish and eight species of vegetation, including four species of algae, and four species of vascular plants (Table 1.). These species are common in the area, and were chosen based on the availability of distribution maps and reported dispersal distances. Focus was on active dispersal by fish because most species in the coastal areas of the Baltic Sea have short or negligible larval dispersal. Connectivity, in terms of movement, is hence primarily through active movements by juveniles or adults. Species listed as being of significant ecological importance, i.e. nested targets (Swedish: preciserade bevarandevärden) were specifically included (SwAM, 2021). Birds, mammals and anadromous fish like sea trout and salmon were excluded from the analyses because most of them undertake long migrations, covering large parts of the Baltic Sea, which makes connectivity analyses on these species redundant.

Fish habitat distribution maps were obtained from Erlandsson et al. (2021). These habitat maps were produced using ensemble species distribution modelling to predict the probability of occurrence of juvenile fish along shallow coastal areas in the Baltic Sea. These probability maps were dichotomized into presence-absence maps by calculating the true skill statistic (TSS) for each species, which serves as a cut-off value for the predictions, over which species are considered to be present, and under which species are considered to be absent. Vegetation habitat distribution maps were obtained from two sources. Vegetation maps for the Gulf of Bothnia were obtained from Florén et al. (2018). Vegetation maps for the Baltic Proper were obtained from Wijkmark et al. (unpublished). We combined vegetation maps from the Gulf of Bothnia and Baltic Proper for species that were available in both datasets, producing vegetation maps for the entire coastal area of the Baltic Sea. In both of these vegetation datasets, species habitat distributions were modelled according to the predicted percentage cover of each given species in a given grid cell. In order to produce conservative estimates in our own analysis, we removed all grid cells where the predicted cover was lower than 10%. All species distribution maps had a spatial resolution of 250 m.

For each species, we utilised the data compiled by Berkström et al. (2019) to estimate active (for fish) and passive (for vegetation) dispersal distances. To determine dispersal distances for species where no information was available, we grouped species according to their life history traits and typical habitat. We then assumed dispersal distances for these species based on information available for other species within the same group.

**Table 1.** All species included in the connectivity models and coherence assessment.

| Scientific name | English name | Swedish name | Assumed dispersal distance | Species group(s) | Figures |
|---|---|---|---|---|---|
| *Abramis brama/Blicca bjoerkna* | Common bream/Silver bream | Braxen/Björkna | 10 km | Fish; Cyprinids | A1 |
| *Alburnus alburnus* | Common bleak | Löja | 10 km | Fish; Cyprinids | A2 |
| *Carassius carassius* | Crucian carp | Ruda | 10 km | Fish; Cyprinids | A3 |
| *Clupea harengus* | Herring | Strömming | 150 km | Fish; Herring | A4 |
| *Esox lucius* | Pike | Gädda | 5 km | Fish; Coastal predatory fish | A5 |
| *Gadus morhua* | Cod | Torsk | 150 km | Fish; Cod | A6 |
| *Gasterosteus aculeatus* | Three-spined stickleback | Storspigg | 150 km | Fish | A7 |
| *Gobiusculus flavescens* | Two-spotted goby | Sjustrålig smörbult | 10 km | Fish | A8 |
| *Gymnocephalus cernuus* | Ruffe | Gärs | 15 km | Fish | A9 |
| *Leuciscus idus* | Ide | Id | 10 km | Fish; Cyprinids | A10 |
| *Gobius niger* | Black goby | Svart smörbult | 10 km | Fish | A11 |
| *Osmerus eperlanus* | Smelt | Nors | 150 km | Fish | A12 |
| *Perca fluviatilis* | Perch | Abborre | 10 km | Fish; Coastal predatory fish | A13 |
| *Phoxinus phoxinus* | Common minnow | Elritsa | 10 km | Fish; Cyprinids | A14 |
| *Platichthys solemdalii* | Baltic flounder | Östersjöflundra | 30 km | Fish; Flatfish | A15 |
| *Pomatoschistus minutus* | Sand goby | Sandstubb | 10 km | Fish | A16 |
| *Pungitius pungitius* | Nine-spined stickleback | Småspigg | 10 km | Fish | A17 |
| *Rutilus rutilus* | Roach | Mört | 10 km | Fish; Cyprinids | A18 |
| *Sander lucioperca* | Pike-perch (Zander) | Gös | 10 km | Fish; Coastal predatory fish | A19 |
| *Scardinius erythrophthalmus* | Common rudd | Sarv | 10 km | Fish; Cyprinids | A20 |
| *Sprattus sprattus* | Sprat | Skarpsill | 150 km | Fish | A21 |
| *Tinca tinca* | Tench | Sutare | 10 km | Fish; Cyprinids | A22 |
| *Chara spp.* | Stoneworts | Sträfsen | 10 km | Vegetation | A23 |
| *Fucus vesiculosus/radicans* | Bladder wrack | Blåstång/Smaltång | 10 km | Vegetation; Large perennial brown algae | A24 |
| *Fucus serratus* | Toothed wrack | Sågtång | 10 km | Vegetation; Large perennial brown algae | A25 |
| *Furcellaria lumbricalis* | Clawed fork weed | Kräkel | 10 km | Vegetation | A26 |
| *Myriophyllum spp.* | Water milfoil | Slingesläktet | 20 km | Vegetation; Vascular plants | A27 |
| *Potamogeton perfoliatus* | Clasping-leaved pondweed | Ålnate | 20 km | Vegetation; Vascular plants | A28 |
| *Stuckenia pectinata* | Sago pondweed | Borstnate | 20 km | Vegetation; Vascular plants | A29 |
| *Zostera marina* | Eelgrass | Ålgräs | 20 km | Vegetation; Eelgrass | A30 |


**Figure 2.** The study area, indicated in blue, for all analyses. The study area encompasses the coastal area of the Swedish Baltic Sea, defined as all sea areas within a 15 km buffer of the Swedish baseline. The island of Gotland and the southernmost part of the Swedish

Baltic Sea coast were excluded as species distribution maps are to a large extent lacking for these areas.

## 2.2. Connectivity models

We measured connectivity using a “degree centrality” approach based on graph theory. Degree centrality is measured by calculating the number of “edges” or connections each node in a network has. In ecology, nodes are typically represented by discrete habitats, and the degree centrality is measured as the number of connections each habitat has to other habitats in the network. Our analysis deviated slightly from the typical approach. In our analysis, all cells in the map were considered nodes in the network. The motivation behind this approach is that it avoids identifying discrete habitat clusters, which can often be accompanied by error. Habitats can have a patchy distribution, and it can often be unclear exactly which areas should be grouped into a single habitat node. In such cases, it is often necessary to make arbitrary assumptions about what is considered discrete habitat (e.g. all habitat patches within a certain distance from one another). Our approach avoids such assumptions. Furthermore, we consider all marine cells in the map nodes, including those that do not contain habitat for the vegetation and juvenile fish species in focus. The benefit of this approach is that it considers dispersal of individuals from source habitats to non-habitat areas. Although these areas may not provide habitat for reproduction, they may be utilized by individuals for other activities, such as feeding, and may also function as stepping-stone locations for dispersal between habitats.

Using this approach, the connectivity model was formulated as follows. Each cell in the map represents a node in the network. All cells in the map (both habitat and non-habitat cells) are considered “receiver” cells, meaning that individuals can disperse to these cells. All cells in the map containing habitat for a given species are considered “source” cells, meaning that individuals can disperse from these cells to any other cells within dispersal range. Cells containing habitat function as both source and receiver cells, meaning that individuals can disperse to and from cells containing habitat. Cells containing no habitat can only receive individuals. It follows, therefore, that connections can only be made between source cells and other source cells, or between source cells and receiver cells, if they are within dispersal range. Connections cannot be made between two receiver cells (i.e. two cells that both contain no habitat).

Distances between cells were calculated using a cost-distance method, which calculates the least-cost path between cells. Using this approach we specified that cells containing land acted as a barrier to dispersal (i.e. it was impossible to travel through these cells). This method is often referred to as travelling “as the wolf runs”, where individuals must avoid obstacles along the path to a destination. This can be contrasted with a linear approach often referred to as travelling “as the crow flies”. This non-linear approach was chosen because it more accurately represents the movement of marine species, for which modes of dispersal are typically restricted to the water body. If, for a given species, the distance between two cells along the least cost path exceeded the maximum dispersal distance (Table 1.), it was assumed that there was no connectivity between the cells.

Within the model, connectivity was weighted according to a dispersal kernel, which allows the model to incorporate expected probabilities of dispersal between cells. We assumed that the probability of dispersal would decline exponentially with distance between cells. As such, we utilised a dispersal kernel based on a negative exponential function. Thus, the connectivity, $k$, between receiver cell, $r$, and source (habitat) cell, $s$, can be represented by the equation:

$$k_{r,s} = \begin{cases} \exp\left(-\frac{1}{\alpha d_{max}} d_{r,s}\right), & d_{r,s} \leq d_{max} \\ 0, & d_{r,s} > d_{max} \end{cases} \tag{1}$$

Where $d_{r,s}$ represents the cost-distance along the least cost path between receiver cell, $r$, and source cell, $s$. The maximum possible dispersal distance is defined by $d_{max}$, such that $k_{r,s} = 0$ when $d_{r,s} > d_{max}$. The constant α dictates the steepness of the decline of the negative exponential curve (Figure 3.). A value of α = 1 produces an approximately linear dispersal kernel, while as α approaches zero, dispersal becomes increasingly unlikely as the distance between cells increases. We assumed α = 0.3, which provides a moderately steep curve (Figure 3.).

Equation 1 defines the pairwise connectivity between each cell in the study region for a given species. Using this method, we produced a connectivity matrix which described the pairwise connectivity of all cells in the study region with all source cells. To calculate the total connectivity of each cell in the study region, we summed the connectivity values (Equation 1) between each cell and all source cells in the map. Connections where the cost-distance was greater than the maximum dispersal distance were set to 0, and thus had no influence on the total connectivity value in that cell. Thus, the total connectivity value, $c$, can be calculated using the following equation:

$$c_r = \sum_{s=1}^{n} k_{r,s} \tag{2}$$

Where $n$ is the total number of cells in the study area. Note that all cells in the study area are receiver cells, including those containing habitat. As such, this equation calculates the total connectivity for all cells, both with and without habitat.

The connectivity models were implemented in the statistical computing software R (RCoreTeam, 2020). The package "gdistance" was used to calculate cost-distances (*d*) between cells along the least cost path (van Etten, 2017). This was done in a pairwise fashion to populate the connectivity matrix. The connectivity matrix consisted of rows for each source cell and columns for each receiver cell. Once the matrix was populated, pairwise connectivities (*k*) were calculated according to Equation 1. Next, the total connectivity (*c*) value in each receiver cell was calculated by summing all *k* values in each column, according to Equation 2. To perform matrix calculations, we utilised the packages "bigstatsr", "biganalytics", and "bigmemory", which are needed for storing and performing computations on extremely large matrices (Kane et al., 2013; Florian, 2018; Emerson and Kane, 2020). Finally, for each species, total connectivity values were standardised to between 0 and 1.

In addition to the individual species connectivity maps, six combined connectivity maps were produced for the following species groups: fish, coastal predatory fish, cyprinids, vegetation, algae, and vascular plants. To create combined maps for multiple species, we calculated the mean standardised connectivity value in each cell across all species in the group. In addition to these, we provide results for notable species and species groups in the region, incorporated into Sweden's "nested targets" (preciserade bevarandevärden; Länsstyrelserna i Norrbottens, Västerbottens, Västernorrlands, Gävleborgs och Uppsala län, 2021; Länsstyrelserna i Stockholm, Södermanland, Östergötland, Kalmar, Gotland, Blekinge och Skåne län, 2021) for which we had habitat distribution maps and dispersal distances. Note also that many of the species present in Sweden's nested target goals are included in the aforementioned groups (Table 1.).

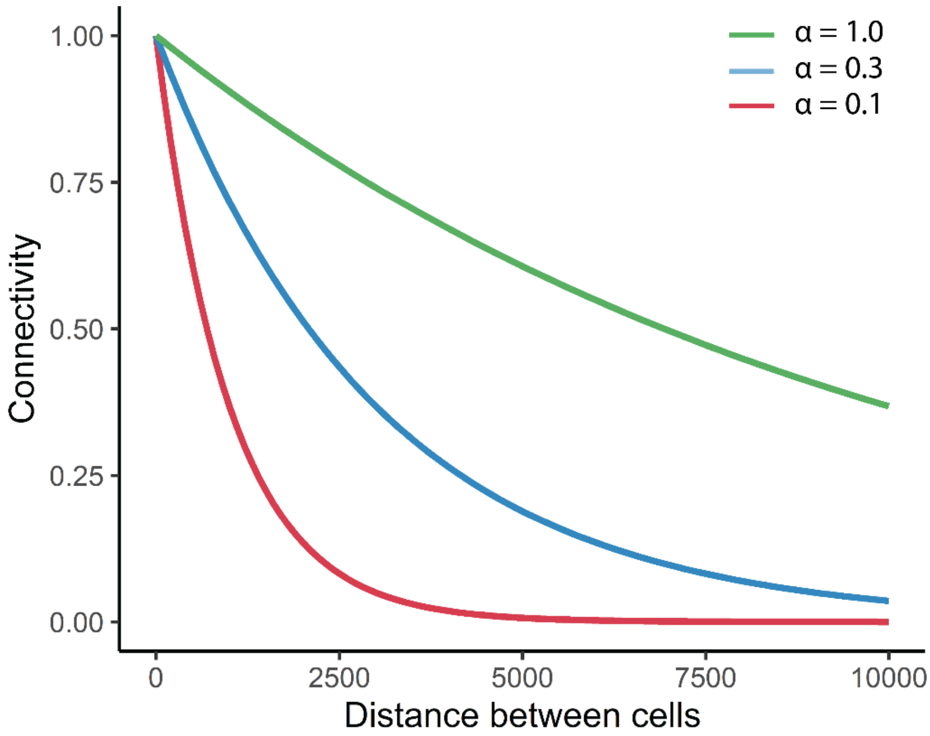


**Figure 3.** Examples of different dispersal kernels describing the relationship between connectivity and the distance between cells. For the connectivity models produced in this report we assumed that α = 0.3 (blue line).

## 2.3. Analysis of the effect of anthropogenic pressures on connectivity

To estimate the effect of anthropogenic pressures on the connectivity of species in the Swedish Baltic Sea, we incorporated spatial pressure data into the connectivity models described above. Spatial pressure maps were obtained from Törnqvist et al. (2020), who produced models of physical disturbance in the Swedish coastal zone. Törnqvist et al. (2020) developed specific spatial models of physical disturbances impacting connectivity, which included impacts of physical obstacles, noise, and changes in hydrological conditions. The model considered various physical disturbances, such as marinas, ports, piers, dredging, dumping activities, and anchorages, among others.

Pressures were incorporated into the connectivity models by adding the pressure layer as a “resistance” layer. In the “gdistance” package in R, the cost-distance between two points is calculated using distance and “conductance”, such that resistance is equal to 1/conductance. Each cell in the raster layer was assigned a conductance value. When conductance equals 1, the cost-distance of traversing that cell is equal to the distance. For example, if the cell resolution is 250 m and the conductance is 1, the cost-distance of traversing that cell is 250. If the conductance in the same cell was 0.5, the cost-distance of traversing the cell would be 500. When the conductance is zero in a cell, it is impossible to travel through that cell, and thus the cell will be avoided in all dispersal routes. Note, in the connectivity models described above, all cells containing land were considered a barrier to dispersal, and were thus assigned a conductance value of 0, while all other cells were assigned a conductance value of 1.

Using the spatial pressure models provided by Törnqvist et al. (2020), we produced an additional conductance layer to that used in the standard connectivity models (Section 2.2). In their model of pressures on the connectivity of coastal habitats, Törnqvist et al. (2020) assigned pressure on a scale of 1 to 5, with 5 indicating the highest intensity of pressures. In our additional conductance layer, we assigned conductance values according to the pressure intensity, where the conductance value, $g$, in cell $i$ is calculated according to the following equation:

$$g_i = 1 - \frac{p_i}{5}$$

Where $p_i$ is the pressure intensity value in cell $i$. As such, when $p = 5$, $g = 0$, when $p = 4$, $g = 0.2$, when $p = 3$, $g = 0.4$, and so forth. Thus, all cells with the maximum pressure intensity of 5 acted as complete barriers to dispersal. All other cells absent of any pressures were assigned a conductance value of 1. It should be noted that data on how different anthropogenic pressures affect the dispersal of individuals of different species is very sparse. Here, we assume a simple linear relationship between pressure intensity and hindrance to dispersal. Although this is a reasonable assumption, outputs from these models should be interpreted with caution, as various pressures might have differing effects on active dispersal, depending on the species being affected and its susceptibility to different pressures and pressure intensities.

To evaluate the change in connectivity in response to anthropogenic pressures, we subtracted connectivity values from the model without pressures by the model with pressures for each species. This produced a map of the change of connectivity in response to pressures, such that higher values represent a greater amount of connectivity loss. We standardised the values for the change in connectivity models to between 0 and 1 for each species. To create combined maps for multiple species, we calculated the mean standardised change in connectivity in each cell across all species in the group.

## 2.4. Coherence assessment: adequacy, replication, representativity, and connectivity

We assessed the coherence of the MPA network in Swedish Baltic coastal waters using four methods: adequacy, replication, representativity, and connectivity. These measures are commonly used in conservation science (Ardron, 2008) and provide some insight into how well protected conservation features are within a protected area network.

Adequacy is typically defined as the capacity for the MPA network to ensure the persistence of conservation features over time (Kukkala & Moilanen 2013). To assess *adequacy* we measured the average and median size of MPAs in the region. We then measured the shortest geodesic distance between each MPA and the nearest MPA (from edge to edge). While this provides only a crude estimate of connectivity between MPAs, it provides some insight, and can be assessed with respect to the typical dispersal distances of species.

The second aspect of coherence, *replication*, is defined as how many instances of a given conservation feature occur within MPAs within the network (Kukkala & Moilanen 2013). We measured replication by calculating, for each species, what proportion of the MPAs in the network contained habitat for each respective species. For fish, juvenile habitat was included since this is a proxy for fish production (Sundblad et al., 2014).

The third aspect of coherence used in this analysis was *representativity*. In a conservation planning context, "representativity" refers to the proportion of occurrences of a conservation feature (e.g. a species' distribution) that occur within a protected area network relative to the total number of occurrences in the study area (Kukkala & Moilanen 2013). To assess the representativity of each species, we calculated the proportion of each species' habitat that occurred within the MPA network. Again, for fish, we focused on juvenile habitats.

To assess the final aspect of coherence, *connectivity*, we measured the total amount of connectivity in the study area for each species using the connectivity models described above. We then calculated the total amount of connectivity within the MPA network as the sum of the connectivity values in each cell within the network. Then, to calculate the percentage of connectivity that is within the MPA network, we divided the total connectivity within the network by the total amount of connectivity within the study area.

Marine Protected Area polygons were obtained from the Swedish Environmental Protection Agency (https://skyddadnatur.naturvardsverket.se/). In the dataset of MPAs, we included Nature Reserves (Swedish: Naturreservat), National Parks (Swedish: Nationalparker), and Biotope Protection Areas (Swedish: Biotopskyddsområden), as defined by Swedish national legislation, and Sites of Community Importance (Swedish: Natura 2000 områden), as defined by the EU Habitats Directive (92/43/EEC). We included only active protected areas specifically designated for the protection of marine areas. We also included only MPAs that intersected with the study area in the analysis (Figure 2.), to avoid underestimating measures, such as representativity, as the habitat models did not include areas outside the study area. Note, however, that we include all MPAs in Sweden in the figures provided in this report.

**Table 2.** Definitions of terms relevant to spatial prioritisation and conservation planning. Most definitions here are based on those by Kukkala and Moilanen (2013).

| Term | Definition |
|---|---|
| Conservation feature | The ecological subject of the spatial prioritisation, typically represented as a spatial layer/map. E.g. species distributions, habitats, connectivity models, species abundance maps. These may be represented discretely (e.g. presence/absence) or continuously (e.g. biomass). |
| Adequacy | The capacity for the protected area network to ensure the persistence of conservation features over time. |
| Replication | The number of instances that a given conservation feature occurs within the protected area network. E.g., if a species is present in a protected area, that is counted as a single instance. |
| Representativity | The proportion of occurrences of a conservation feature (e.g. a species' distribution) that occurs within a protected area network relative to the total number of occurrences in the study area. This is typically measured as the percentage area of a species' distribution that occurs within the protected area network. |
| Coherence | Short for "ecological coherence". Coherence is a term used to describe the overall capacity for a protected area network to facilitate the persistence of habitats, species, and ecosystem functions. Coherence is typically assessed according to the following four criteria: adequacy, replication, representativity, and connectivity. |
| Complementarity | The degree to which protection of a new location, or combination of locations, contributes to protection targets for unrepresented conservation features. Importantly, locations can contribute greatly to targets, even though they may have low species richness, because they contain a complementary set of conservation features that are rare and poorly represented in the existing protected area network. |
| Redundancy | The opposite to complementarity. Locations containing species already represented in the protected area network, and for which targets have already been reached are considered redundant. |
| Irreplaceability | The degree to which removal of a given location from the study area increases the difficulty to reach targets in a spatial prioritisation. Highly irreplaceable sites tend to include many species, rare species, and high biodiversity values (e.g. high connectivity) for many species. |
| Objective | The broader aim of a spatial prioritisation, such as the conservation of species. |
| Target | The desired percentage or proportion of a feature that is to be protected. |
| Efficiency | Efficiency is the degree to which conservation targets can be met for a given cost or area. Highly efficient solutions reach targets with the least amount of required cost or area. Modern conservation planning tools allow users to determine highly efficient solutions, and in the case of the "prioritizr" package (with the Gurobi optimizer), users can determine the optimal solution to maximise efficiency. Other tools, such as Zonation and Marxan, allow users to determine near-optimal solutions, in terms of efficiency. |

## 2.5. Prioritisation of MPAs

One of the objectives of this study was to identify priority areas for the expansion of the MPA network. To do so, we utilised the "prioritizr" package in R using the Gurobi optimizer (Hanson et al., 2021). The prioritizr package is used for solving conservation problems, and provides solutions that are guaranteed to be optimal. As such, prioritizr outperforms other tools, such as Marxan and Zonation, which can only find approximate, sub-optimal, solutions, and provides great utility for identifying the most efficient areas for prioritisation and expansion of protected area networks.

A key concept inherent in all conservation planning tools is complementarity. Complementarity is defined as the degree to which protection of a new location, or combination of locations, contributes to protection targets for unrepresented conservation features (e.g. species' habitats). Complementarity is often contrasted with the concept of redundancy. Selecting an area for protection would be considered redundant if the species present in that location are already protected elsewhere, and if the targets for that species have already been met. Instead, conservation planning tools focus on selecting additional locations containing species that are not already adequately protected. This approach can be contrasted with ranking methods, where locations are selected for protection based on the ranking of a given biodiversity metric, such as species richness. Today, conservation planning tools allow users to create much more efficient solutions using the concept of complementarity, which is incredibly useful for determining optimal locations for protection in large regions with multiple species.

We performed spatial prioritisations based on the output maps produced with the connectivity models described above. These connectivity maps were treated as conservation features in the prioritisation. To identify priority areas for protection, we calculated the "irreplaceability" of each cell in the study area using "eval_replacement_importance" function in the prioritizr package. Irreplaceability is a measure of the relative importance of each cell on the map for reaching conservation objectives. It is calculated by removing an individual cell from the map and measuring the increased difficulty to reach the objectives as a result, and repeating this process iteratively for all cells in the map. For example, cells containing multiple species present nowhere else tend to have high irreplaceability, whereas cells containing few and more widespread species tend to have low irreplaceability.

Prioritisation maps were produced for all species groups (Table 1.). To create the irreplaceability maps, we set feature representativity targets to 90%. Thus, if the target is achieved, 90% of the connectivity of all species in the group would be protected. We set the target to 90% because the objective was to produce irreplaceability maps that cover the majority of the connectivity of all species, rather than to create an explicit spatial prioritisation based on an arbitrary target. Instead, the irreplaceability maps serve as a priority map that can be used by managers for different species groups regardless of their targets.

In addition to irreplaceability maps for each species group, we performed spatial prioritisations to expand the existing MPA network in the study region. In this analysis, cells (i.e. planning units) within existing MPAs were “locked in” for protection, meaning that they are always included in the prioritization solution. We then iteratively repeated the prioritisation while increasing the area that could be selected for protection, corresponding to an increase in the area of the MPA network by 5%, 10%, 15%...100%, i.e. where a 100% increase in the area of the network means that the solution is double the size of the existing MPA network. For these scenarios, the objective function in prioritizr was to maximise the protection of features using the specified area (i.e. budget). For each iteration we then measured the amount of connectivity that was protected in the solution for each species.

# 3. Results

## 3.1. Connectivity models

A total of 30 connectivity models were produced, one for each species (Table 1.). Maps of the connectivity models are provided in Appendix 1 (Figures A1-A30). For all species, connectivity was extremely positively skewed, in terms of frequency. That is, connectivity was generally concentrated in a few small areas, while the majority of the study area contained areas of low connectivity. Below we provide results for six species groups: fish, coastal predatory fish, cyprinids, vegetation, large perennial brown algae, and vascular plants, where connectivity values in each cell represents the mean for all species in the group. We also provide results for individual species included in Sweden's nested target goals (preciserade bevarandevärden), including herring (*Clupea harengus*), cod (*Gadus morhua*), Baltic flounder (*Platichthys solemdalii*), stoneworts (*Chara spp.*), clawed fork weed (*Furcellaria lumbricalis*), and eelgrass (*Zostera marina*).

### 3.1.1. Fish

*Species included: common bream/silver bream (Abramis brama/Blicca bjoerkna), common bleak (Alburnus alburnus), crucian carp (Carassius carassius), herring (Clupea harengus), pike (Esox lucius), cod (Gadus morhua), three-spined stickleback (Gasterosteus aculeatus), two-spotted goby (Gobiusculus flavescens), ruffe (Gymnocephalus cernuus), ide (Leuciscus idus), black goby (Gobius niger), smelt (Osmerus eperlanus), perch (Perca fluviatilis), common minnow (Phoxinus phoxinus), Baltic flounder (Platichthys solemdalii), sand goby (Pomatoschistus minutus), nine-spined stickleback (Pungitius pungitius), roach (Rutilus rutilus), pike-perch (Sander lucioperca), common rudd (Scardinius erythrophthalmus), sprat (Sprattus sprattus), tench (Tinca tinca)*

Connectivity of fish species was particularly concentrated in shallow nearshore areas of the Baltic Proper (Figure 4.). Connectivity of fish was lower in the Gulf of Bothnia compared to the Baltic Proper, which reflects the lower occurrence of the species in this northern basin. However, within the Gulf of Bothnia, notable connectivity hotspots occurred in: Rånefjärden and Siknäsfjärden, north of Luleå, and the southern part of the Gräsö Archipelago. These are topographically complex areas with a large proportion of wave-sheltered habitats, which are rare in the rest of the area. In the Baltic Proper, the most notable connectivity hotspots for fish occurred in: northern and southern Stockholm Archipelago, Sankt Anna Archipelago, Bråviken, Tjust Archipelago, particularly around the islands north of Västervik, Misterhults Archipelago, particularly south of Eknö, and the Mönsterås Archipelago. Sankt Anna Archipelago contained the highest levels of connectivity for fish in the study area.

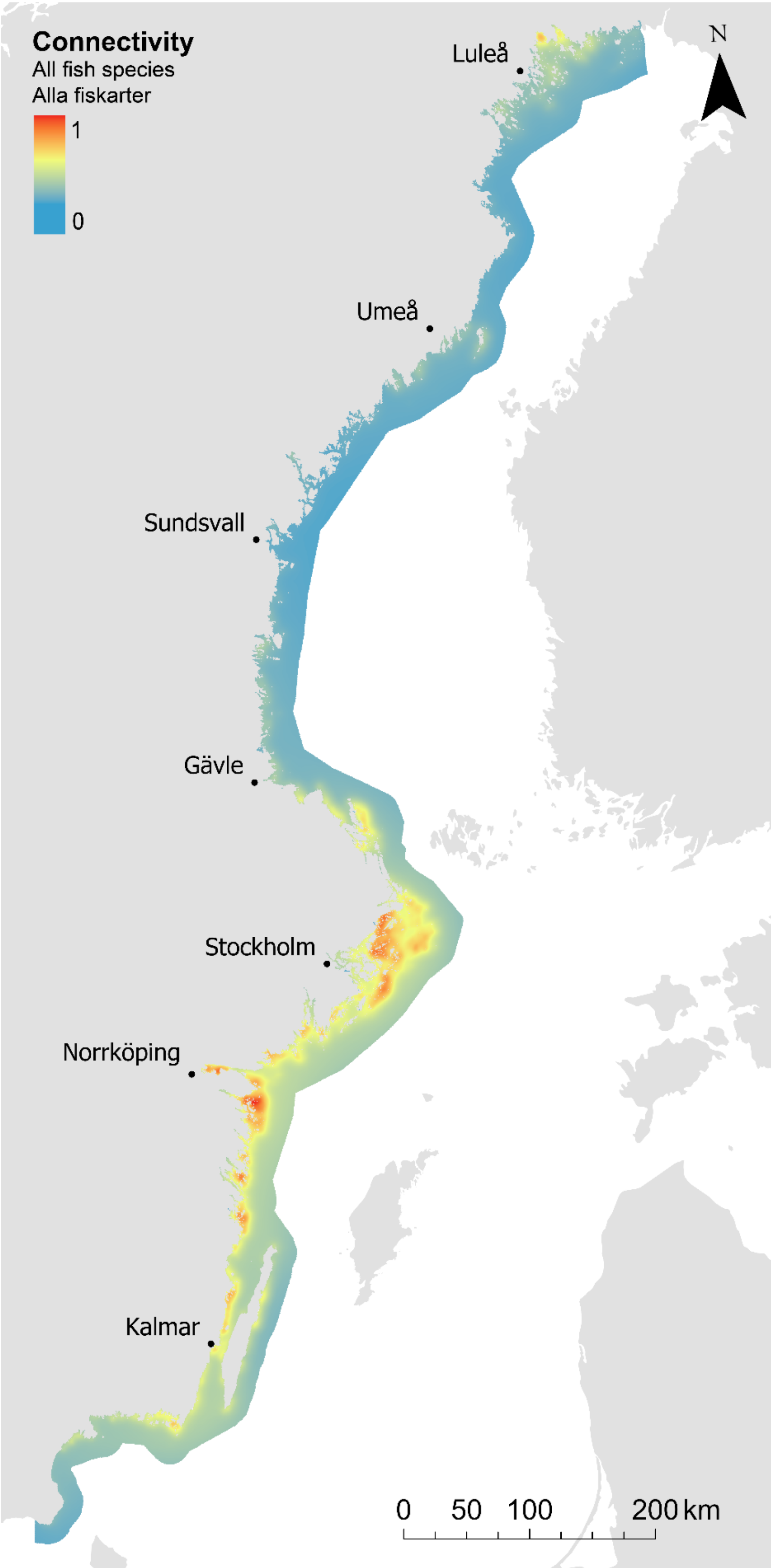


**Figure 4.** Map of the modelled connectivity of all fish species included in this study (Table 1.).

### 3.1.2. Coastal predatory fish

*Species included: pike (Esox lucius), perch (Perca fluviatilis), pike-perch (Sander lucioperca)*

In the Gulf of Bothnia, notable connectivity hotspots for coastal predatory fish occurred in: Rånefjärden and Siknäsfjärden, north of Luleå; Storfjärden, north-east of Piteå; and Galtfjärden, south-east of Östhammar (Figure 5.). The highest connectivity for coastal predatory fish in the study area was in Rånefjärden. In the Baltic Proper, connectivity hotspots occurred in: the northern part of the Stockholm Archipelago; Bråviken, east of Norrköping; Trännöfjärden in Sankt Anna Archipelago; the area north of Västervik in Tjust Archipelago; Misterhults Archipelago in the area surrounding Älö; Dragsviken, north of Kalmar; and Danmarksfjärden and Gåsefjärden, near Karlskrona.


**Figure 5.** Map of the modelled connectivity of all predatory coastal fish species included in this study (Table 1.).

### 3.1.3. Cyprinids

*Species included: common bream/silver bream (Abramis brama/Blicca bjoerkna), common bleak (Alburnus alburnus), crucian carp (Carassius carassius), ide (Leuciscus idus), common minnow (Phoxinus phoxinus), roach (Rutilus rutilus), common rudd (Scardinius erythrophthalmus), tench (Tinca tinca)*

In the Gulf of Bothnia, hotspots for the connectivity of cyprinids occurred in: Rånefjärden and Siknäsfjärden, north of Luleå; Lövstabukten, southeast of Gävle; Östhammarfjärden, south-east of Östhammar (Figure 6.). In the Baltic Proper, hotspots for the connectivity of cyprinids occurred in: Norrfjärden, in northern Stockholm Archipelago; Bråviken, east of Norrköping; Trännöfjärden in Sankt Anna Archipelago; and the area north of Västervik in Tjust Archipelago. Bråviken contained the highest levels of connectivity for cyprinids in the study area.


**Figure 6.** Map of the modelled connectivity of all cyprinid species included in this study (Table 1.).

### 3.1.4. Vegetation

*Species included: stoneworts (Chara spp.), bladder wrack (Fucus vesiculosus/radicans), toothed wrack (Fucus serratus), clawed fork weed (Furcellaria lumbricalis), water milfoil (Myriophyllum spp.), cperfoliate pondweed (Potamogeton perfoliatus), sago pondweed (Stuckenia pectinata), eelgrass (Zostera marina)*

Connectivity of the species of vegetation included in this analysis was relatively low in the Gulf of Bothnia compared to the Baltic Proper (Figure 7.). However, within the Gulf of Bothnia the highest areas of connectivity occurred in Enhammarsfjärden, southeast of Hudiksvall, and in Östhammarfjärden, southeast of Östhammar. In the Baltic Proper, hotspots of connectivity for vegetation occurred in: the northern part of Stockholm Archipelago; the entrance to Bråviken; Sankt Anna Archipelago; Gundingen, the area north of Västervik in Tjust Archipelago; Misterhults Archipelago; Mönsteråsviken and the surrounding islands; and the islands surrounding Karlskrona. The highest levels of connectivity for vegetation in the study area occurred in the Stockholm Archipelago, particularly around the islands surrounding Träsköfjärden.


**Figure 7.** Map of the modelled connectivity of all species of vegetation included in this study (Table 1.).

### 3.1.5. Large perennial brown algae

*Species included: bladder wrack (Fucus vesiculosus/radicans), toothed wrack (Fucus serratus)*

Connectivity was relatively limited in the Gulf of Bothnia for the algae species included in this analysis (Figure 8.). Notable hotspots for algae in the Gulf of Bothnia occurred in the coastal area north of Hudiksvall and particularly north of Söderhamn. Moderate levels of connectivity of algae also occurred in the Gräsö archipelago. In the Baltic Proper, hotspots of connectivity occurred in: northern and central Stockholm Archipelago; the entrance to Bråviken; Sankt Anna Archipelago; the islands surrounding Karlskrona; and the coastal area south of Karlshamn.


**Figure 8.** Map of the modelled connectivity of all species of algae included in this study (Table 1).

### 3.1.6. Vascular plants

*Species included: water milfoil (Myriophyllum spp.), perfoliate pondweed (Potamogeton perfoliatus), sago pondweed (Stuckenia pectinata)*

Connectivity of vascular plants was relatively limited in the Gulf of Bothnia (Figure 9.). The highest levels of connectivity in the Gulf of Bothnia occurred around Galtfjärden and Singöfjärden, southeast of Östhammar. Within the Baltic Proper, connectivity of vascular plants was concentrated in the following areas: Stockholm Archipelago; Svärdsfjärden, west of Nynäshamn; Sankt Anna Archipelago; Gundingen, the area north of Västervik in Tjust Archipelago; Misterhults Archipelago; and the island surrounding Mönsteråsviken, south of Oskarshamn. The highest levels of connectivity of vascular plants in the study area occurred in the northern and central parts of the Stockholm Archipelago.


**Figure 9.** Map of the modelled connectivity of all species of vascular plants included in this study (Table 1).

### 3.1.7. Species specified in Sweden’s nested targets (preciserade bevarandevärden)

*Herring (Clupea harengus)*
Connectivity of herring was concentrated around the Stockholm Archipelago, extending from Gävle in the northto Oskarshamn in the south (Figure A4). Because herring is a pelagic species with a large home range size and capable of dispersing large distances, connectivity is high across the region. There was also a notable level of high connectivity of herring in the area northeast of Luleå.

*Cod (Gadus morhua)*
Connectivity of cod was concentrated in the area surrounding Karlskrona (Figure A6). This area of high connectivity extended from Kalmar in the north to Simrishamn in the south. The spatial patterns of connectivity for cod were noticeably different from most other species included in this analysis, in that most species have high levels of connectivity in Stockholm Archipelago, whereas cod connectivity was highest in the south; in the Kalmar, Blekinge, and Skåne counties, as well as the coastal areas closest to the main spawning area in the Bornholm basin.

*Baltic flounder (Platichthys solemdalii)*
For Baltic flounder, the highest levels of connectivity occurred in Sankt Anna Archipelago in Östergötland County and south of Oskarshamn in Kalmar County (Figure A15). Connectivity of Baltic flounder was moderately high along the entire coastline between northern Stockholm Archipelago down to Skåne. Baltic flounder was not predicted to occur in the habit models north of Stockholm Archipelago, therefore there was a lack of connectivity.

*Pike (Esox lucius)*
In the Gulf of Bothnia, pike connectivity was concentrated in shallow, wave-sheltered areas around Luleå, Umeå, Sundsvall, and Östhammar (Figure A5). Pike connectivity was very high along the entire coastline of the Baltic Proper, with hotspots occurring particularly in the south in Kalmar, Blekinge, and Skåne counties. Specifically, the highest levels of connectivity of pike occurred in: the coastline between Kalmar and Mönsterås; Gåsefjärden, southeast of Karlskrona; Tromtöfjärden, south-west of Karlskrona; and in northern Hanöbukten, southeast of Kristianstad.

*Perch (Perca fluviatilis)*
Perch, being a widespread species throughout the study area, showed very high levels of connectivity across much of the region (Figure A13). Levels of connectivity were exceptionally high in Rånefjärden and Siknäsfjärden, north of

Luleå. This hotspot of connectivity for perch represents an area of great conservation value, as the nearest connectivity hotspot for the species occurs much further south in the Stockholm Archipelago. As such, populations in Rånefjärden and Siknäsfjärden, although highly connected locally, are extremely isolated, and loss of populations in these areas would likely have highly detrimental effects on recruitment to other sub-populations in the Gulf of Bothnia. In the Gulf of Bothnia, other connectivity hotspots for perch occurred in: Storfjärden, north of Piteå; Galtfjärden and Singöfjärden, southeast of Östhammar; and southern Gräsö Archipelago. In the Baltic Proper, connectivity of perch was very high throughout much of the Stockholm Archipelago. Other notable hotspots occurred in: Bråviken, north.east of Norrköping; Sankt Annas Archipelago; Gudingen, north of Västervik; Mistehults Archipelago; Dragsviken, north of Kalmar; and in the sea area surrounding Karlskrona.

*Eelgrass (Zostera marina)*

Eelgrass connectivity was very high in the sea area between Kalmar and Öland, particularly in the area between Mönsterås in the north and Hagby in the south (Figure A30). Areas with high connectivity for eelgrass also occurred in the sea area between Karlshamn and Karlskrona in Blekinge County, and in the area around Sölvesborg on the border between Blekinge County and Skåne County. Other areas of low connectivity occurred along the coast in the Baltic Proper. The northern distribution range of eelgrass in the Baltic Sea is in the northern Baltic Proper, why there is no connectivity for eelgrass in the Gulf of Bothnia.

*Stoneworts (Chara spp.)*

Connectivity of stoneworts was highly restricted to a few small areas (Figure A23). Most notably, the highest levels of connectivity occurred south of Misterhults Archipelago around Simpevarp in Kalmar County. Other notable connectivity hotspots for stoneworts occurred in: Stockholm Archipelago between the islands Ljusterö and Möja; east of the island Yxnö and south-west of the island Finnö in Östergötland County; and Gudingen sea area, north of Västervik in Kalmar County

*Clawed fork weed (Furcellaria lumbricalis)*

Connectivity of clawed fork weed was also highly restricted to a few small areas (Figure A26). The highest levels of connectivity occurred along the northeastern coast of Listerlandet peninsula, which is south of Karlshamn in Blekinge county. Other areas of high connectivity of clawed fork weed occurred around the Örarevet sea area in Kalmar County and in the sea area between Sölvesborg and Åhus (east of Kristianstad) in Skåne County.

*Bladder wrack (Fucus vesiculosus/radicans)*

Connectivity of the bladder wrack was concentrated mostly in the south part of the Gulf of Bothnia and northern part of the Baltic Proper, with the highest levels of connectivity occurring in the Stockholm Archipelago (Figure A24). The highest levels of connectivity in the Gulf of Bothnia occurred in the sea area northeast of Söderhamn and the sea area southeast of Strömsbruk, near Hudiksvall. In the Baltic Proper, hotspots occurred in: the northern and southern parts of Stockholm Archieplago; eastern Bosofjärden, outside Norrköping; and in Sankt Annas Archipelago.

## 3.2. Change in connectivity in response to anthropogenic pressures

Anthropogenic pressures, in this case physical disturbance, had a relatively large predicted impact on connectivity, particularly for certain species (Table 3.). The species that had the greatest predicted reduction in connectivity was *Carassius carassius* (Crucian carp/ruda), which had 25% less connectivity when anthropogenic pressures were incorporated into the connectivity models. Note that percentages were used because all connectivity values from the model output were standardised to between 0 and 1, so that it is possible to compare between species. This is necessary because some species are naturally more widespread and abundant, and so have higher absolute values of connectivity. Other species for which connectivity was severely affected included a number of cyprinids: *Rutilus rutilus* (Roach/Mört), *Scardinius erythrophthalmus* (Common rudd/Sarv), *Abramis brama/Blicca bjoerkna* (Common bream/Silver bream/Braxen/Björkna), and *Alburnus alburnus* (Common bleak/Löja). Also, large predators like *Sander lucioperca* (pike-perch/gös), *Perca fluviatilis* (perch/abborre) *and Esox lucius* (pike/gädda) had 19%, 17% and 16% less connectivity, respectively, when incorporating physical disturbance into the models. These are all species that are dependent on shallow wave-sheltered areas for their reproduction. These are also the areas where most human pressures are concentrated, as these bays are often used for jetties and marinas, and are in many cases dredged to enable boat traffic. Habitat-forming submerged aquatic vegetation (SAV) with limited dispersal (macrophytes and macroalgae), was also highly affected by physical disturbance in our connectivity models.

The species for which connectivity was predicted to be least affected by anthropogenic pressures was *Gadus morhua* (cod/torsk). This is likely the result of the long dispersal capabilities of cod, meaning that concentrated areas of physical disturbance are unlikely to impede its ability to disperse, in combination with cod using deeper and wave-exposed habitats as nursery areas. Other species less affected by anthropogenic pressures included *Furcellaria lumbricalis* (clawed fork weed/kräkel), *Platichthys solemdalii* (Baltic flounder/Östersjöflundra), and *Gasterosteus aculeatus* (three-spined stickleback/storspigg).

There were abundant predicted losses in connectivity along the entire Swedish east coast (Figure 10.). Predicted losses were more severe in the Baltic Proper than in the Gulf of Bothnia, although relatively severe losses were still predicted in the Gulf of Bothnia. In the Gulf of Bothnia, predicted losses were most severe in the areas surrounding Luleå, Piteå, Umeå, Härnösand, Hudiksvall, Söderhamn, Norrsundet, Gävle, and Forsmark (north of Öregrund). In the Baltic proper, predicted losses were most severe in the areas surrounding Stockholm (and in the Stockholm Archipelago), Nynäshamn, Nyköping, Norrköping, Västervik, Mönsterås, Kårehamn (Öland), Kalmar, and Karlskrona.

**Table 3.** Predicted change in connectivity of species in response to anthropogenic pressures. Note that percentages were used because all connectivity values from the model output were standardised to between 0 and 1, so that it is possible to compare between species. This is necessary because some species are naturally more widespread and abundant, and so have higher absolute values of connectivity.

| **Scientific** | **English** | **Swedish** | **Percentage change in connectivity in response to anthropogenic pressures** |
|---|---|---|---|
| *Abramis brama/Blicca bjoerkna* | Common bream/Silver bream | Braxen/Björkna | -20% |
| *Alburnus alburnus* | Common bleak | Löja | -20% |
| *Carassius carassius* | Crucian carp | Ruda | -25% |
| *Clupea harengus* | Herring | Strömming | -6% |
| *Esox lucius* | Pike | Gädda | -16% |
| *Gadus morhua* | Cod | Torsk | -2% |
| *Gasterosteus aculeatus* | Three-spined stickleback | Storspigg | -5% |
| *Gobiusculus flavescens* | Two-spotted goby | Sjustrålig smörbult | -6% |
| *Gymnocephalus cernuus* | Ruffe | Gärs | -10% |
| *Leuciscus idus* | Ide | Id | -12% |
| *Gobius niger* | Black goby | Svart smörbult | -7% |
| *Osmerus eperlanus* | Smelt | Nors | -12% |
| *Perca fluviatilis* | Perch | Abborre | -17% |
| *Phoxinus phoxinus* | Common minnow | Elritsa | -7% |
| *Platichthys solemdalii* | Baltic flounder | Östersjöflundra | -4% |
| *Pomatoschistus minutus* | Sand goby | Sandstubb | -8% |
| *Pungitius pungitius* | Nine-spined stickleback | Småspigg | -7% |
| *Rutilus rutilus* | Roach | Mört | -21% |
| *Sander lucioperca* | Pike-perch (Zander ) | Gös | -19% |
| *Scardinius erythrophthalmus* | Common rudd | Sarv | -21% |
| *Sprattus sprattus* | Sprat | Skarpsill | -6% |
| *Tinca tinca* | Tench | Sutare | -21% |
| *Chara spp.* | Stoneworts | Sträfsen | -15% |
| *Fucus vesiculosus/radicans* | Bladder wrack | Blåstång/Smaltång | -6% |
| *Fucus serratus* | Toothed wrack | Sågtång | -14% |
| *Furcellaria lumbricalis* | Clawed fork weed | Kräkel | -3% |
| *Myriophyllum spp.* | Water milfoil | Slingesläktet | -17% |
| *Potamogeton perfoliatus* | Clasping-leaved pondweed | Ålnate | -14% |
| *Stuckenia pectinata* | Sago pondweed | Borstnate | -13% |
| *Zostera marina* | Eelgrass | Ålgräs | -10% |

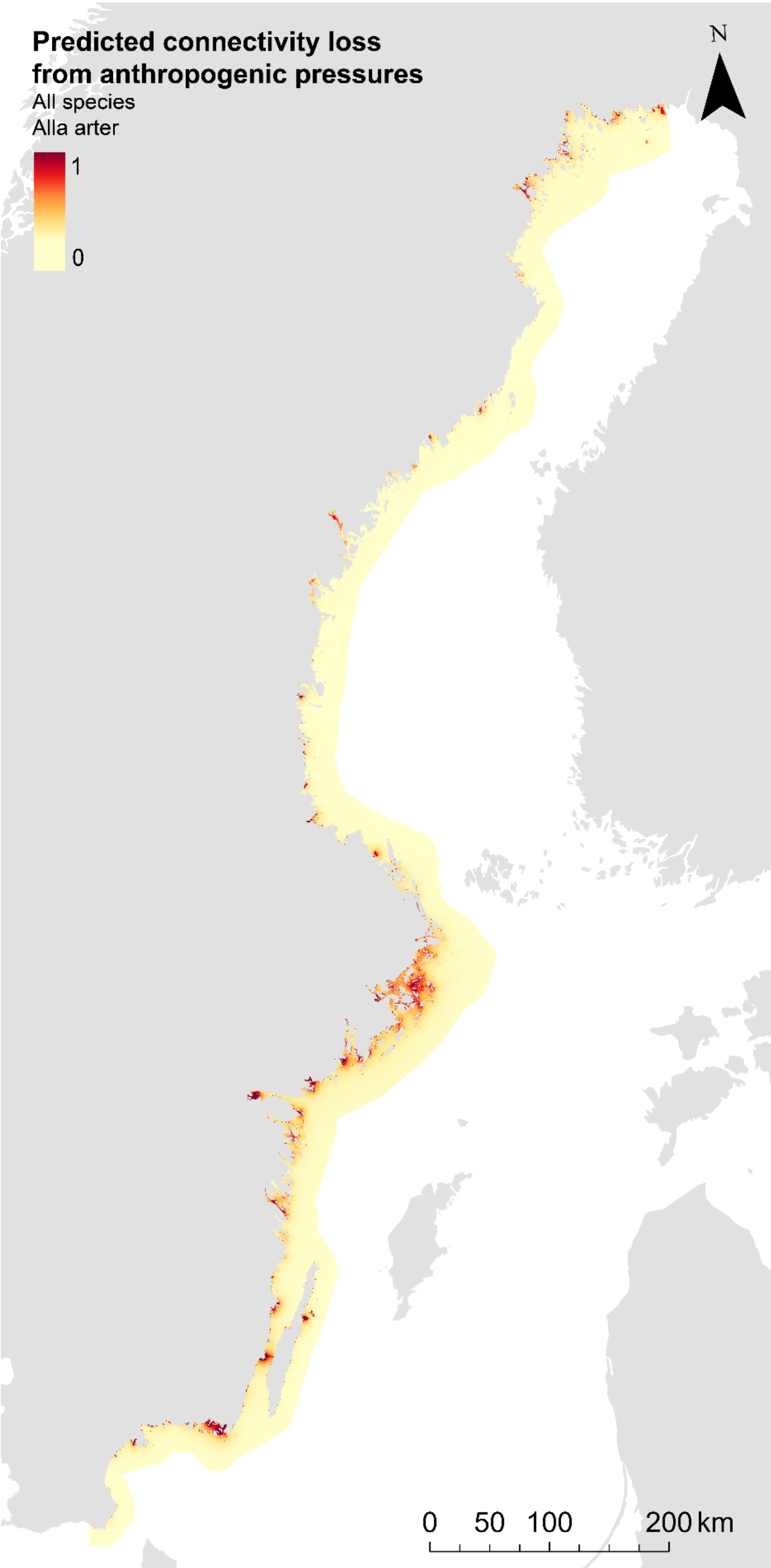


**Figure 10.** Map of the predicted connectivity loss from anthropogenic pressures for all species included in the study area. To combine connectivity models for multiple species,

all connectivity values were standardised, and, as such, values in the map represent relative values rather than an absolute measure of connectivity loss.

## 3.3. Coherence of the MPA network

### 3.3.1. Adequacy and replication

The study area contained 307 marine protected areas (MPAs), of which 21 were strictly protected MPAs (classified as IUCN category Ia or Ib). For IUCN category Ia and Ib removal of species or modification, extraction or collection of resources (e.g. through fishing, harvesting or dredging) is generally not permitted. However, collection for scientific purposes is allowed in category Ia and in category Ib, in some circumstances, sustainable resource use by indigenous people to conserve their traditional, spiritual and cultural values is allowed (Day et al., 2019). Additionally, for IUCN category Ia, anchoring, which can damage bottom habitat, is generally not permitted.

The distance between MPAs in the study area was highly positively skewed (Figure 11.), meaning that the vast majority of MPAs were a short distance from the other nearest MPA. The mean and median distance between MPAs was 1.86 km and 0.45 km, respectively. The typical dispersal distances for the species included in this study were greater than the distances between most of the MPAs and their nearest neighbour, indicating that the MPA network is mostly adequate for facilitating between-MPA dispersal. The vast majority (over 96%) of MPAs were within 10 km of the nearest MPA. For the remaining 4%, spacing may not be sufficient to maintain connectivity.

MPA size was also highly positively skewed (Figure 11.), meaning that the vast majority of MPAs were small. The mean and median size of MPAs was 21.94 $km^2$ and 4.74 $km^2$, respectively. The high mean value is explained by the presence of a small number of very large MPAs, such as Svenska Högarna in Stockholms Län, Gräsö östra skärgård in Uppsala Län, and Örefjärden-Snöanskärgården in Västerbottens Län.

Replication of species included in this study was highly variable (Table 4.). The average replication of species was 47%, meaning that, on average, across species, 47% of the MPAs contained at least one occurrence of a given species. For strict MPAs, the average was 44%. Some species were widespread across the MPA network, such as *Pomatoschistus minutus* (sand goby/sandstubb), which was present in 91% of MPAs, and 100% of strict MPAs. Other species were present in only a small percentage of MPAs, such as *Sander lucioperca* (pike-perch/Gös), which was present in only 12% of MPAs, and 10% of strict MPAs. In general, there was high replication within the MPA network for the following species: *Pomatoschistus minutus* (sand goby/sandstubb), *Clupea harengus* (herring/strömming), *Gobiusculus flavescens* (two-spotted goby/sjustrålig smörbult), *Sprattus sprattus* (sprat/skarpsill), *Stuckenia pectinata* (sago pondweed/borstnate), *Myriophyllum spp.* (water milfoil/ slingesläktet), and *Chara spp.* (stoneworts/ sträfsen). There was low replication within the MPA network for the following species: *Sander lucioperca* (pike-perch/gös), *Scardinius erythrophthalmus* (common rudd/sarv), *Carassius carassius* (crucian carp/ruda), *Gadus morhua* (cod/torsk), *Fucus serratus* (toothed wrack/sågtång), and *Furcellaria lumbricalis* (clawed fork weed/kräkel). These poorly replicated species all have very specific habitat requirements, some being associated with sheltered, turbid bays with a high influx of freshwater, whilst others with a preference for more exposed, saline waters of the southern Baltic.

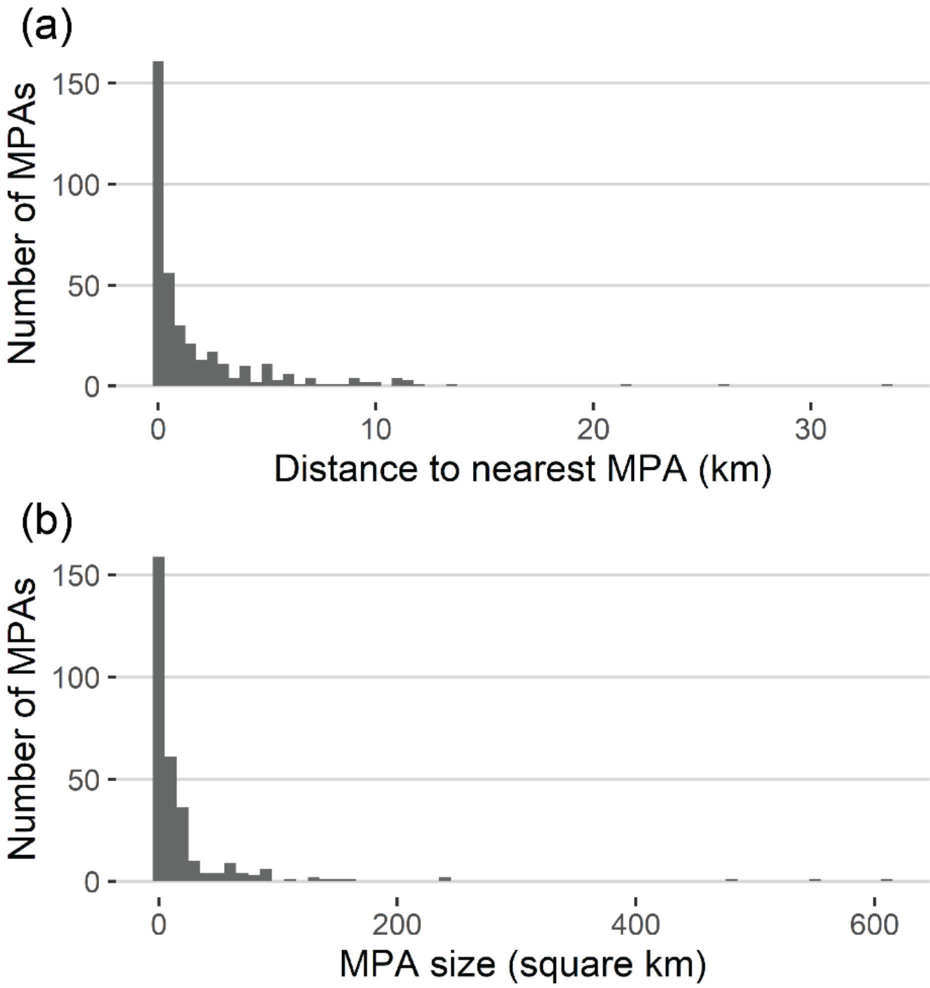


**Figure 11.** The number of MPAs within the study area within difference classes of: (a) distance to the nearest other MPA, and (b) total size.

**Table 4.** Replication of species within the marine protected area network in the study area. Replication was measured as the percentage of MPAs where habitat for each species is present. Strict MPAs here refer to those classified as IUCN category Ia or Ib protected areas.

| Scientific name | English name | Swedish name | Percentage of MPAs with habitat | Percentage of strict MPAs with habitat |
|---|---|---|---|---|
| *Abramis brama/Blicca bjoerkn* | Common bream | Braxen | 31% | 19% |
| *Alburnus alburnus* | Common bleak | Löja | 36% | 29% |
| *Carassius carassius* | Crucian carp | Ruda | 19% | 5% |
| *Clupea harengus* | Herring | Strömming | 88% | 90% |
| *Esox lucius* | Pike | Gädda | 59% | 33% |
| *Gadus morhua* | Cod | Torsk | 20% | 10% |
| *Gasterosteus aculeatus* | Three-spined stickleback | Storspigg | 65% | 86% |
| *Gobiusculus flavescens* | Two-spotted goby | Sjustrålig smörbult | 76% | 90% |
| *Gymnocephalus cernuus* | Ruffe | Gärs | 63% | 81% |
| *Leuciscus idus* | Ide | Id | 30% | 48% |
| *Gobius niger* | Black goby | Svart smörbult | 56% | 57% |
| *Osmerus eperlanus* | Smelt | Nors | 62% | 67% |
| *Perca fluviatilis* | Perch | Abborre | 54% | 38% |
| *Phoxinus phoxinus* | Common minnow | Elritsa | 36% | 57% |
| *Platichthys solemdalii* | Baltic flounder | Östersjöflundra | 59% | 33% |
| *Pomatoschistus minutus* | Sand goby | Sandstubb | 91% | 100% |
| *Pungitius pungitius* | Nine-spined stickleback | Småspigg | 53% | 52% |
| *Rutilus rutilus* | Roach | Mört | 49% | 38% |
| *Sander lucioperca* | Zander (pike-perch) | Gös | 12% | 10% |
| *Scardinius erythrophthalmus* | Common rudd | Sarv | 18% | 10% |
| *Sprattus sprattus* | Sprat | Skarpsill | 73% | 62% |
| *Tinca tinca* | Tench | Sutare | 23% | 19% |
| *Chara spp.* | Stoneworts | Sträfsen | 64% | 52% |
| *Fucus vesiculosus/radicans* | Bladder wrack | Blåstång | 31% | 48% |
| *Fucus serratus* | Toothed wrack | Sågtång | 14% | 10% |
| *Furcellaria lumbricalis* | Clawed fork weed | Kräkel | 18% | 10% |
| *Myriophyllum spp.* | Water milfoil | Slingesläktet | 65% | 43% |
| *Potamogeton perfoliatus* | Clasping-leaved pondweed | Ålnate | 44% | 43% |
| *Stuckenia pectinata* | Sago pondweed | Borstnate | 71% | 57% |
| *Zostera marina* | Eelgrass | Ålgräs | 42% | 14% |

### 3.3.2. Representativity and connectivity

Determining sufficient targets for representativity is often difficult, because standards and goals for representativity are often arbitrary, except in cases where appropriate targets for the persistence of species can be determined through empirical analysis. However, reviews of the scientific literature on appropriate area-based targets for conservation have concluded that targets to protect conservation features should, at an absolute minimum, be 30%, and in many cases should be up to 50% or even 70% to preserve ecological function, prevent extinction risk, and prevent regime shifts (Svancara et al., 2005; Woodley et al., 2019). That is to say, we should aim to have a minimum target of 30%, while also aiming to improve beyond this target, if possible. A minimum target of 30% also aligns with the EU Commission's recent commitment to protect 30% of European waters by 2030.

The average representativity of species included in this study was 17% in all MPAs. Only three species had more than 30% of their distribution within MPAs: *Phoxinus phoxinus* (common minnow/elritsa), *Fucus serratus* (toothed wrack/sågtång), and *Furcellaria lumbricalis* (clawed fork weed/kräkel, Table 5.). The most poorly represented species were *Gadus morhua* (cod/torsk), *Carassius carassius* (crucian carp/ruda), *Tinca tinca* (tench/sutare), *Chara spp.* (stoneworts/sträfsen), *Myriophyllum spp*. (water milfoil/slingesläktet), and *Potamogeton perfoliatus* (clasping-leaved pondweed/ålnate). The representativity of species within strict MPAs was poor, with an average of only 2% across all species.

The amount of connectivity protected within the MPA network was relatively consistent across species (Table 5.). The mean amount of connectivity within the MPA network was 16% across all species, and only 2% for strict MPAs. Species for which connectivity was relatively well protected included: *Gobiusculus flavescens* (two-spotted goby/sjustrålig smörbult), *Gobius niger* (black goby/svart smörbult), *Phoxinus phoxinus* (common minnow/elritsa), *Fucus serratus* (toothed wrack/sågtång), and *Furcellaria lumbricalis* (clawed fork weed/kräkel). Species for which connectivity was relatively poorly protected were: *Gadus morhua* (cod/torsk), *Platichthys solemdalii* (Baltic flounder/Östersjöflundra), *Rutilus rutilus* (roach/mört), and *Zostera marina* (eelgrass/ålgräs).

**Table 5.** Representativity of species within the marine protected area network in the study area. Representativity was measured in terms of the percentage of habitat within the MPA network, and the percentage of connectivity within the MPA network. Strict MPAs here refer to those classified as IUCN category Ia or Ib protected areas.

| Scientific name | English name | Swedish name | Habitat area (km$^2$) | Habitat | | Connectivity | |
|---|---|---|---|---|---|---|---|
| | | | | % in MPAs | % in strict MPAs | % in MPAs | % in strict MPAs |
| *Abramis brama/Blicca bjoerkn* | Common bream | Braxen | 873 | 16% | 0% | 18% | 1% |
| *Alburnus alburnus* | Common bleak | Löja | 990 | 14% | 0% | 18% | 1% |
| *Carassius carassius* | Crucian carp | Ruda | 339 | 9% | 0% | 13% | 1% |
| *Clupea harengus* | Herring | Strömming | 3869 | 21% | 2% | 12% | 3% |
| *Esox lucius* | Pike | Gädda | 1931 | 15% | 1% | 16% | 1% |
| *Gadus morhua* | Cod | Torsk | 6397 | 4% | 2% | 7% | 3% |
| *Gasterosteus aculeatus* | Three-spined stickleback | Storspigg | 1867 | 27% | 3% | 11% | 2% |
| *Gobiusculus flavescens* | Two-spotted goby | Sjustrålig smörbult | 3022 | 26% | 3% | 24% | 3% |
| *Gymnocephalus cernuus* | Ruffe | Gärs | 3023 | 18% | 2% | 17% | 3% |
| *Leuciscus idus* | Ide | Id | 690 | 16% | 2% | 17% | 2% |
| *Gobius niger* | Black goby | Svart smörbult | 2644 | 22% | 2% | 22% | 3% |
| *Osmerus eperlanus* | Smelt | Nors | 1817 | 13% | 1% | 12% | 3% |
| *Perca fluviatilis* | Perch | Abborre | 2134 | 14% | 1% | 14% | 1% |
| *Phoxinus phoxinus* | Common minnow | Elritsa | 398 | 34% | 5% | 25% | 3% |
| *Platichthys solemdalii* | Baltic flounder | Östersjöflundra | 7127 | 19% | 3% | 13% | 3% |
| *Pomatoschistus minutus* | Sand goby | Sandstubb | 4301 | 20% | 2% | 19% | 3% |
| *Pungitius pungitius* | Nine-spined stickleback | Småspigg | 1338 | 24% | 2% | 23% | 2% |
| *Rutilus rutilus* | Roach | Mört | 1378 | 12% | 0% | 11% | 0% |
| *Sander lucioperca* | Zander (pike-perch) | Gös | 579 | 13% | 0% | 13% | 0% |
| *Scardinius erythrophthalmus* | Common rudd | Sarv | 170 | 14% | 1% | 14% | 1% |
| *Sprattus sprattus* | Sprat | Skarpsill | 2416 | 25% | 2% | 12% | 2% |
| *Tinca tinca* | Tench | Sutare | 761 | 9% | 1% | 13% | 1% |
| *Chara spp.* | Stoneworts | Sträfsen | 983 | 8% | 0% | 18% | 1% |
| *Fucus vesiculosus/radicans* | Bladder wrack | Blåstång | 385 | 18% | 3% | 17% | 3% |
| *Fucus serratus* | Toothed wrack | Sågtång | 37 | 32% | 6% | 26% | 7% |
| *Furcellaria lumbricalis* | Clawed fork weed | Kräkel | 67 | 35% | 1% | 22% | 1% |
| *Myriophyllum spp.* | Water milfoil | Slingesläktet | 1042 | 9% | 0% | 15% | 1% |
| *Potamogeton perfoliatus* | Clasping-leaved pondweed | Ålnate | 1296 | 8% | 1% | 12% | 1% |
| *Stuckenia pectinata* | Sago pondweed | Borstnate | 1043 | 13% | 1% | 15% | 1% |
| *Zostera marina* | Eelgrass | Ålgräs | 427 | 14% | 0% | 11% | 1% |

## 3.4. Priority areas for establishment and expansion of MPAs

When including all species in the prioritisation, several key areas were identified as essential for maximising connectivity in the study area. In the Gulf of Bothnia, Rånefjärden and Siknäsfjärden, north of Luleå were identified as high priority areas. Rånefjärden is classified as a Natura 2000 Site of Community Importance (SCI), and represents a good candidate for strengthening of protection, particularly given the lack of other priority areas in the Gulf of Bothnia. Likewise, Siknäsfjärden represents a good candidate for the establishment of a new protected area. Given the proximity of these locations to one another, and their isolation from other areas of high connectivity, these two locations should be considered a priority in the region. In addition to these locations, the following areas were identified as high priority areas in the Gulf of Bothnia: Ledskär, east of Karlholm, which is partly protected as a SCI for the protection of birds; the area between the southern part of Gräsö and Öregrund; and the area south-east of Östhammarsfjärden.

In the Baltic Proper, the following key priority areas were identified: the area north-west of Yxlö Island and Furusund in the Stockholm Archipelago; Bråviken, east of Norrköping (contains nature reserve); the areas east and west of Yxnö in Sankta Anna Archipelago; the area surrounding Smågö in Gudingen, north of Västervik (contains SCI and nature reserve); the area south-west of Eknö in Misterhults Archipelago; Mönsteråsviken, south of Oskarshamn; Östrafjärden, east of Karlskrona; and the area surrounding Bockön, east of Karlshamn (partly contains SCI).

In the analysis of MPA expansion, we found that targeted expansion of the MPA network could provide substantial improvements to the connectivity of species. The current MPA network within the study region covers an area of 4,919 km$^2$. If the MPA network was expanded by 25% (1,230 km$^2$) according to the optimal prioritisation (Figures 12. & 13.), the mean connectivity of species would be increased by 54%. Similarly, a 50%, 75%, and 100% expansion of the MPA area would increase species connectivity by 162%, 234%, and 263%, respectively. The relationship between the percentage of MPA expansion and the increase in connectivity followed a sigmoidal trajectory, meaning that connectivity rapidly improved up until the area of the network was expanded by about 50% (~2,450 km$^2$), at which point it became increasingly more difficult to improve connectivity. These data indicate that connectivity hotspots (i.e. the areas described above) are highly restricted and uncommon, and that if they are not incorporated into the MPA network, connectivity is unlikely to improve. This was partially influenced by the inclusion of some highly connected and long-dispersing species, such as cod, sprat, and smelt, for which protection of connectivity requires a large amount of MPA area.

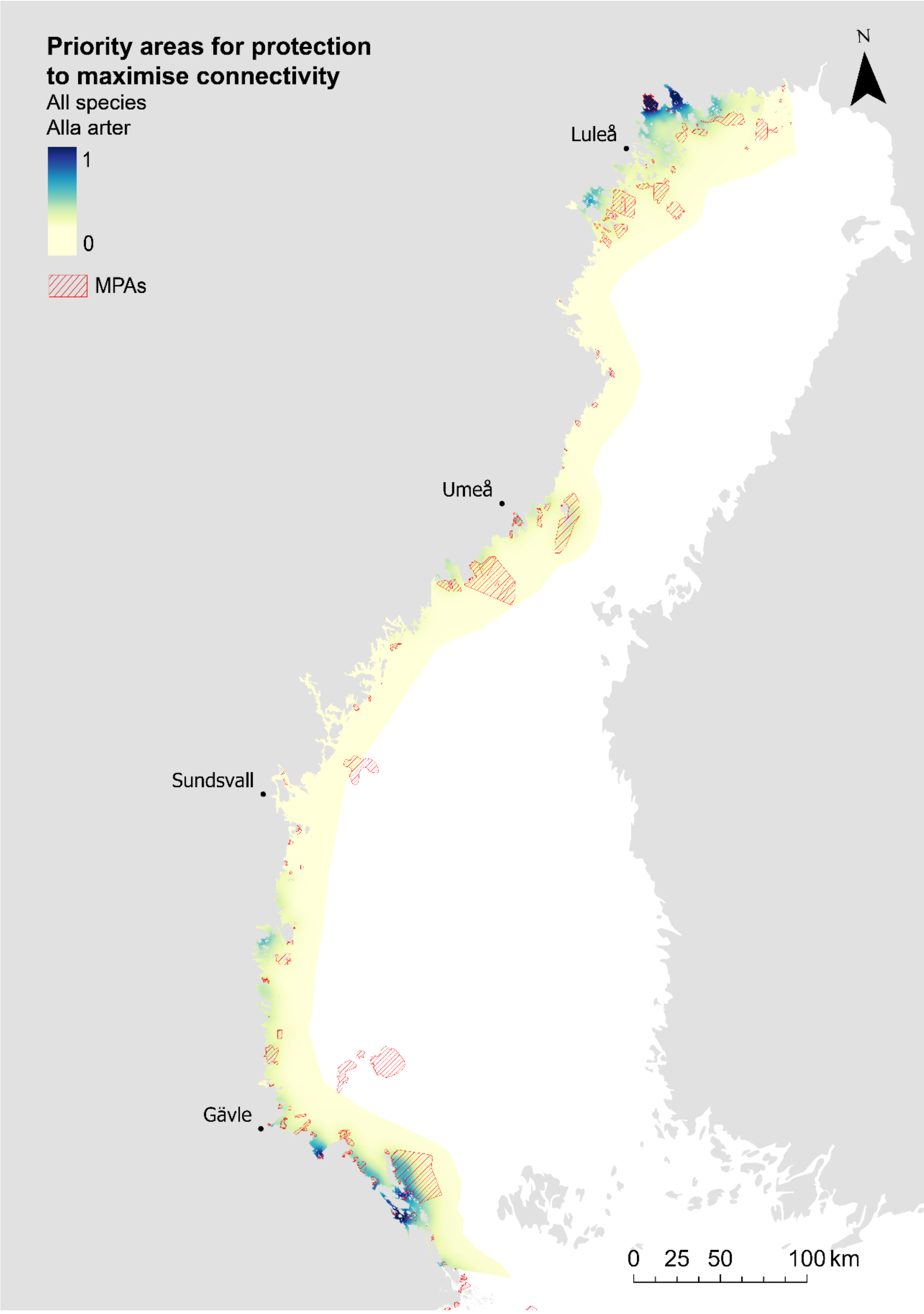


**Figure 12.** Priority areas for expansion of the MPA network in the Gulf of Bothnia to maximise connectivity of all species. Dark blue areas indicate areas of high priority, and represent good candidates for expansion or strengthening of the MPA network.

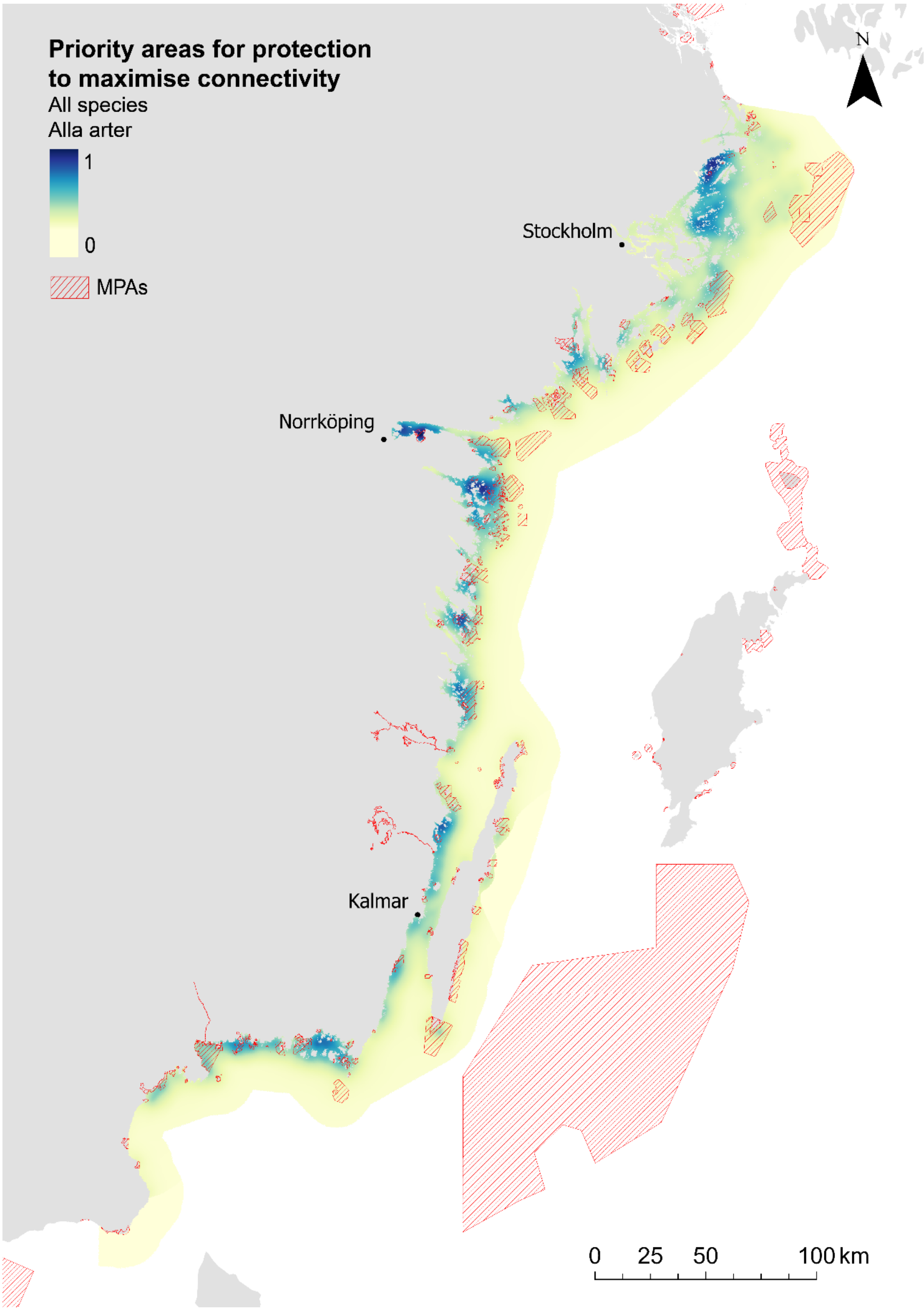


**Figure 13.** Priority areas for expansion of the MPA network in the Baltic Proper to maximise connectivity of all species. Dark blue areas indicate areas of high priority, and represent good candidates for expansion or strengthening of the MPA network.

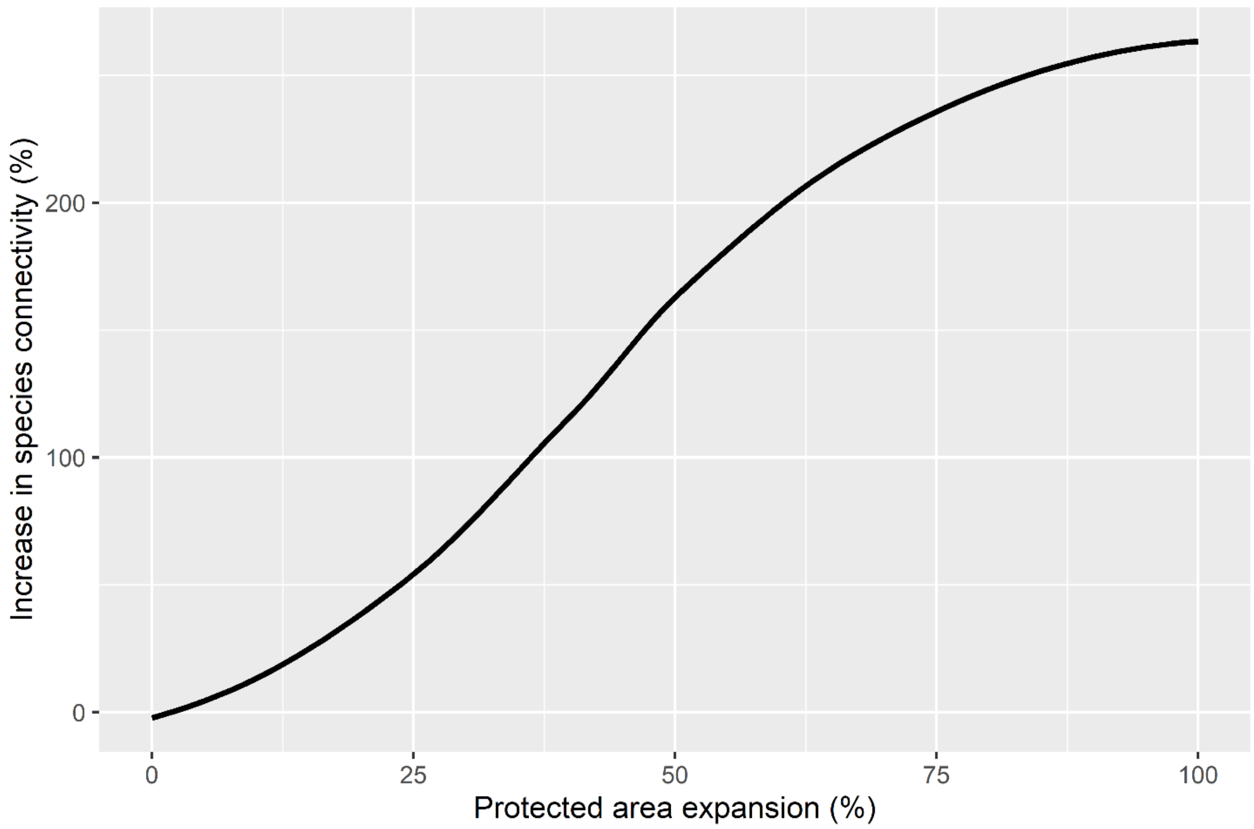


**Figure 14.** The percentage increase in connectivity that can be achieved through optimal expansion of the existing MPA network. The percentage of protected area expansion is relative to the total area of the current MPA network, i.e. where a 100% expansion is a doubling in the size of the network. The optimal expansion was determined using the "prioritizr" package in R using the Gurobi optimiser.

# 4. Discussion

Previous connectivity studies and coherence assessments in the Baltic Sea have focused on only a few species in restricted geographical areas or on larval dispersal. However, connectivity of the majority of species in the brackish waters of the Baltic Sea coastal area is driven by active dispersal, and specific analyses are needed to quantify the connectivity of these species. This report is the first to assess large-scale connectivity and ecological coherence of the MPA network in the Baltic Sea with a focus on coastal habitat-forming species and species with active dispersal. The results of this study show that connectivity hotspots often coincided with human development and activities, and that physical disturbance had a large impact on connectivity for most species, particularly those of freshwater origin and with limited mobility. In our analyses, we found that the MPA network was insufficient according to several of the coherence criteria, particularly in terms of representativity, which was generally below levels recommended in the scientific literature, and in terms of connectivity, which could be substantially improved. Importantly, we found lack of coherence for several ecologically important species, such as cod, pike, perch, and eelgrass. With targeted protection in only a few priority areas, the coherence of the network could be greatly improved.

## 4.1. Connectivity models

For most species, high-connectivity areas were generally concentrated in a few hotspots along the Swedish coast, while connectivity was low in most of the study area. The connectivity models were based on either juvenile fish habitats, since they represent production areas from which fish move as they grow (i.e. source areas), or habitat-forming vegetative species, most of which are found in shallow, wave-sheltered areas. The connectivity is hence highest in these regions, with hotspots in shallow bays, inlets and archipelagos.

Most of the fish species included in this report have relatively small home range sizes (20 km or less). Macrophyte and macroalgal seeds and spores generally disperse less than 10 m from the mother plant (Berkström et al., 2021). However, algae and eelgrass may break off and float long distances before attaching to the bottom in areas with optimal conditions (Tatarenkov et al., 2005; Jahnke et al., 2018). Therefore a dispersal distance of 10-20 km was applied to these species based on distances related to sexual and asexual dispersal and population distributions (Berkström et al., 2021). These low dispersal distances, in combination with specific habitat requirements, where many species are dependent on shallow sheltered environments, leads to connectivity hotspots occurring in a few concentrated areas. This is exacerbated by the complex coastline of Sweden, which contains vast archipelago areas. These islands and complex coastlines act as a barrier to dispersal for individuals and propagules restricted to the water column, meaning that it is often necessary to travel greater distances to reach habitats that are relatively nearby "as the crow flies".

The nested targets (Swedish: preciserade bevarandevärden) specified within the Swedish framework for MPAs were specifically considered in the analyses. They consist of species of notable ecological importance. These nested targets have been discussed and decided jointly by multiple stakeholders (SwAM, 2021). In order to assess ecological connectivity, information on life-history characteristics such as habitat use, life-cycle and dispersal/migration patterns are needed (Schellekens et al., 2017) in combination with full-coverage maps of species distributions. The current report was therefore limited to include nested targets and other species for which such information is available.

The list of nested targets is based on broader conservation targets, focusing on coarser habitat and biotope types prioritized on a European, regional and national level. Nested targets consist of functional groups or as single species if they require additional attention and protection beyond the protection of that of the habitat it depends on. For example, eelgrass and *Chara* species are on the list of nested targets as well as herring, cod and Baltic flounder, and are also included in the current report. They belong to one or more of the following five categories of species, that; 1) Sweden is legally obliged to protect through the EU Birds and Habitats directives, 2) Sweden has committed to protect under the regional seas conventions (i.e. HELCOM and OSPAR), 3) are critical to species that are threatened in the respective marine regions (Gulf of Bothnia, Baltic Proper and Swedish west coast), 4) are endemic or threatened in Sweden, and 5) that are considered keystone species, i.e. critical for ecosystem functioning and ecological representativity (SwAM, 2021). The number of nested targets is limited to 50, in order to keep the process manageable and align with existing legislation and priorities.

Species which perform extreme long-distance migrations, such as birds, marine mammals and fish, like the European eel, salmon, and sea trout, were not included in our analyses. Connectivity models of these species would be not be of great value because they can migrate across large portions of the Baltic Sea, which means that connectivity patterns can only be discerned over extremely large extents (e.g. global), and that MPAs are unlikely to be able to cover dispersal routes. Instead, spawning rivers for salmon and trout and nesting and resting sites for birds and marine mammals should be a priority for maximizing the connectivity of these species. Additionally, these species are likely to follow specific migration routes and homing behavior that would require more complex connectivity modelling than the approach we used in this report (Siira et al., 2009; Östergren et al., 2012).

Berkström et al. (2021) collated all available information on dispersal and migration distances for species in the Baltic Sea, Skagerrak and Kattegat. These distances together with available species distribution maps, created by the Dept. of Aquatic Resources at the Swedish University of Agricultural Sciences (SLU Aqua) for fishes and AquaBiota Water Research for vegetation species, were combined to produce connectivity models in the current report (Florén et al., 2018; Erlandsson et al., 2021). The greatest strength of the connectivity models developed in this report is their incorporation of land barriers to dispersal, which, to our knowledge, has never been done using a degree-centrality, graph theoretic approach at such high scale and resolution. However, the connectivity models were limited based on the quality of the dispersal information and habitat models used as inputs. Many of the species included in this report are lacking empirical data on active dispersal distances, which is typically acquired through mark-recapture studies. Further, there are several uncertainties associated with the habitat models, including that they are based on relatively limited datasets of field surveys, some of the predictor variables for the models are at coarse resolution, and that the resolution of the models (250 m) is relatively coarse compared to the topographically complex areas these species inhabit. Additionally, the cutoff values determined in the species habitat models might be subject to change if they were produced in different regions (e.g. separate habitat maps for the Baltic Proper and Gulf of Bothnia).

## 4.2. Change in connectivity in response to anthropogenic pressures

Anthropogenic pressures causing physical disturbance of the seabed, had a relatively large predicted impact on connectivity, particularly for certain species. The majority of these species are of freshwater origin and have shorter migration distances (e.g. crucian carp, roach, common rudd, common bream/silver bream, common bleak) than marine species like cod, flounder and herring, which perform long migrations between the open sea and coastal areas during their life cycle (Aro, 1989; Candolin and Voigt, 2003). Also large predators like pike, pike-perch and perch had a pronounced decrease in connectivity when incorporating physical disturbance into the models. This is not surprising considering most human pressures are concentrated along the coast, often in shallow sheltered bays and inlets where human development coincides with important breeding, spawning, nursery and feeding grounds (Bulleri and Chapman, 2010; Kraufvelin et al., 2021) and cause conflict of interest between development and habitat conservation (Sundblad and Bergström, 2014; Hansen et al., 2018).

More stationary species, spending the majority of their life cycle in coastal areas, are likely more affected by habitat loss and fragmentation than highly mobile species unless the highly mobile species are strongly dependent on specific habitat types in the coastal zone. Hansen et al. (2018) found that recreational boating degraded vegetation important for fish recruitment in the Baltic Sea and Eriander et al. (2017) found that small-scale coastal development, e.g. docks and marinas, had a negative effect on eelgrass on the Swedish west coast. Eelgrass is also an important feeding and nursery habitat for many marine species (Staveley et al., 2016; Perry et al., 2018). Habitat-forming submerged aquatic vegetation (SAV) with limited dispersal (macrophytes and macroalgae), was also highly affected by physical disturbance in our connectivity models. Connectivity will be reduced when habitats become fragmented or diminished and populations of organisms decline. This isolation may in turn have consequences on genetic diversity, viability of populations and ultimately ecosystem functioning (Biggs et al., 2009; Carim et al., 2016). A reduction in large predators like pike, pike-perch and perch can have cascading effects in Baltic Sea coastal food webs, where lower predation can result in an increase of mesopredators like the three-spined stickleback, a reduction in important grazers (stickleback prey) and an increase in epiphytic algae, which will further degrade the vegetative nursery habitats through shading and smothering (Donadi et al., 2017; Eklöf et al., 2020).

## 4.3. Coherence of the MPA network

The MPA network was found to be non-coherent in terms of *representativity* and *connectivity* for species included in this study, while *adequacy* and *replicability* were somewhat sufficient. MPAs in the study area were sufficiently close to neighbouring areas, but generally small in size. Focus was on species performing active migrations and on habitat-forming macroalgae and macrophytes. Representativity of habitats was generally within the target of 10% protection by 2020 for all but six species (out of 30 in total), but all but three species were below the new target of 30% protection by 2030 in the EU Biodiversity strategy and what is generally recommended by conservation scientists (Svancara et al., 2005; Wenzel et al., 2016; European Commission, 2020). Regarding strict MPAs with a target of 10 % protection, representativity was very poor, with an average of 2% across species. The average representativity of species habitats included in this study was 17% in all MPAs, and an average of 16% of species connectivity was protected. In a scorched earth scenario, if all habitats outside MPAs were to disappear, connectivity would likely be insufficient to maintain the populations for most species. Only three species had greater than 30% of their distribution within MPAs, including common minnow (*Phoxinus phoxinus*), toothed wrack (*Fucus serratus*), and clawed fork weed (*Furcellaria lumbricalis*), which are all species that have their main distribution in wave-exposed areas in the outer archipelagos. These results illustrate the fact that most MPAs are situated in the more remote areas of the archipelagos, while areas closer to the mainland have a much poorer coverage. Since the most diverse and productive habitats, including most connectivity hotspots, are found in such shallow and wave-sheltered areas, there is an obvious need for strengthening the MPA network in these locations.

Determining sufficient targets for representativity is difficult, because standards and goals for representativity are usually arbitrary. Svancara et al. (2005) reviewed 159 articles and assessed differences between policy-driven and evidence-based approaches and found that the average percentages of area recommended for evidence-based targets were nearly three times as high as those recommended in policy-driven approaches. There is a general consensus among conservation scientists that targets should be at least 30% (Svancara et al., 2005; Wenzel et al., 2016; Woodley et al., 2019), although this is highly dependent on the ecology of the species, its conservation status, and the efficacy of protection measures, both in terms of the level of protection and of how well the regulations are complied with. This implies that we should have at least 30% of the distribution of a species protected from unnatural disturbances to ensure its persistence. This also aligns with the EU Commissions new goal of 30% protection of the ocean by 2030 in the new EU Biodiversity Strategy (European Commission, 2020).

Our results are in line with previous coherence assessments in the region in which the network fulfilled one of the four coherence criteria (adequacy, representativity, replication, and connectivity) in some cases, but far from all criteria. In general, the connectedness of the MPA network was evaluated in previous studies. However, focus was on passive dispersal or very few species (one or five key species). The first two studies in the Baltic Sea were conducted in 2007 (Bergström et al., 2007; Piekäinen and Korpinen, 2007) followed by assessments by HELCOM (HELCOM, 2010; 2016) and studies focusing on larval dispersal (Corell et al., 2012; Nilsson Jacobi et al., 2012; Jonsson et al., 2020; Assis et al., 2021). A coherence assessment in a limited area of the Baltic Proper, The Swedish–Finnish archipelago, was performed for pike, perch, pike-perch and roach by Sundblad et al. (2011) using species distribution models of juvenile habitat (recruitment areas), similar to our study. They also found that both the representativity and the connectivity of the network were poor with respect to the studied fish species. Recently Virtanen et al. (2018) assessed the MPA network along the Finnish Baltic coast using the software Zonation and included a large data set from the Finnish national monitoring program where juvenile and nursery habitats, like our study, were included. They found that 27% of the most valuable features were covered by the MPA network.

A few large MPAs exist along the Swedish Baltic Sea coast. However, the majority are rather small, which may limit self-recruitment for some species. The estimates of home ranges include movement ranges for most individuals, i.e. represent close-to-maximum values rather than mean values. This means that self-recruitment may still be sufficient in areas that are much smaller than the home ranges we use in our analyses. For example, in a no-take area in the Stockholm archipelago there was a strong positive effect on fish populations in an area that was 1.7 $km^2$ for both pike and pike-perch (Bergström et al., 2016), even though their home range estimates in our models are a lot larger (5 and 10 km, respectively).

## 4.4. MPA network expansion

With spatial conservation prioritization, efficient allocation of conservation resources can be done (Lehtomäki and Moilanen, 2013). Along the Swedish Baltic coast, the priority areas identified in our analysis were found to be insufficiently protected. The connectivity of the network could be greatly improved with targeted protection in just a few important locations. If the MPA network was expanded by 25% according to the optimal prioritisation, the mean connectivity of species within the network would be increased by 54%. In a recent study by Virtanen et al. (2018) it was found that expanding the MPA network along the Finnish Baltic Sea coast by as little as 1%, would double the mean conservation cover of ecologically important areas. This would increase the protection levels of habitat types based on the IUCN Red List of Ecosystems, key species, threatened species and fish reproduction areas. Our study included many of, but not all, these species and habitats and it is likely that if included, the percentage increase with percent expansion would be greater. Leathwick et al. (2008) found that the most cost-effective scenario, using the prioritisation tool Zonation, in New Zealand would deliver conservation benefits nearly 2.5 times greater than those from equivalent-sized areas that had recently been implemented at the request of fishers. It would also come with a lower cost. These examples highlight the importance of using prioritisation tools before establishing an MPA network, if possible. In the Baltic Sea, however, a large network of protected areas has already been established and using prioritisation tools to suggest areas for expansion is more realistic and feasible, and can still provide important guidance for efficient ways of strengthening the MPA network.

We found some examples where MPAs are very well placed, e.g. Rånefjärden north of Luleå. This area is well connected locally, but very isolated from other priority areas and hence becomes a very important area to protect. Siknäsfjärden, also north of Luleå, is another connectivity hotspot representing a good area for establishing a new MPA and expanding the network. These two areas would contribute to a “connectivity portfolio” (Harrison et al., 2020) in the northern parts of the Gulf of Bothnia by being part of a wider network, rather than isolated single MPAs. In this way they can together dampen stochastic dispersal or migration events and provide a more consistent supply of organisms to replenish populations (Harrison et al., 2020), particularly in the Gulf of Bothnia, where priority areas are rather isolated from the rest of the priority areas in the Baltic Sea.

Most MPAs in the network covering Swedish Baltic coastal waters have weak protection, particularly in priority areas. When expanding the MPA network it is therefore important to apply an ecosystem-based management approach and regulate fisheries in parts of the MPA network in order to reach conservation goals. Edgar et al. (2014) found that the conservation benefits of MPAs increased exponentially with the accumulation of five key features; no-take, well enforced, old (>10 years), large (>100 km$^2$), and isolated by deep water or sand, where high protection and high enforcement resulted in highest benefits. In northern Europe, nature conservation and fisheries management are traditionally separated with most MPAs lacking fisheries regulation (Sørensen and Thomsen, 2009; Seitz, 2014). This highlights the need to involve relevant stakeholders across management units to promote successful outcomes of MPAs (Grip and Blomqvist, 2020). Jameson et al. (2002) also highlighted that the two most important aspects to consider in the planning of MPAs is where to place them and how to manage them. Most ecosystems would greatly benefit from combining both natural resource management and fisheries management, advocated in ecosystem-based fisheries management (Halpern et al., 2010; Baskett and Barnett, 2015; Grip and Blomqvist, 2020).

Another important aspect of MPAs is that the regulations need to be strong enough to protect against activities causing physical disturbance. Development interests in the coastal zone are strong, and constructions are often granted exemptions in practice (Eriander et al., 2017). Similarly, boating is a major pressure that is rarely regulated, but may have a large impact on habitat-forming vegetation and fish recruitment (Hansen et al., 2018). A central focus for expansion of the network will thus be on stricter regulations within the MPAs. Accordingly, one target of the expansion of the MPA network in the EU Biodiversity Strategy is that 10% of the marine waters should be strictly protected.

Applying an ecosystem-based management approach when expanding and managing the MPA network would also greatly benefit the green infrastructure of the region by preserving a network of natural and semi-natural areas contributing to ecosystem functioning and delivering a wide range of ecosystem services (Chatzimentor et al., 2020). Here structural connectivity, i.e. the spatial configuration of habitats and the functional connectivity, i.e. the ability of organisms and material to move and disperse (Kindlmann and Burel, 2008), would contribute to the maintenance of population function in the region. Connectivity, together with environmental protection and ecosystem multifunctionality, has been highlighted as one of the most important aspects to consider in work related to green infrastructure (Lai et al., 2018).

In the current project, connectivity hotspots have been identified through the production of connectivity models for a broad range of species, and using optimised spatial conservation prioritisation. However, areas with lower connectivity at specific locations can also be an important focus for protection and restoration efforts, through the addition of stepping-stone habitats between connectivity hotspots. For example, our analyses identified important connectivity hotspots in Rånefjärden and Siknäsfjärden in the north, which are extremely isolated from the hotspot in Stockholm Archipelago. As such, areas of moderate connectivity between these two hotspots, such as the habitats around Umeå, Hudiksvall, and Östhammar, represent key stepping-stone habitats for facilitating more rare, long distance dispersal events that influence gene flow and long-term population dynamics. Sometimes protection of an area against physical disturbance may be enough to restore species and habitats in the areas, while in other cases specific restoration efforts may be necessary for a species to recolonize a previously disturbed area. There have been restoration attempts of coastal wetlands and eelgrass beds in Swedish waters as a means to decrease fragmentation and increase connectivity (Nilsson et al., 2014; Eriander et al., 2017; Jahnke et al., 2018; Jahnke et al., 2020). Restoration efforts on eelgrass and macroalgae have also been done in Kiel Fjord, Germany, to reconstruct biotopes and create "wildlife corridors" in an urbanized area (Krost et al., 2018). Their study is one of the first attempts to reconstruct sublittoral wildlife corridors where present sublittoral maps were compared to historical maps and literature to facilitate the process.

## 4.5. Future directions

*Test different resolutions in connectivity models*

The resolution of the connectivity models and prioritisation maps in the current study was 250 m, the same as that of the species distribution models used. The primary limitation on resolution is the computing power, computer memory, and time required to run the connectivity models, which require several days of computing time for a single species. The computing time can be reduced either by decreasing the resolution, or reducing the extent of models (i.e. smaller study area). The current resolution is likely adequate for the design and planning of MPA network expansion in a regional context. However, to be useful at more local scales, it would be desirable to run connectivity models for a selection of key species with a higher resolution, i.e. 50 or 25 m for a smaller spatial extent (e.g. specific counties).

*Combine active and passive dispersal in future assessments*

Currently, most large-scale coherence assessments of the Baltic Sea have focused on larval dispersal (e.g. Corell et al., 2012; Nilsson Jacobi et al., 2012; Jonsson et al., 2020). Combining larval dispersal with our connectivity models of active dispersal would provide a more comprehensive assessment and is encouraged in future assessments.

*Conduct assessment on Swedish west coast based on active migrations*

Larval dispersal has also been in focus on the Swedish west coast, with no connectivity assessments based on active migrations, nor connectivity within the coastal areas (Moksnes et al., 2014; Moksnes et al., 2015; Jonsson et al., 2016; Assis et al., 2021). Although larval dispersal is more common on the Kattegat and Skagerrak coast compared to the Baltic Sea because of the marine conditions (as marine species to a larger extent have pelagic larval stages than freshwater species), there are still several keystone species and species of commercial importance that mainly disperse by performing active migrations within the coastal habitats and between the coast and open sea environments.

*Incorporate climate change*

Climate change is accelerating range shifts in marine biodiversity and threatening important ecosystem services (Doney et al., 2012; Viitasalo, 2019). Species in the Baltic Sea are already pushing environmental tolerance limits, and are therefore highly sensitive to climate change. The rate of warming in the Baltic Sea exceeds the global mean, and additional climate-related changes like precipitation changes affecting salinity, shorter ice periods and extended bottoms with hypoxic conditions are also apparent (Andersson et al., 2015; Reusch et al., 2018). These changes affect spatial distributions, spawning behaviour, and habitat selection of species (Härmä et al., 2008; Olsson et al., 2012; Viitasalo, 2019), most likely affecting connectivity in the region (Berkström et al., 2021). Taking future climate-related changes in species distributions, as well as in circulation patterns affecting larval dispersal, into account when expanding the MPA network will be central for increasing the resilience of the Baltic Sea ecosystem to the combined impact from climate change and other human pressures.

*Improved spatial prioritisation*

When developing spatial prioritisations, there are always limitations that must be considered. First, prioritisations must be based on a specific set of species, habitats, or other specified conservation features. Thus, implicit in the prioritisation is the assumption that these species adequately represent the full spectrum of biodiversity in the region. In our analysis, we have included 30 species of various lifestyles and ecological functions. However, the addition of more species would provide even greater accuracy to the prioritization. Another important consideration is the relative importance of different species for conservation. In our analysis, we treated all species as equal in importance. However, the prioritization could be improved by designating higher weights to species of specific ecological importance. These weights could be determined through, for example, workshops with experts and stakeholders. Finally, in our analysis we have used the spatial prioritization software "prioritizr", as it offers the ability to determine optimal solutions to conservation planning problems. Other tools are available, such as Marxan and Zonation, which are likely to produce different prioritisations. However, these tools utilize heuristics that are near-optimal, which was our motivation for electing to use prioritizr. Further research is needed comparing these tools and quantifying the degree to which solutions differ. This work could also be expanded by exploring the use of indicator species, which, when included in the prioritization, might effectively maximize representativity and connectivity of all species, even those not included in the prioritization.

# 5. Conclusions

In conclusion, our report is the first large-scale coherence assessment to include coastal habitat-forming species and species performing active migrations in the Baltic Sea. Large-scale connectivity patterns were determined by species distribution maps combined with dispersal estimates in connectivity models. Hotspot areas for connectivity were identified, and these were generally concentrated in a few, relatively small areas. These hotspot areas are, however, at the same time central for coastal development and human activities, as they are often situated in bays, inlets and topographically complex archipelagos. Physical disturbance had a large impact on connectivity models of most species, particularly those of freshwater origin and with limited mobility. The MPA network was found to be mostly non-coherent in terms of representativity and connectivity for most species while adequacy and replicability were somewhat sufficient. MPAs in the study area were sufficiently spaced, but generally of small size. This is in line with previous assessments in the Baltic Sea. The average representativity of species in this study was 17% in all MPAs, below what is generally recommended (30% according to scientific literature, and the targets of the new EU Biodiversity Strategy) for all but three species (out of 30 in total). Representativity was also very poor regarding strict MPAs, with an average of 2% across species. The same was true for MPA cover of connected habitats. The target for strict protection is 10% by 2030. However, the spatial prioritization analyses show that great improvements to connectivity and representativity can be made by expanding the MPA network in a few well-chosen priority areas. The current report may form the basis for identifying and strengthening a functional MPA network and marine green infrastructure, as well as important decision support for spatial planning and ecosystem-based management in the Baltic Sea.

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# Appendix 1. Connectivity maps all species


**Figure A1** Map of the modelled connectivity of *Abramis brama* (English: Common bream, Swedish: Braxen) and *Blicca bjoerkna* (English: Silver bream, Swedish: Björkna)


**Figure A2** Map of the modelled connectivity of *Alburnus alburnus* (English: Common bleak, Swedish: Löja).


**Figure A3** Map of the modelled connectivity of *Carassius carassius* (English: Crucian carp, Swedish: Ruda).

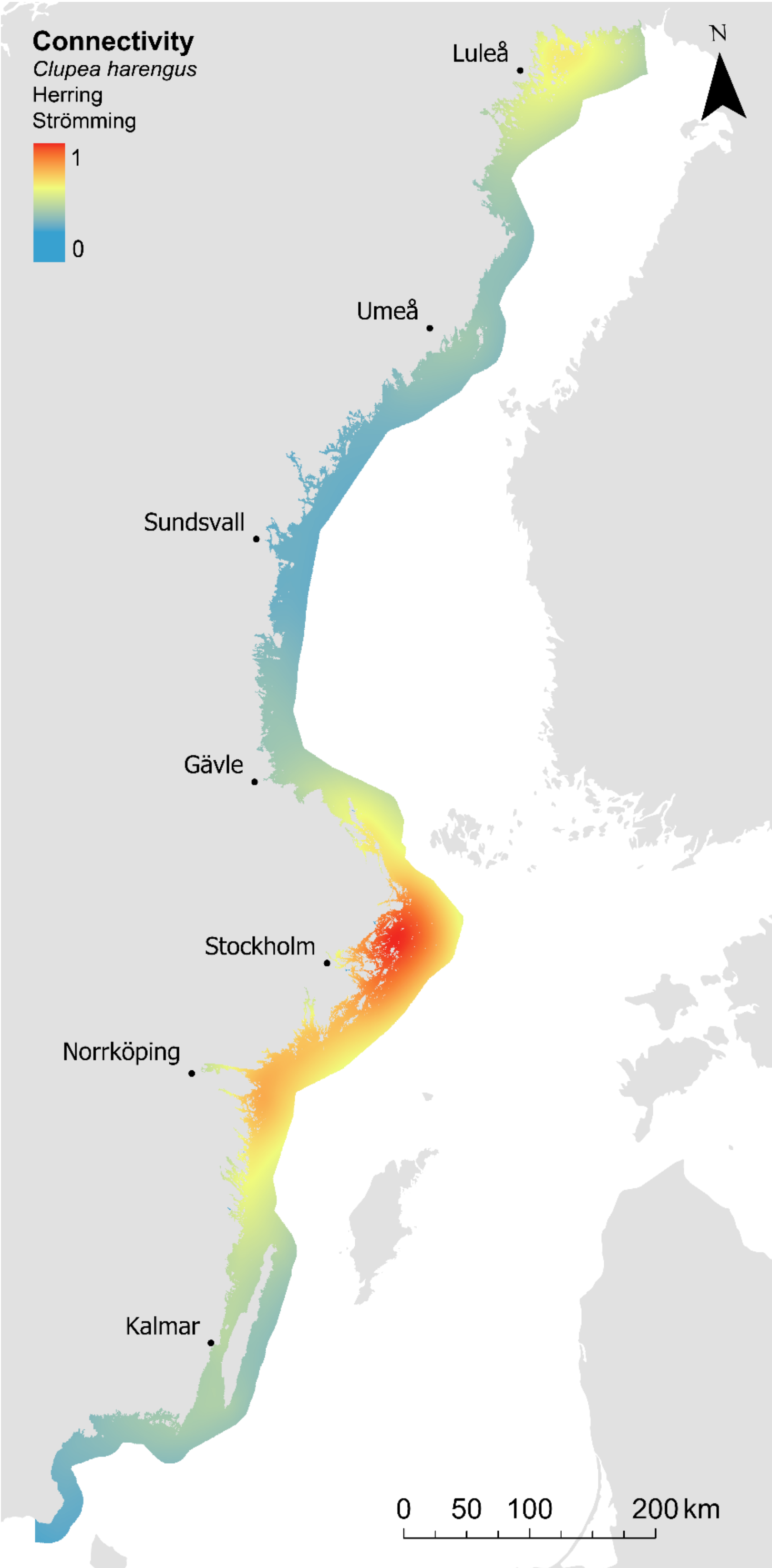


**Figure A4** Map of the modelled connectivity of *Clupea harengus* (English: Herring, Swedish: Strömming).


**Figure A5** Map of the modelled connectivity of *Esox lucius* (English: Pike, Swedish: Gädda).


**Figure A6** Map of the modelled connectivity of *Gadus morhua* (English: Cod, Swedish: Torsk).

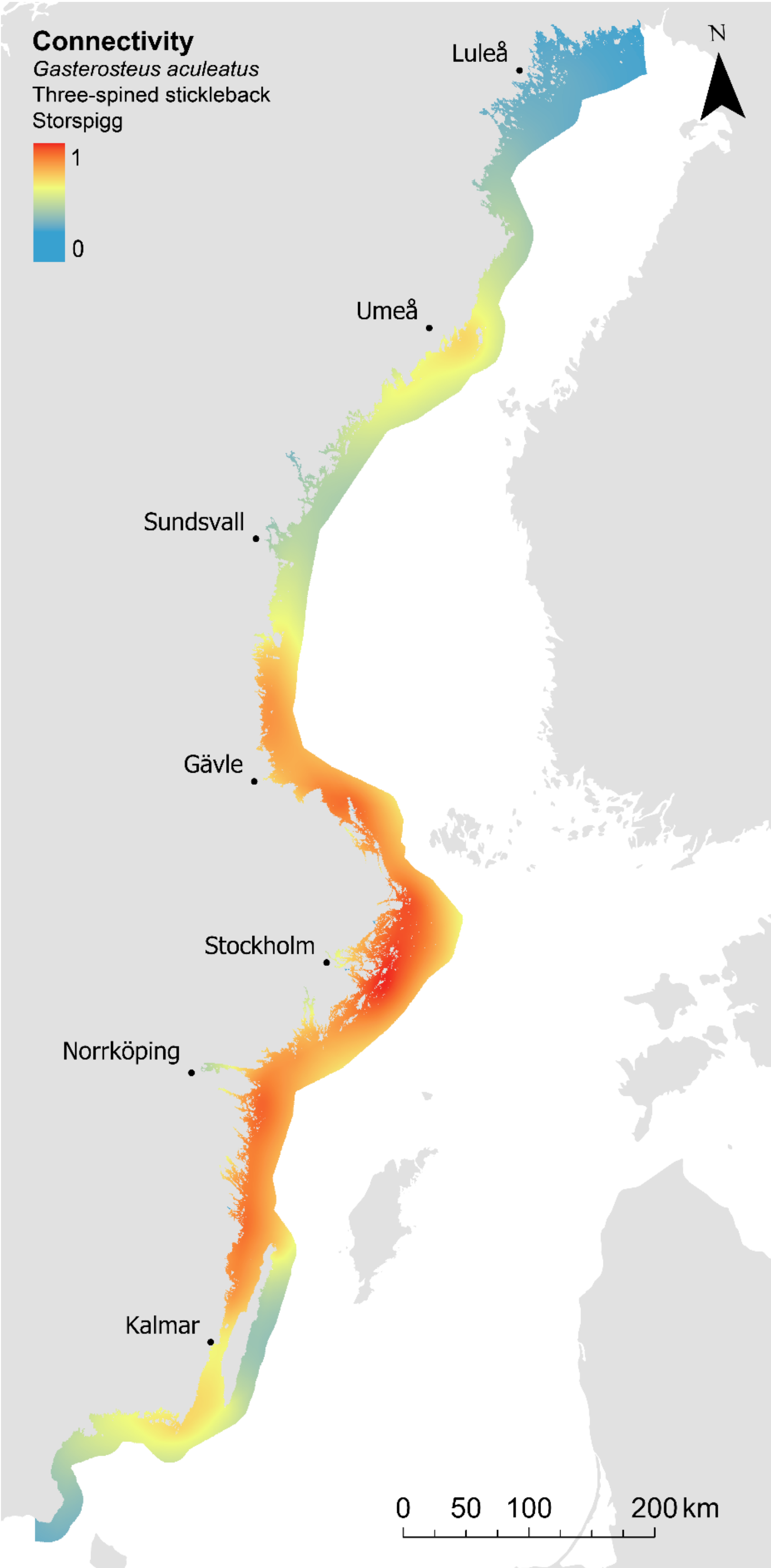


**Figure A7** Map of the modelled connectivity of *Gasterosteus aculeatus* (English: Three-spined stickleback, Swedish: Storspigg).


**Figure A8** Map of the modelled connectivity of *Gobiusculus flavescens* (English: Two-spotted goby, Swedish: Sjustrålig smörbult).

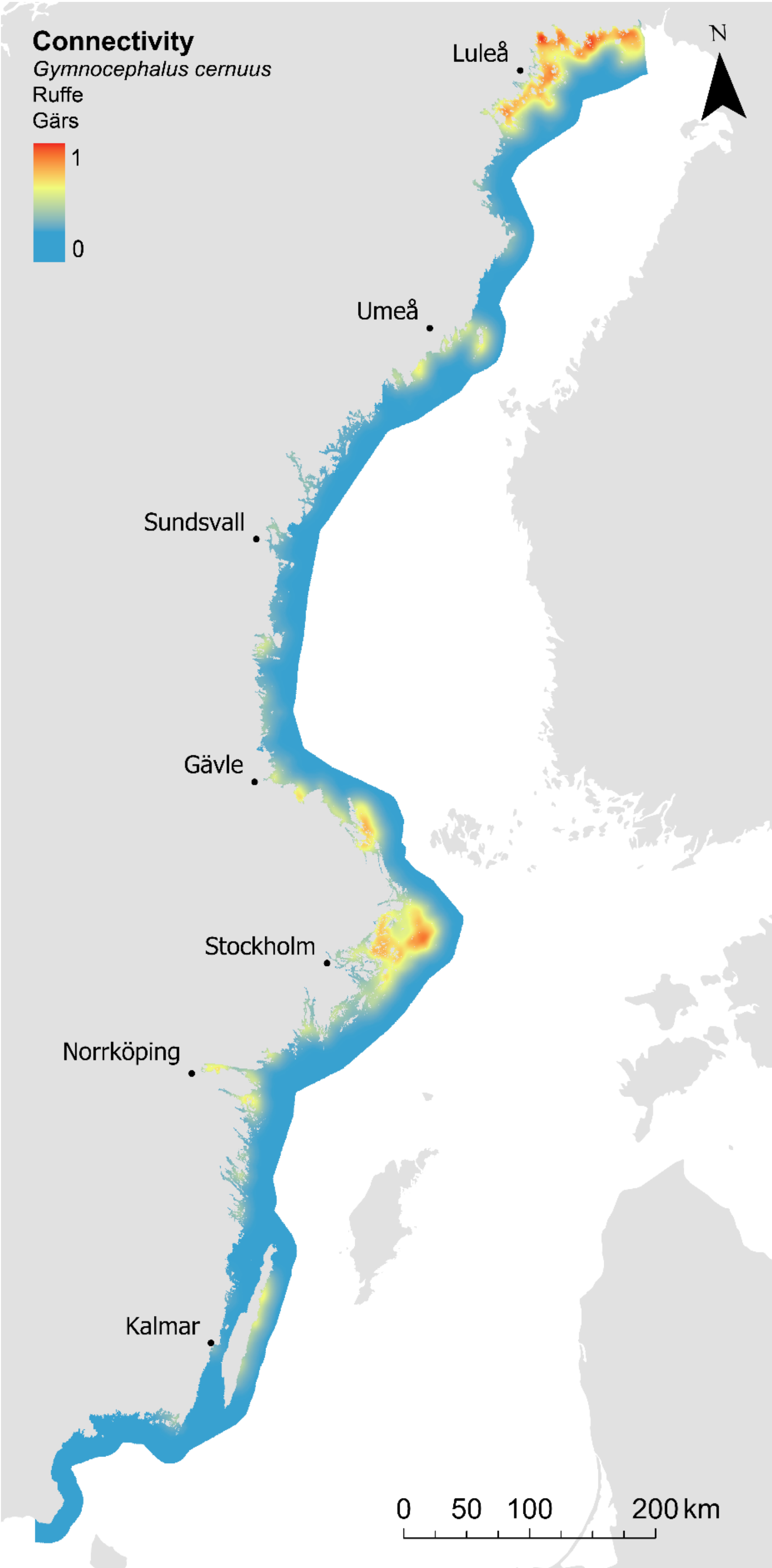


**Figure A9** Map of the modelled connectivity of *Gymnocephalus cernuus* (English: Ruffe, Swedish: Gärs).


**Figure A10** Map of the modelled connectivity of *Leuciscus idus* (English: Ide, Swedish: Id).

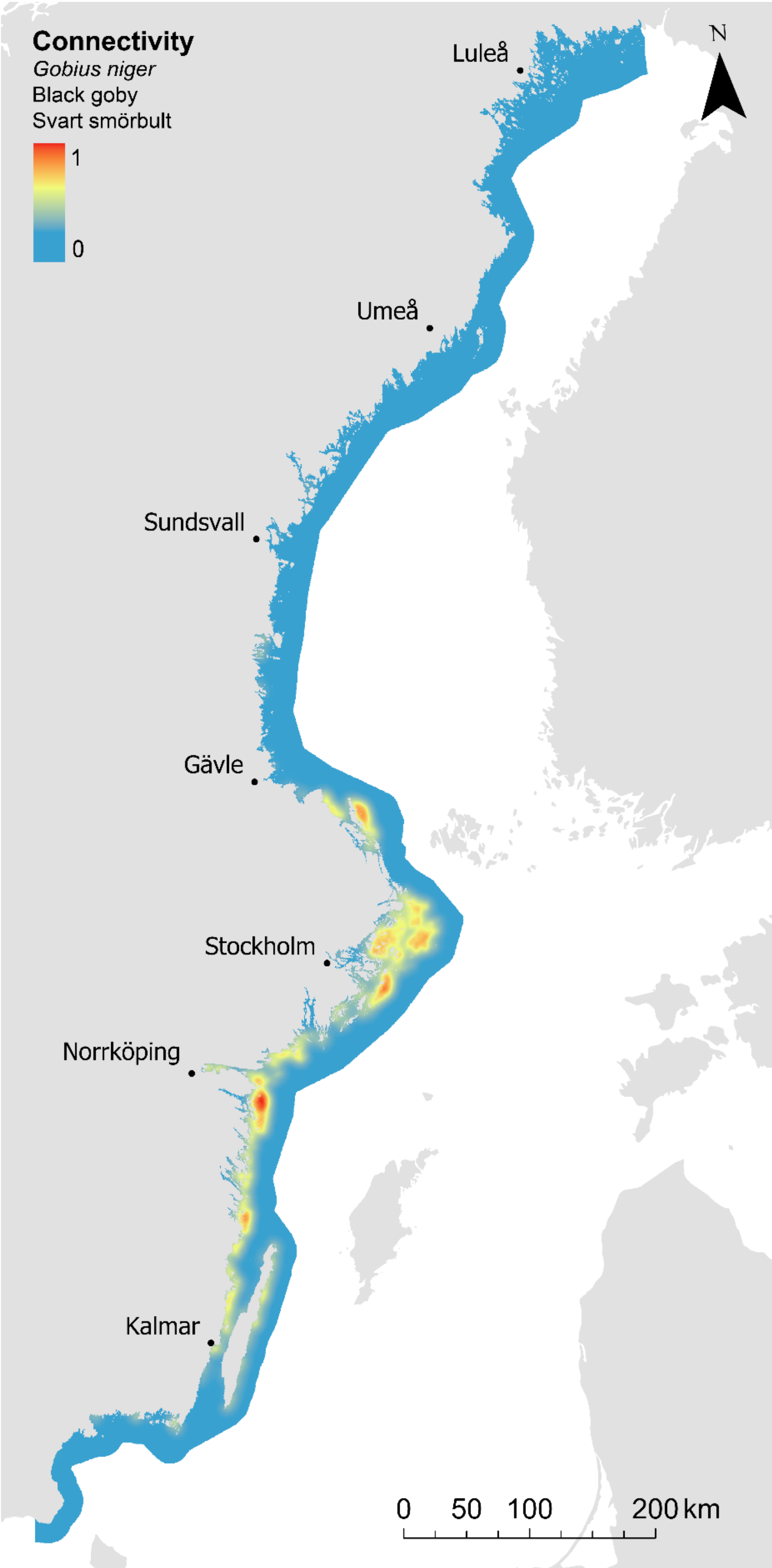


**Figure A11** Map of the modelled connectivity of *Gobius niger* (English: Black goby, Swedish: Svart smörbult).

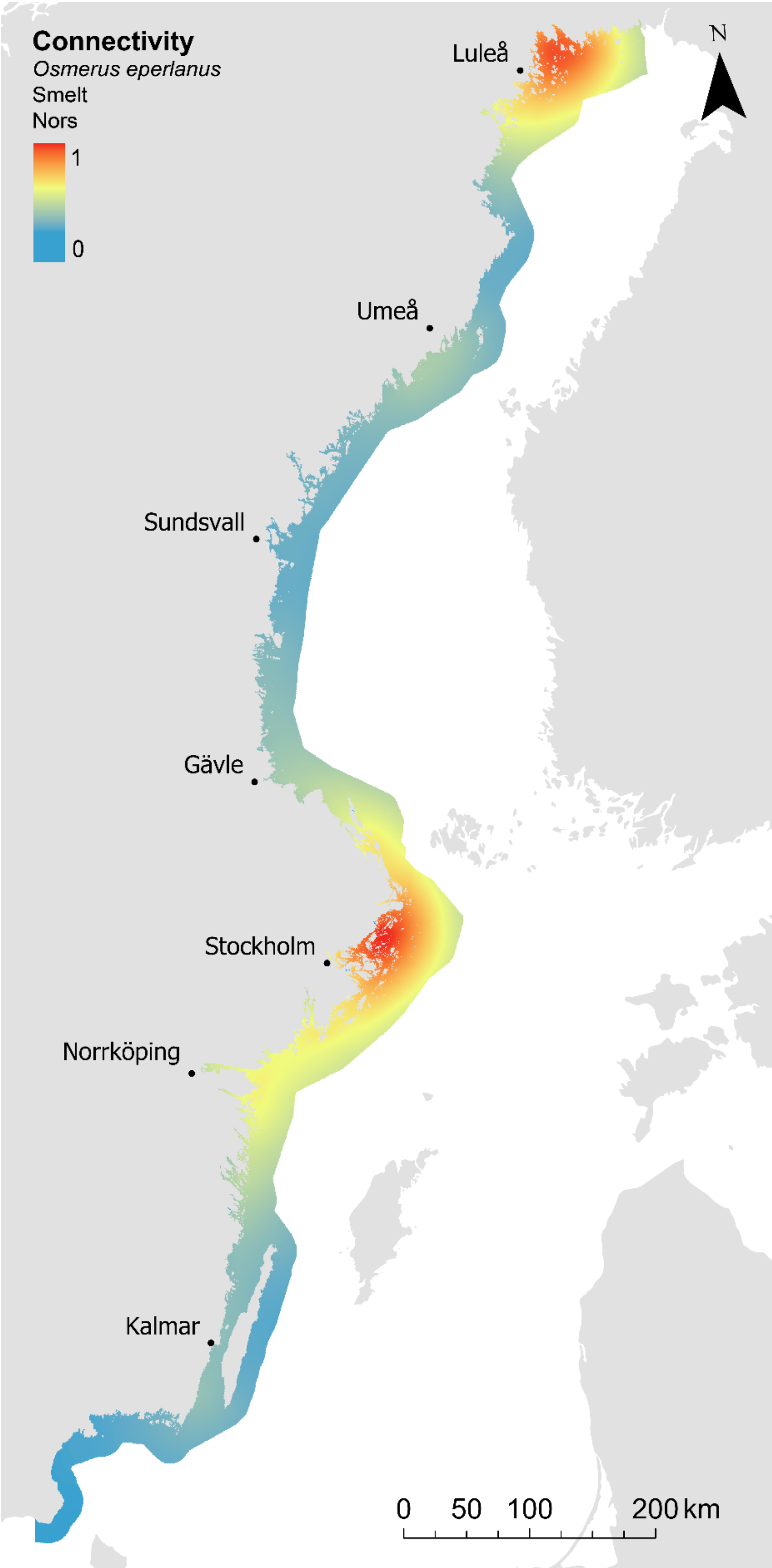


**Figure A12** Map of the modelled connectivity of *Osmerus eperlanus* (English: Smelt, Swedish: Nors).


**Figure A13** Map of the modelled connectivity of *Perca fluviatilis* (English: Perch, Swedish: Abborre).


**Figure A14** Map of the modelled connectivity of *Phoxinus phoxinus* (English: Common minnow, Swedish: Elritsa).

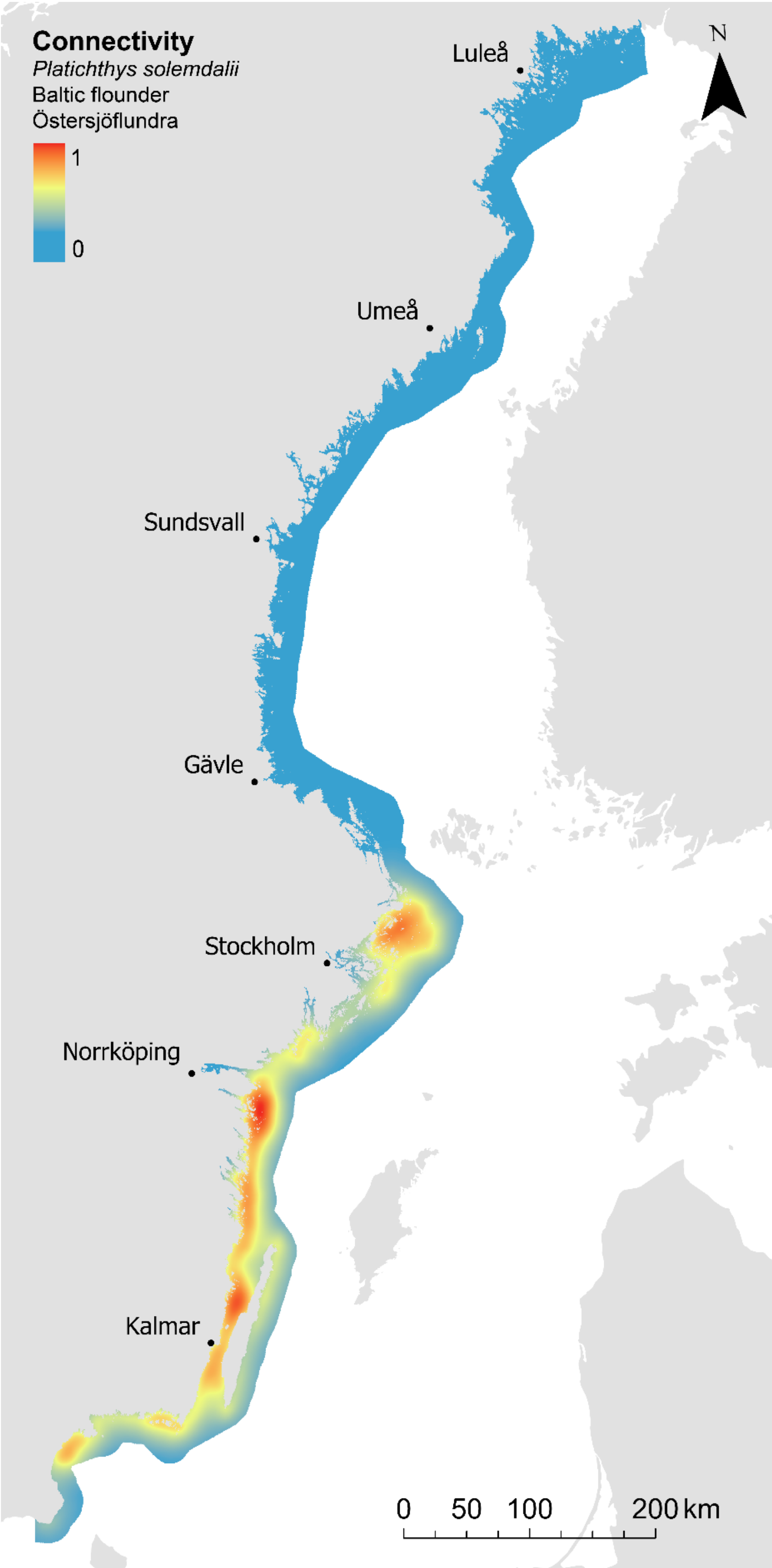


**Figure A15** Map of the modelled connectivity of *Platichthys solemdalii* (English: Baltic flounder, Swedish: Östersjöflundra).

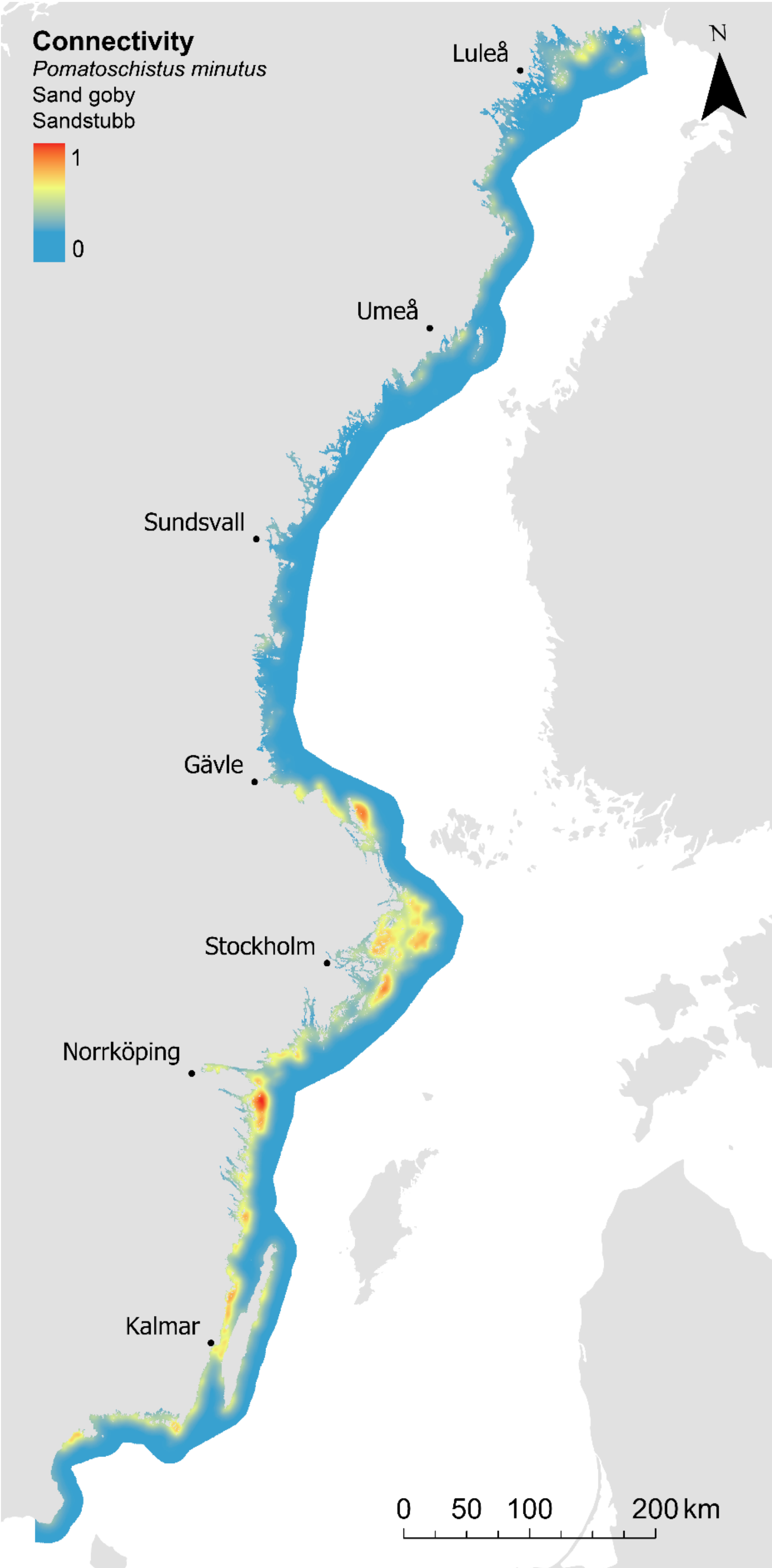


**Figure A16** Map of the modelled connectivity of *Pomatoschistus minutus* (English: Sand goby, Swedish: Sandstubb).

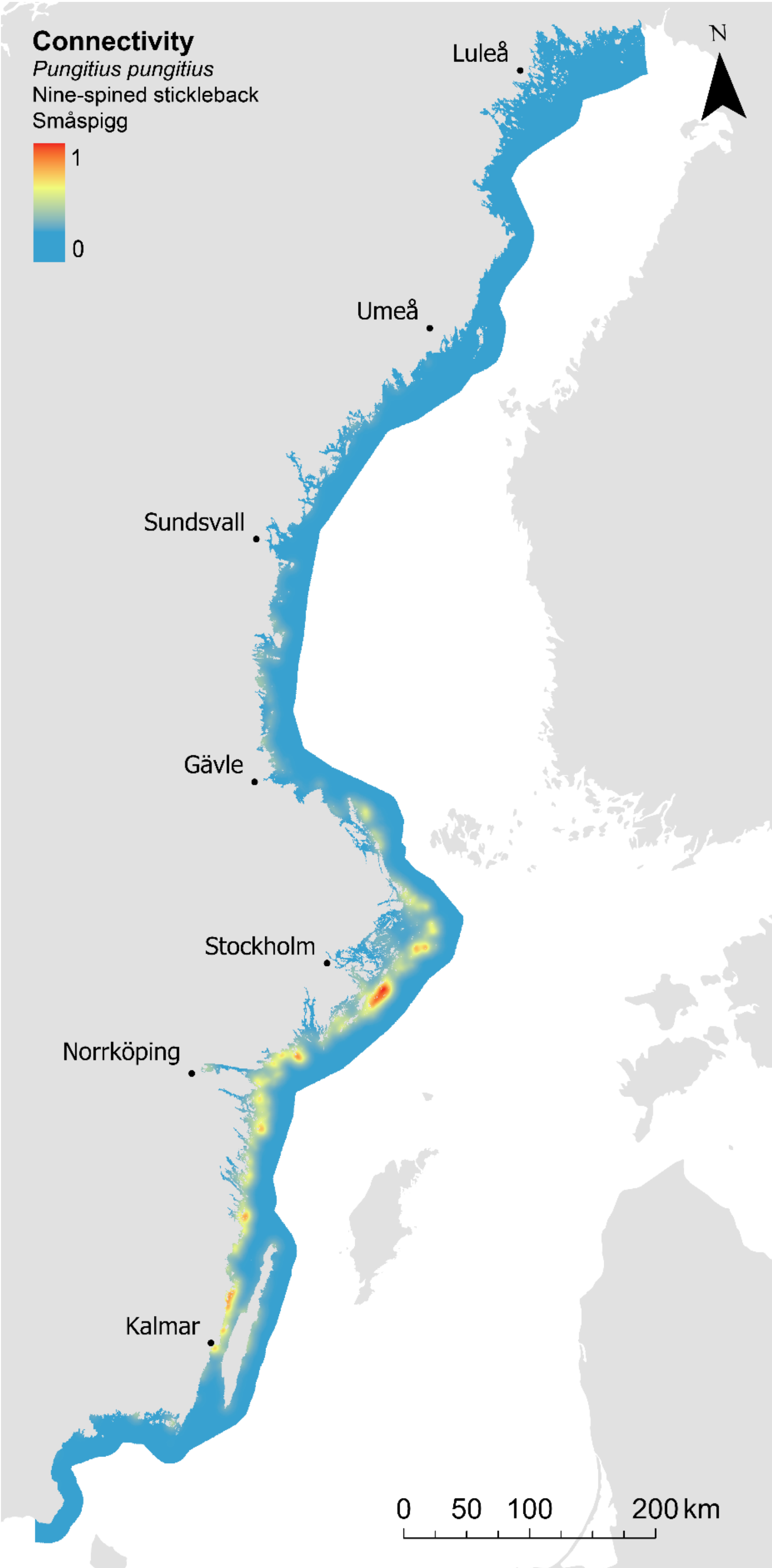


**Figure A17** Map of the modelled connectivity of *Pungitius pungitius* (English: Nine-spined stickleback, Swedish: Småspigg).


**Figure A18** Map of the modelled connectivity of *Rutilus rutilus* (English: Roach, Swedish: Mört).


**Figure A19** Map of the modelled connectivity of *Sander lucioperca* (English: Zander/Pike-perch, Swedish: Gös).


**Figure A20** Map of the modelled connectivity of *Scardinius erythrophthalmus* (English: Common rudd, Swedish: Sarv).

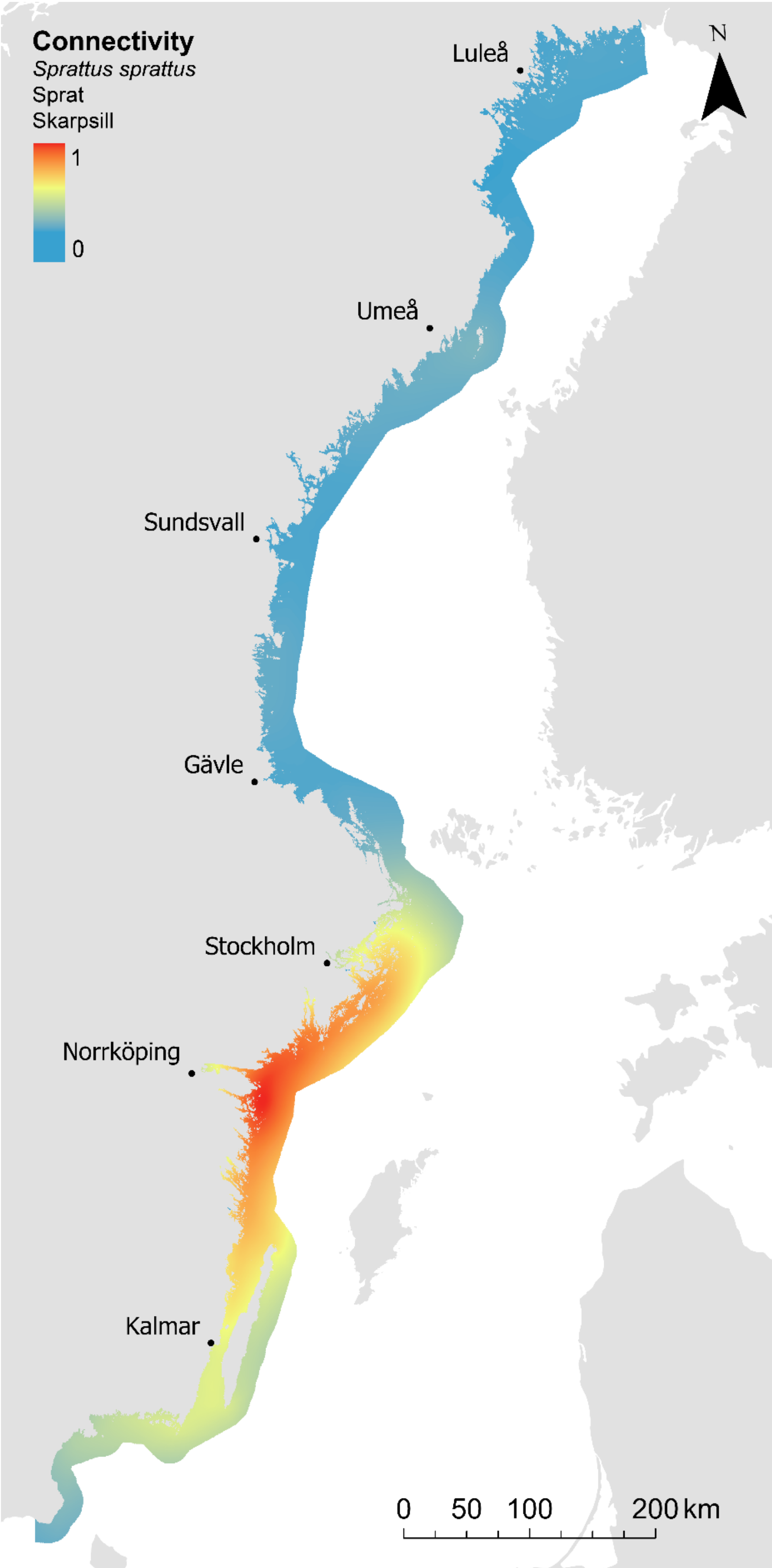


**Figure A21** Map of the modelled connectivity of *Sprattus sprattus* (English: Sprat, Swedish: Skarpsill).


**Figure A22** Map of the modelled connectivity of *Tinca tinca* (English: Tench, Swedish: Sutare).


**Figure A23** Map of the modelled connectivity of *Chara* spp. (English: Stoneworts, Swedish: Sträfsen).


**Figure A24** Map of the modelled connectivity of *Fucus vesiculosus/Fucus radicans* (English: Bladder wrack, Swedish: Blåstång/Smaltång).


**Figure A25** Map of the modelled connectivity of *Fucus serratus* (English: Toothed wrack, Swedish: Sågtång).


**Figure A26** Map of the modelled connectivity of *Furcellaria lumbricalis* (English: Clawed fork weed, Swedish: Kräkel).


**Figure A27** Map of the modelled connectivity of *Myriophyllum* spp. (English: Water milfoil, Swedish: Slingesläktet).


**Figure A28** Map of the modelled connectivity of *Potamogeton perfoliatus* (English: Clasping-leaved pondweed, Swedish: Ålnate).

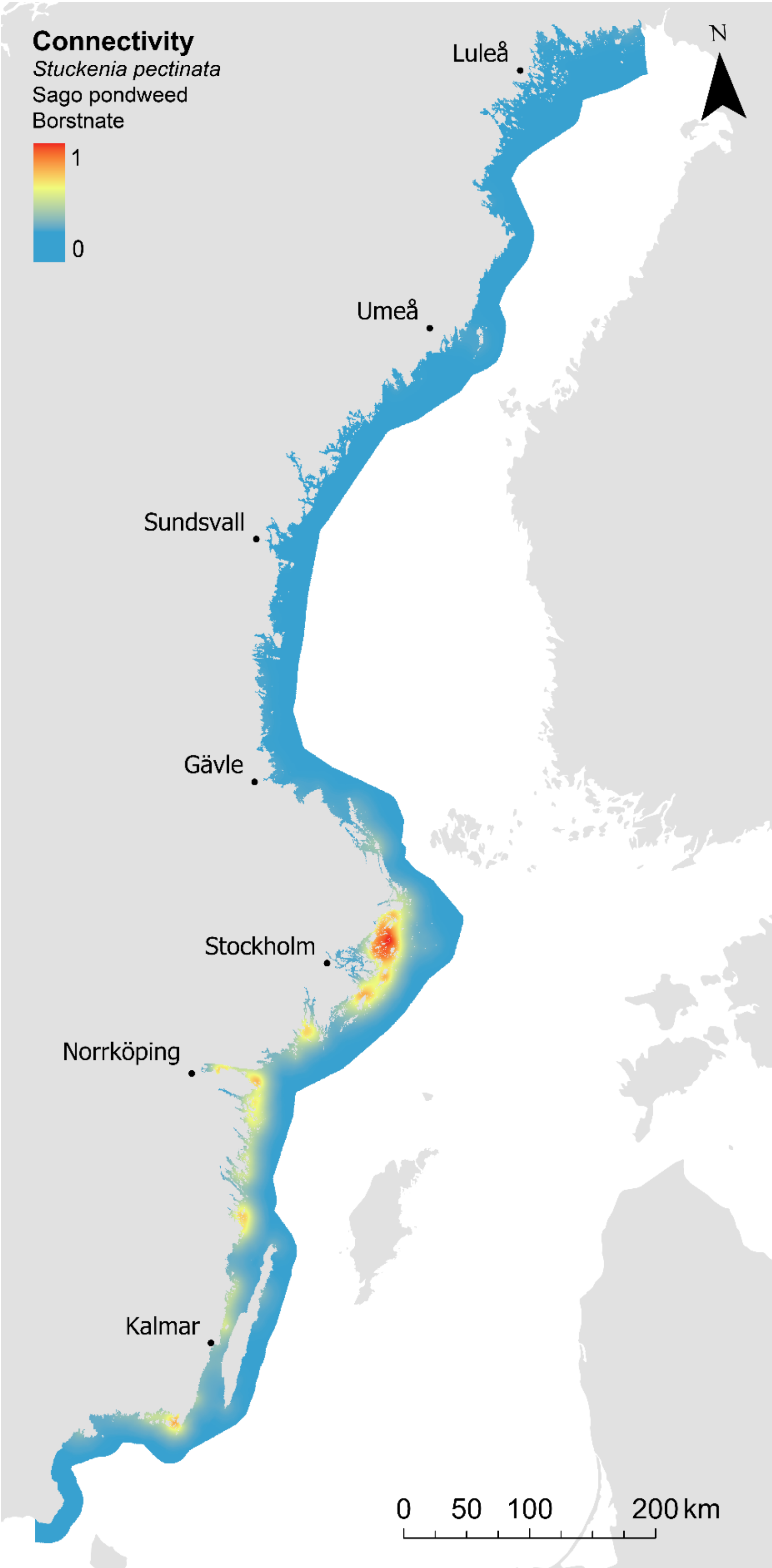


**Figure A29** Map of the modelled connectivity of *Stuckenia pectinata* (English: Sago pondweed, Swedish: Borstnate).


**Figure A30** Map of the modelled connectivity of *Zostera marina* (English: Eelgrass, Swedish: Ålgräs).

# Appendix 2. Guide – how to consider connectivity in the development of the Swedish MPA network

In order for MPAs to be effective conservation tools, two main aspects need to be considered; 1) where they are located and 2) how they are managed (Jameson et al., 2002). To locate MPAs as efficiently as possible, the following connectivity aspects should be considered when developing the Swedish MPA network:

- Acknowledge the different types of connectivity including active migrations and passive drift and the differences in distances associated with these modes of dispersal, with passive dispersal generally covering longer distances and active migrations generally shorter.
- Acknowledge passive dispersal being dictated by currents, time of year, amount of time larvae/spores spend in the pelagic and at what depth they are located (Kinlan and Gaines 2003).
- Acknowledge if species are of freshwater or marine origin, since the majority of marine species disperse via larvae while freshwater species spread mostly via active migrations.
- Acknowledge the movements and needs of different life-stages; i.e. include all habitats needed during an organism's lifecycle (spawning, nursery and feeding) to make sure the MPA network is ecologically coherent, unless these habitats are found in adequate condition outside the MPA network and within the organism's dispersal range (Félix-Hackradt et al., 2018).
- Important to separate between typical home ranges and maximum migration distances, where home ranges reflect scales relevant for population dynamics while maximum distances are more important for the genetic variation between populations.
- Connectivity within single MPAs is important for species with short dispersal ranges and found in fragmented habitats, while connectivity between MPAs and the surrounding area is important for dispersal and genetic exchange between populations across larger areas (Andersson et al., 2008).
- An MPA may either be larger than an organisms' dispersal range in order to keep a viable population within the MPA or consist of a network of MPAs placed with distances equivalent to organisms' dispersal ranges in order to connect populations within the network (Carr et al., 2017).
- Physical disturbance from jetties, dredging and boat traffic can have negative effects on habitats functioning as nursery, feeding or spawning grounds with a decrease in ecological connectivity if reduced or fragmented.
- Disturbance of the connectivity of species with larval dispersal acts primarily through disturbance on benthic/demersal life stages of the species, while the actual dispersal of

larvae is more resilient to human activities. For these species, focus should thus be put on protecting the habitats of these benthic/demersal life stages.

- Unprotected connectivity hotspots with dense habitats and many connections are high priority areas for expansion of the MPA network. These hotspots may act as source areas for more remote habitats, and are resilient to different pressures acting on the populations. Hotspot areas are identified by the spatial prioritization analyses of this report.
- Stepping stone areas, i.e. isolated areas with suitable habitat for a species that are important for connecting larger hotspot areas, are also a priority for expansion of the MPA network.
- Dispersal and distribution ranges of species may be affected by climate change due to changes in temperature, salinity and water movement (Bruno et al. 2018). Due to many species living close to their physiological salinity limits, the effects of climate change may be particularly severe in the Baltic Sea. By placing MPAs in climate refuges the effects of climate change may be counteracted (Hammar and Mattson, 2017). More in-depth analyses of the effects of climate change on species distributions and connectivity are needed.