EUROPEAN UNION

Interreg
Botnia-Atlantica
European Regional Development Fund

What will the sea look like in 2120?

Ecological connectivity and resilience of marine protected areas in the central Gulf of Bothnia

Carlos Paz von Friesen, Tytti Turkia, Maria Eggertsen, Johnny Berglund,
Emma Anderssén, Anna Bonde, Lotta Nygård & Anette Bäck

ECONNECT 2120

Authors: Carlos Paz von Friesen[1], Tytti Turkia[2], Maria Eggertsen[1], Johnny Berglund[1],
Emma Anderssén[2], Anna Bonde[3], Lotta Nygård[4] & Anette Bäck[2]

[1] County administrative board of Västerbotten, Länsstyrelsen Västerbotten
[2] Metsähallitus, Forststyrelsen, Parks & Wildlife Finland
[3] South Ostrobothnia Centre for Economic Development, Transport, and the Environment
[4] County administrative board of Västernorrland, Länsstyrelsen Västernorrland

Contact information:
Anette Bäck, Metsähallitus, anette.back@metsa.fi
Johnny Berglund, Länsstyrelsen Västerbotten, johnny.berglund@lansstyrelsen.se

Cover image: Juuso Haapaniemi
Cite: Paz von Friesen, C., Turkia, T., Eggertsen, M., Berglund, J., Anderssén, E., Bonde, A., Nygård, L., & Bäck, A. 2022. What will the sea look like in 2120: Ecological connectivity and resilience of marine protected areas in the central Gulf of Bothnia. The ECOnnect project's final report. Interreg Botnia-Atlantica project.

Registration No. MH 5039/2022

What will the sea look like in 2120?

Ecological connectivity and resilience of marine protected areas in the central Gulf of Bothnia

EUROPEAN UNION
Interreg Botnia-Atlantica
European Regional Development Fund
Österbottens förbund
Pohjanmaan liitto
Havs och Vatten myndigheten
Centre for Economic Development, Transport and the Environment
Länsstyrelsen Västerbotten
Länsstyrelsen Västernorrland
METSÄHALLITUS
FORSTSTYRELSEN

Foreword

Climate change is the greatest environmental crisis of the 21st century. The changes due to climate change are already happening everywhere in the world both on land and in water and our actions today will determine our future. It is expected that the effects of climate change such as temperature increases will be greater in the Gulf of Bothnia than in any other part of the Baltic Sea. The aim of the project ECOnnect was to study what the sea in the central Gulf of Bothnia will look like in 2120. This was done by analysing present and future environmental conditions and species distribution, ecosystem services, and connectivity in the central Gulf of Bothnia. The results from the project indicate that climate change will make the sea warmer, the ice-cover thinner and the salinity slightly lower. Species will react differently to these changes depending on their living requirements. Lower salinity affects marine species such as the blue mussel which are already living at the limit of their tolerance for low salinity, while reduced ice-cover will benefit perennial algae, for instance. Changes in ecosystem services are in many parts expected to follow the changes in species distribution. Some areas might experience an increase in ecosystem services while others may undergo a decrease. A drastic change in ecosystem services is however not expected. Kvarken is an important route for species to spread between Sweden and Finland. Marine protected areas are undisturbed areas for marine life. The better placed the protected areas are the better habitat network they create for species, which increases the chances for species survival in the future.

Three reports presenting the results from each work package and a summary report highlighting the main outcome from each report were produced within the project (all can be found at econnect2120.com). This report focuses on the evaluation of existing and future networks of protected areas from a connectivity perspective. The other two reports concentrate on the possible changes to future environmental parameters and species distribution and on identifying the present ecosystem services in the area and how these might change in the future.

The project was financed through the Interreg Botnia-Atlantica cross-border cooperation programme. It started in June 2018 and ended in May 2022. The project was a continuation of long-term cross-border collaboration between Finland and Sweden in Kvarken aiming at strengthening the management of the joint sea area. The project partners were Metsähallitus Parks & Wildlife Finland, the South Ostrobothnia Centre for Economic Development, Transport and the Environment, the County Administrative Board of Västerbotten, and the County Administrative Board of Västernorrland. The project area was confined to Ostrobothnia and Central Ostrobothnia in Finland and Västerbotten and Västernorrland county in Sweden.

The ECOnnect project would like to thank Interreg Botnia-Atlantica, the Regional Council of Ostrobothnia, the Swedish Agency for Marine and Water Management, and the participating organizations for making this project possible. We would also like to give thanks to SMHI and FMI who produced the climate models and to everyone else who have helped us in one way or another.

Contents

Abbreviations and Acronyms

BRT	Boosted regression trees, a method of species distribution modelling
BSAP	The HELCOM Baltic Sea Action Plan
FMI	Finnish Meteorological Institute
MPA	Marine Protected Area
RCP 8.5	Representative Concentration Pathway 8.5, the worst-case climate scenario
SMHI	Swedish Meteorological and Hydrological Institute

1. Introduction

1.1. The Baltic Sea

The Baltic Sea is a shallow sea characterized by brackish water (Leppäranta & Myrberg 2009). There are nine countries surrounding the Baltic Sea with around 85 million people living in the drainage area. The drainage area is about four times larger than the sea, and this puts great pressure on the biodiversity and ecosystem functions of the sea (HELCOM 2017). Environmental problems from human activities affecting the Baltic Sea include eutrophication, pollution, maritime traffic, introduction of non-indigenous species, fishing and hunting, habitat loss and disturbance, climate change, marine litter, etc. (Leppäranta & Myrberg 2009; HELCOM 2017).

Due to the brackish water, species diversity in the Baltic Sea is low compared to marine or freshwater environments (Kautsky & Kautsky 2000; HELCOM 2009). Nevertheless, the biodiversity is higher than expected in a brackish system because of the high variability in types of habitats and the unique salinity gradient (HELCOM 2018a). Moreover, the Baltic Sea has been estimated to be a very productive ecosystem providing a variety of ecosystem services. These include e.g. fish, water and climate regulation, nutrient recycling, and recreational opportunities (HELCOM 2009).

Marine species like *Fucus* spp. and the blue mussel (*Mytilus trossulus x edulis*) are examples of key species throughout almost the entire Baltic Sea as they form habitats (HELCOM 2009) and provide a food source for many other species (Waldeck & Larsson 2013; Wikström & Kautsky 2007). Areas where a few key species have a large influence on the ecosystem (HELCOM 2009), or where there is low species diversity (Peterson et al. 1998), like in the Baltic Sea, can be defined by their low resilience to stress factors (HELCOM 2009). One stress factor that could have a large impact on the Baltic Sea is climate change.

1.2. Project background

The aim of the ECOnnect project was to study the possible effects of climate change on the aquatic environment in the central Gulf of Bothnia hundred years ahead. The project area (Fig. 1) is especially interesting when it comes to climate change as some marine species in the area of Kvarken are already living near their tolerance limit regarding salinity. The low mean salinity in the project area is optimal for neither the marine nor freshwater species living together in the area (Kautsky & Kautsky 2000). A possible decrease in salinity due to climate change could have a great effect on the species distribution in the area. Additionally, the temperature has a great impact on the environment and ecosystems due to the seasonality and duration of ice cover. The aim of the project was to generate information that could assist community planners in adapting to the effects of climate change. The goal was also to make the results accessible for the public. The goals of the project were achieved by producing models of possible future distributions of underwater species and species groups in the area as well as maps of possible changes to physical parameters, such as the temperature, salinity, and sea ice cover. The models were based on future climate scenarios from the Swedish Meteorological and Hydrological Institute (SMHI) and the Finnish Meteorological Institute (FMI). Furthermore, the project studied the possible future ecological connectivity between biotopes and keystone species and marine protected areas (MPAs) and investigated the impact of climate change on important marine ecosystem services in the project area.

The climate models used in this project are based on the climate scenario RCP8.5 and the nutrient reduction schemes according to the HELCOM Baltic Sea Action Plan (BSAP). The RCP8.5 is the worst-case climate scenario created by IPCC in the Fifth Assessment Report (AR5) (Collins et al. 2013). The BSAP is a collection of actions and measures for the

HELCOM contracting parties to achieve a healthy marine environment in the Baltic Sea with a special emphasis on eutrophication mitigation (HELCOM 2020). The results from the ECOnnect project are based on assumptions that concentrations of greenhouse gases in the atmosphere will continue to increase in the future following RCP8.5, but a good environmental status concerning eutrophication will exist in the Baltic Sea.

The decision to focus on RCP8.5 and BSAP was made based on present trends and trajectories. While there are ambitious goals for climate change mitigation such as the EU's policy to reach carbon neutrality by 2050, the measures may be too little and too late. Climate change has been acknowledged as a serious threat for decades, but this awareness of the problem and its solutions have unfortunately not turned into sufficient action. Moreover, we wanted to use the worst-case scenario to study what totally neglecting the climate crisis might cause for the sensitive Kvarken area and to draw attention to how climate change, eutrophication, the state of the marine ecosystems and human well-being are intertwined. In contrast, eutrophication of the Baltic Sea has been taken seriously for a while, and inputs of nitrogen and phosphorus to the sea decreased by 22 % and 24 % respectively in the 1995–2014 period (HELCOM 2018b). Therefore, it seems possible to achieve the goals of the BSAP in future decades. Nevertheless, much of the work against eutrophication and other environmental stressors remain. We also wanted to show how important it is to reduce the nutrient input to lessen the stress on the marine environment to avoid cumulative effects of eutrophication and climate change.

Further information about RCP8.5 and BSAP can be found in the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia* where species distributions have been modelled in the reference period and in the future.

Communicating the purpose of the project and the results to both community planners and environmental and climate experts, as well as to the general public was an important part of the project from the start. Social media was the main channel for communication and an online workshop for community planners and environmental and climate experts was organized at the beginning of 2021. The project results are presented in different reports, on the SeaGIS2.0 map portal, the project's webpage and in a story map. The reports include detailed information about the project's methods and results, and the models can be studied more closely in the SeaGIS2.0 map portal. The produced data is open and free to be used further in other climate related projects. In order to make the results available and interesting to a broader public with different backgrounds, several videos and animations were created about the different topics of the project. A story map was created to display the communication material produced and the main results from the project in an inspiring way.

1.3. Project area including Kvarken

The project area extends from north of Skellefteå in Sweden and Kokkola (Karleby) in Finland to south of Sundsvall in Sweden and Kristiinankaupunki (Kristinestad) in Finland (Fig. 1).

Within this central part of the Gulf of Bothnia lies Kvarken. Kvarken is a shallow transitional area separating the Bothnian Sea from the Bothnian Bay. The coastline and topography of Kvarken are constantly changing and are shaped by the ongoing land uplift, which makes the land rise at a rate of around 9 mm/year (Poutanen & Steffen 2014). Kvarken contains several marine protected areas, including Natura 2000 areas, and important bird and biodiversity areas (Kallio et al. 2019). Moreover, Kvarken is classified as an Ecologically or

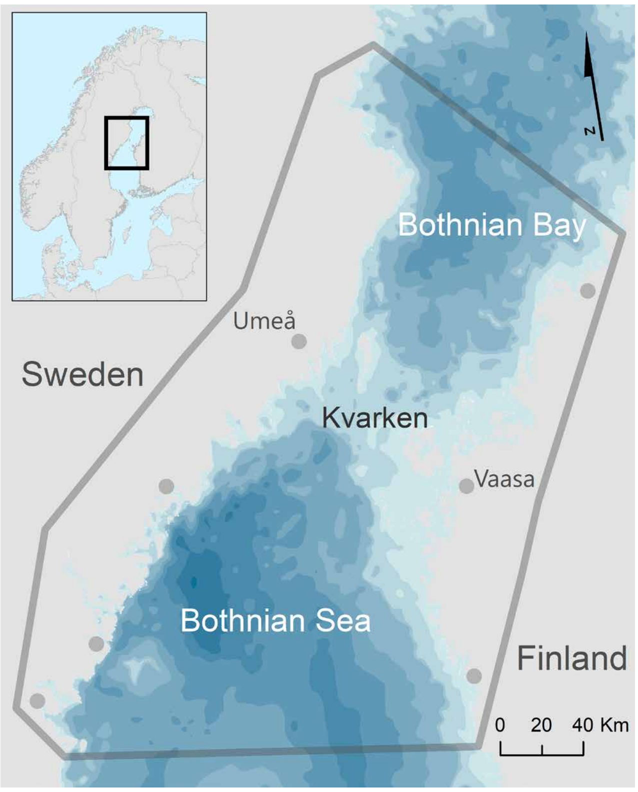


Figure 1. The ECOnnect project area is situated in the central Gulf of Bothnia in the northern Baltic Sea.

Biologically Significant Area (EBSA) (The Convention on Biological Diversity 2021).

The archipelago on the Finnish side of the project area is shallow and consists of thousands of small islands, whereas the landscape on the Swedish side is much steeper with fewer islands (Poutanen & Steffen 2014; Donadi et al. 2020). The UNESCO World Heritage Site High Coast / Kvarken Archipelago is located here (UNESCO 2021). On the Finnish side of the project area lies several EMMA areas (Finnish ecologically significant marine underwater areas): Revöfjärden, Rönnskäret, Mikkelinsaaret, and Kvimofjärden (Lappalainen et al. 2020).

There are variations in the salinity in the project area due to the shallow depth and strong currents in Kvarken. The salinity declines from 5 to 4 ‰ when moving only ca 10 kilometres northwards from Bergö, located south of Vaasa. The salinity is higher on the eastern side of the project area as the Coriolis effect steers the incoming saltwater from the south towards the Finnish west coast and the rivers on the Swedish east coast bring a lot of fresh water into the sea (Rinkineva & Bader 1998). The mean salinity in Kvarken is 3–4 ‰ which is lower than the mean salinity in the Baltic Sea (Kautsky & Kautsky 2000). The declining salinity from the Baltic proper to the Gulf of Bothnia affects the living conditions for species. Therefore, Kvarken is a border area for the distribution of several species (Rinkineva & Bader 1998), for example, for blue mussels and brown algae *Fucus* spp. (HELCOM 2017). The majority of the species within the project area are freshwater species that can tolerate brackish conditions, for example, fish species such as perch (*Perca fluviatilis*), bream (*Abramis brama*), and roach (*Rutilus rutilus*) and underwater vegetation such as pondweeds (*Potamogeton* spp.) and stoneworts (Charales) (Viitasalo et al. 2017). Since both marine and freshwater species are to some extent living outside of their optimal conditions regarding salinity, both groups of species face physiological stress. This stress can result in the smaller size of the species, for example, compared to areas where the species are not as exposed to stress factors (Westerbom et al. 2002).

The mean and maximum depth in the project area is 64 m and 298 m, respectively (SeaGIS2.0). The shallow parts of the project area provide areas with warmer temperatures, especially in the spring, unlike the otherwise cold waters in the Gulf of Bothnia. These warmer areas are important for species reproduction, for example for several fish species. The ice that covers the project area during winter has a great impact on the sea, affecting for example the sedimentation process and scraping away underwater vegetation from shallow areas where land-fast ice has formed. The main currents in the Gulf of Bothnia travel northward along the eastern coast and southward along the western coast. There are also smaller and more local currents that affect local conditions, such as sedimentation. The currents are typically strong in Kvarken as it is the passage for water going between the Bothnian Sea and the Bothnian Bay (Rinkineva & Bader 1998).

1.4. Future effects of climate change

In the future, atmospheric changes due to climate change could include changes in air temperature and precipitation. In the oceans and seas, changes in water temperature, sea level, storm surges, and sea ice cover can be expected (HELCOM & Baltic Earth 2021; Meier et al. 2021). Increasing levels of carbon dioxide in the atmosphere are also causing ocean acidification, which leads to a decrease in the water pH (HELCOM 2017), but it is uncertain how much the pH might change in the Baltic Sea (HELCOM & Baltic Earth 2021). These changes, in turn, are expected to lead to changes in marine species and communities (Viitasalo & Bonsdorff 2021).

The greatest changes to water temperature in the Baltic Sea are predicted to occur in the Gulf of Bothnia in the summer (Meier et al. 2021). The surface layers will warm more than the deep waters, and mean summer surface water temperatures in the northern parts of the Baltic Sea could increase by over 3 °C under the RCP8.5 scenario (Meier et al. 2021). Climate models have large uncertainties regarding water balance, and because runoff is the greatest factor affecting salinity there are large uncertainties even concerning whether the salinity will decrease or increase. It is projected that precipitation will increase in the summer as well as in the winter in the northern part of the Baltic Sea, which could result in a salinity decline. However, with rising temperatures there could also be an increase in evaporation which would reduce the river-runoff and would not cause a decline in salinity. In addition, sea level rise affects salt inflows into the Baltic Sea, which could compensate the effect of increased runoff, further complicating the predictions of future salinity.

Rising sea levels are mainly caused by melting of glaciers and the thermal expansion of sea water as it gets warmer. In the Gulf of Bothnia, the potential sea level rise is expected to be compensated for by the ongoing land uplift (Meier et al. 2021). The sea level rise in the project area is further discussed in the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia*. Future changes in storm surges will depend on the sea level rise and increased wind speed. At present, it is not well understood how winds may change in the future, but increasing wind speed is considered possible by several recent studies, especially in the autumn (reviewed in HELCOM & Baltic Earth 2021; Meier et al. 2021). Sea level rise is the factor affecting changes in storm surges the most (von Storch et al. 2015), and one could assume that if the sea level rises, storm surge levels could also rise. This is, however, very uncertain.

Ice cover is highly dependent on the air temperature in the winter. The ice cover today is already smaller and thinner than the historical average, and the duration of the ice cover has shortened. In winter 2020, the annual maximum sea ice extent was at its lowest since 1720, when measurements began (Meier et al. 2021). Additionally, during the last 30 years the mean extent of the sea ice has been the lowest ever (Meier et al. 2021). The increasing temperature in the future is expected to accelerate these changes in the sea ice (HELCOM & Baltic Earth 2021; Meier et al. 2021).

How ocean acidification can affect species and ecosystems in the Baltic Sea is still highly uncertain (HELCOM & Baltic Earth 2021), but the available data implies that many species in the Baltic Sea are generally tolerant to a lower pH, but that for example some shell-building species may suffer (Navenhand 2012). It is also expected that brackish water communities will be less affected by ocean acidification as they are already adapted to variations in CO_2 and pH (Bermudez et al. 2016). However, some studies have also found evidence that acidification in combination with warming waters will have more detrimental effect on Baltic Sea communities than acidity alone (Viitasalo & Bonsdorff 2021).

According to the future models produced for this project for the years 2070–2099, the mean bottom water temperatures in the summer will increase by 3°C, ice-thickness will decrease by more than 80 % and salinity is on average projected to decline by 0.52 ‰, or -10 %, compared to the reference period 1976–2005. These are the most important climate induced changes that the marine environment in the project area is expected to face in the future. If the BSAP will be successfully applied, nutrient inputs into the sea would decline and light availability increase, which would benefit many plants and algae. This report does not go into detail for all the expected future environmental changes, but as these (and the species distribution models) are something that the results of this report also rely on, more information on them can be found in ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia*. It is expected that the effects of climate change such as an increase in sea surface temperature will be larger in the Gulf of Bothnia than in any other part of the Baltic Sea, partly because the albedo will decrease as the ice is lost, leading to even more warming (Meier et al. 2012). Climate change will affect the Baltic Sea ecosystems in different ways and together with other human pressures can also affect the resilience of the ecosystems making them even more vulnerable to future changes (HELCOM 2013a; von Storch et al. 2015; HELCOM & Baltic Earth 2021).

2. Ecological connectivity

2.1. Theoretical background and key concepts of ecological connectivity

Ecological connectivity is key for the survival and conservation of many species, both on land and in the sea (Taylor, 1993). There are several different types of connectivity, but ecological connectivity typically refers to the links created by species and ecological processes among habitat patches in a landscape (Taylor et al. 1993). These movements can be performed for various reasons and during different life stages, for example when young individuals are seeking a territory of their own, when searching for a mate, and during feeding migrations and the use of different dispersal strategies (e.g. as seeds or propagules) (Hodgson et al. 2009; Wade et al. 2015). The ability of a species to disperse to new habitats can be critical for its survival, especially if existing habitats are becoming degraded (Heller & Zavaleta, 2009). When facing a future of predicted increased habitat loss and degradation due to climate change, connectivity and local migrations to less impacted areas play an increasingly important role for the long-term survival of species (Krosby et al. 2010).

The breakdown of a large and continuous habitat, for example a forest or a seagrass meadow, into several smaller patches is termed fragmentation (Rosenberg et al. 1997; Franklin et al. 2002). Habitat fragmentation is increasing globally due to anthropogenic activities (Haddad et al. 2015). This is considered a major threat to biodiversity because too small habitat patches may not provide enough resources for the organisms living in them (Rosenberg et al. 1997). Small habitat patches also support only small populations, which can be prone to problems like inbreeding and stochastic dynamics. All these problems can also lead to a decreased resilience, meaning that populations have lower tolerate for disturbance and recover slowly after damages to the system. However, conservation of connectivity may mitigate and buffer negative effects on plants and animals. Effective conservation of connectivity requires information about the dispersal and movement of the species as well as identification of the areas where conditions for connectivity are good.

Climate change is one of the largest challenges that conservation managers are facing today (Heller & Zavaleta 2009). Predicted changes in the Gulf of Bothnia include a substantial increase in sea surface temperature, increased land run-off and reduction and earlier melting of ice-cover (Andersson et al. 2015). Because of the profound effect these factors can have on different biotopes, the abundance, quality, and distribution of certain habitats may be altered in near future (Takolander et al. 2017; Jaatinen et al. 2020; see also the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia*). Climate change may decrease habitat suitability for some species but may also create new habitats for others. For example, a decrease in salinity may enable freshwater species to extend their range southwards in the Baltic Sea (Mackenzie et al. 2007). However, colonization of new areas may not be possible if there is no existing connectivity or no possibilities that connectivity can be established in the affected areas (Hiddink and Coleby 2012). Currently, there is little knowledge of the connectivity in the Gulf of Bothnia or how it may be altered with climate change.

Traditional conservation efforts such as the establishments of protected areas may not be sufficient to buffer the consequences of climate change. It may also be unrealistic to try to encompass all species inside protected areas if their geographical distribution ranges are very large. Conservation with protected areas becomes even more challenging if species' ranges will change in the future, for example if some species move to higher latitudes because of warmer temperatures or to lower latitudes due to decreased salinity (Heller and Zavaleta 2009). An alternative approach is instead to focus management efforts on maintaining and enabling connectivity across *seascapes*, by the creation of a network of protected areas, thus ensuring that there are possibilities for dispersal among protected habitats (Heller & Zavaleta 2009; Wade et al. 2015). In this report, the term seascape is used, following Pittman 2017, to describe "spatially heterogenous and dynamic spaces that can be delineated at a wide range of scales". The project area was divided into six seascapes following national borders and the sea basins, described in section 3.1.

The different spatial scales that connectivity operates on have to be considered when designing habitat networks. Short-range connectivity occurs within habitat networks, whereas long-range connectivity describes movements across habitat networks (Rayfield et al. 2016). The former reduces the risks of local extinctions and enables recolonization of new habitat patches whereas the latter facilitates annual migrations and climate-driven range shifts (Rayfield et al. 2016). Connectivity over large spatiotemporal scales is also crucial for gene flow among different parts of a species' range. Consequently, the conservation of species and their habitats is only efficient if both short-range and long-range connectivity are maintained or increased. Therefore, ecological connectivity is key to successful establishment of long-term, viable networks of protected areas that are resilient to climate change.

Ecological connectivity can be defined in different ways depending on the context and research area. Three main theories constitute the foundation that connectivity builds upon: **island biogeography, metapopulation theory** and **landscape ecology** (Wade et al. 2015).

Island biogeography presents the view that biodiversity is dependent on the size of a habitat patch (an island) and its isolation or proximity to other habitat patches (the mainland) (MacArthur & Wilson 1967). Even though the theory was originally developed for islands, this concept is widely applied in ecology, defining landscapes as high-quality habitat patches that are embedded in unhospitable and unsuitable habitats, referred to as the matrix (Wade et al. 2015). However, this is a rather "black and white" approach, and in reality, nature is not that conservative (Prugh et al. 2008). Properties of the matrix itself need to be taken into account, because the matrix will always be used to some degree by organisms, and a more nuanced approach is adopted today, which considers to what extent the matrix is used by the populations (Prugh et al. 2008; Franklin & Lindenmayer 2009).

Metapopulation theory describes regional small populations of the same species that are geographically separated but still connected by movement or dispersal patterns and thus create a larger population network called a metapopulation (Levins 1968, 1969, Hanski 1998). Because local populations are generally small, they always face the risk of extinction, which is compensated by the recolonization of other habitat patches (Hanski 1998). Populations in patches that are very isolated face a larger risk of extinction because of the limited supply of new recruits (Hanski 1998). This means that populations in highly fragmented and isolated habitats are more vulnerable to extinctions than populations in habitats that are less fragmented (Hanski 1998).

Stable metapopulation models have equal extinction and recolonization rates, which means that any population in a habitat patch could go extinct, but this is compensated by the colonization of other habitat patches (Hanski 1998). The number of inhabited patches will therefore remain the same, and there is no risk that the species would go extinct on metapopulation scale (Levins 1969; Hanski & Simberloff 1997). An important aspect to metapopulation theory is also the concept of **source and sink populations** (Gaggiotti 1996). In short, this means that in some populations (sinks), mortality rates may exceed recruitment rates, but this is compensated by the inflow of new recruits from populations that have a surplus of recruits (sources) (Pulliam & Danielson 1991). Source populations can therefore sustain sink populations if there is connectivity among these (Pulliam & Danielson 1991).

Landscape ecology combines the key concepts of island biography and metapopulation theory (Wade et al. 2015). By doing so, it uses the 'isolation and sizes of patches'- concepts from island biogeography and the dispersal concept from metapopulation theory, which is merged into a patch-corridor-matrix view, commonly referred to as a 'landscape mosaic' (Forman 1995). Similar to island biogeography theory, patches are still habitats distinctly different from the surrounding matrix (which is the dominating landscape type), and patches are connected by corridors, i.e. habitat types of preferred habitats that cross the matrix that consists of less preferred habitats (Wade et al. 2015). Less preferred habitats are not always categorized into 'matrix', and an alternative approach to island biogeography is to define a landscape mosaic as a patchwork of habitats of different degrees of habitat quality (Fischer et al. 2004) instead of isolated islands (Wade et al. 2015).

Since the 1970s, parts and pieces of landscape ecology concepts have been applied in aquatic environments, which has emerged as **seascape ecology** during the last decade (Pittman et al. 2011; Pittman 2017). Similar to landscape ecology, the seascape ecology focuses on the spatial arrangement of habitat mosaics and their effects on ecological patterns and processes, but in aquatic habitats (Pittman 2017). In doing so, it includes physical characteristics of the marine environment, such as hydrographic and chemical properties, and landscape characteristics that can be correlated with the ecology, life-histories and biodiversity in those ecosystems (Pittman 2017). The seascape ecology concept promotes a holistic view of the seascape where different spatial scales are considered, and builds upon four core concepts: context, configuration, the consideration of scale and connectivity (Pittman et al. 2021). Seascape context refers to the impacts of the surroundings, such as the degree of isolation of a habitat patch (Turner et al. 2001). Configuration describes the spatial arrangement of the seascape, and the consideration of scale defines the size of the seascape, which may differ largely, depending on research question and focus species (Jackson et al. 2017). For example, a whole seascape for a very small species may be considered as a single patch for a larger and more mobile one (Jackson et al. 2017).

One large difference between terrestrial and marine habitats is that marine populations are generally more open than terrestrial ones (Roberts 1997). Many marine species are dependent on pelagic dispersal of seeds, larvae or propagules which are driven by currents and oceanic circulation patterns and can cross vast distances (Roberts 1997). Marine connectivity may therefore cross national and international borders and local populations may be dependent on population dynamics in other locations (Roberts 1997). However, in fragmented coastal areas, large-scale hydrodynamic patterns may have less impact on connectivity while other factors such as habitat quality and sizes of habitat patches might be more important (Virtanen et al. 2020).

Another difference between terrestrial and marine environments is that coastal habitats are usually more fragmented due to natural causes such as strong waves and currents and variations in depth and substrate. This needs to be taken into consideration within marine management efforts.

2.2. Structural, functional and genetic connectivity

In short, connectivity refers to the movements of organisms and ecological processes across landscapes and habitat patches (Hodgson et al. 2009; Berkström et al. 2013) (Fig. 2).

Connectivity is considered a key feature for the survival of metapopulations in fragmented landscapes (Taylor et al. 1993; Metzger & Décamps 1997). Landscape and seascape connectivity embrace several aspects of movements and linkages, such as structural, functional or genetic connectivity. These concepts may be divided and classified further into various subgroups, but the categorization into structural and functional connectivity is the most general classification (Wade et al. 2015).

- **Structural connectivity** (or landscape connectivity) is related to the geographical characteristics of the environment. It refers to the arrangement and sizes of patches or habitats in a landscape (or a seascape) and to what extent

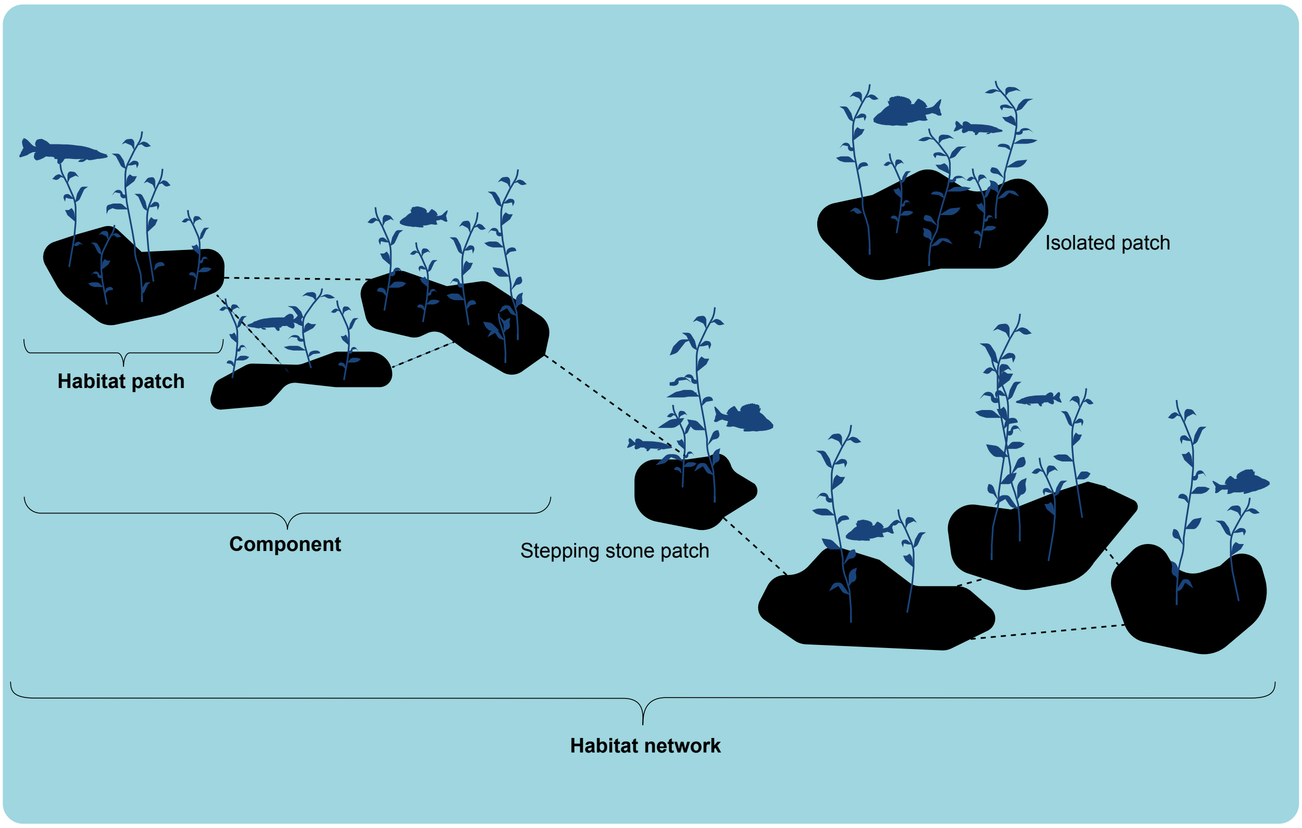


Figure 2. Conceptual figure illustrating the arrangement of patches on different spatial scales within a seascape and definitions to consider within connectivity. Black areas illustrate habitat patches and the lines among these illustrate how connectivity might link different habitat patches together in a seascape. Modified from Saura & Pascual-Hortal (2007).

the different patches or habitats are connected (Wade et al. 2015). Structural connectivity includes both the sizes of patches and distances among those. In aquatic environments, links among habitat patches can also be constituted by different physical processes and properties of the water itself, such as currents and fronts (Carr et al. 2017). Organisms that have passive dispersal, e.g. propagules, eggs and seeds that are carried by currents will therefore be highly affected by the structural connectivity in a seascape.

- **Functional connectivity** (or actual connectivity) is species-specific and describes the movements of a species which may depend on landscape characteristics and behavioural patterns (Wade et al. 2015). It encompasses several different types of movements, such as daily habitat migrations, seasonal migrations, demographic migrations, gene flow and range shifts.
- **Genetic connectivity** refers to the flow of genes among populations of the same species, which often results from population connectivity, for example dispersal of spores or larvae or migrations of juveniles or adults.

2.3. How can connectivity be quantified?

Marine habitats are linked to different degrees by the constant movements and spreading of species. Even organisms that are sessile for the majority of their life cycle, such as aquatic plants and algae, have seeds and propagules that can be transported by currents, water movements and other spreading vectors. But how can these processes be measured and quantified? Connectivity can be quantified in different ways depending on research questions and the type of connectivity being investigated.

Furthermore, there are different aspects to consider. Connectivity in a seascape can be characterized by different measurements and indices. The spatiotemporal scale depends on which type of connectivity should be measured (populations, habitats or a complete ecosystem, for example), and also depends on the species. Even the goal of the analysis can influence which scale or scales are relevant for the analysis. A multi spatiotemporal scale approach can be necessary in a connectivity analysis to get a holistic answer. Aquatic plants and algae may have very short dispersal ranges compared to mobile vertebrates such as fish: eggs of bladderwrack (*Fucus vesiculosus*) are usually only transported a few meters whereas a perch may move over distances spanning tens of kilometers (Berkström et al. 2019). However, this short dispersal distance is for one life cycle, and after several life cycles an individual's genes can eventually be spread much further.

Connectivity is highlighted as a key component to consider within conservation efforts, especially in the design of marine protected areas (MPAs) (Berglund et al. 2012; Carr et al. 2017; Virtanen et al. 2021). Different spatial metrics, indices and methods that are based on ecological knowledge and theory are used for this purpose. For example, patch size is an important prerequisite for connectivity ("the bigger the better"), as well as habitat quality and the distances among patches (Hodgson et al. 2009). A variety of different tools and methods are available for answering these questions (see section 2.6). The processes and patterns in the sea can be modelled by using a combination of different structural connectivity metrics (the spatial arrangement of habitat patches). Functional connectivity is hard to analyse, because it requires in situ information about spreading. This kind of data can be collected directly by tagging individuals, or in an indirect way through a genetic analysis which investigates how closely related different populations are and combines this information to actual connectivity between areas or patches distributed in the seascape.

Specific tools can be applied for addressing different spatiotemporal scales, aspects or characteristics of seascape connectivity, which means that one metric or tool might be needed to quantify the degree of habitat fragmentation in a seascape, and another to investigate connectivity bottlenecks. Similarly, the mapping of short-range connectivity (movements and dispersal within habitat networks) and long-range connectivity (movements and dispersal among habitat networks) require different tools (Rayfield et al. 2015) that operate on different spatiotemporal scales.

Also, it is important to keep in mind that all species distribution models are built upon predictions that are in turn based on observations, and the quality and accuracy of the observation data affects the result. Connectivity analyses based on species distribution models therefore provide the *probability* that connectivity exists in an area or the *likelihood* that there is a certain degree of connectivity, but they do not state that there *is connectivity* in an area. Depending on the degree of uncertainty of the models, the accuracy of predictions may differ slightly. However, the results from the models and the analyses are considered to give relatively accurate information. Furthermore, the analyses of connectivity have a focus on seascapes rather than on habitat patches. This gives a stronger confidence in the results. It is tempting to try to get results on a finer scale, but in the present analyses, especially considering uncertainties of the future scenarios, the results are more reliable on a larger scale, in this case on different seascapes (Fig. 3).

2.4. Barriers disrupt connectivity

The likelihood for an organism, a propagule, or a seed to reach a certain location generally decreases with distance from the source, i.e. the more isolated a habitat patch is, the less connectivity there is (Hanski & Gilpin, 1997). This is the reason why highly fragmented seascapes may have a very low degree of connectivity. However, the shortest distance between two locations in a landscape may actually not be the most likely route for dispersal or migrations, and other approaches might be needed to correctly predict connectivity (Hanski & Gilpin, 1997; McRae et al. 2008; Thiele et al. 2018). One reason for this is that some areas or habitat types might create barriers for species that are unable or unwilling to cross them. For example, in coral reef habitats which commonly consist of clearly defined patches of coral structures scattered across a structurally less complex matrix (e.g. sand) many reef-associated fishes will stay close to reef structures and avoid crossing the sand where they are more exposed to predators. Barriers are not the same for all species though. For flatfish that prefer soft bottoms, the coral reef may instead create a barrier.

In aquatic habitats, barriers may not always be related to the topography of habitats but can also be constituted of differences in water properties, such as the salinity. Salinity gradients form barriers for several species in the Baltic Sea (Snickars et al. 2015). For example, there is a steep salinity decrease originating from the transition zone between the North Sea and the Baltic Sea that continues all the way into the Gulf of Bothnia, resulting in a dramatic decline in the number of marine species (Ulrich et al. 2017). Other important factors that may act as barriers or limit species distribution in the Baltic Sea are depth and wave exposure (Florin et al. 2009; Snickars et al. 2010).

Large areas with deep and turbulent water may be perceived as a hostile environment for some species with limited dispersal, even though such an environment may not disrupt dispersal per se. On the contrary, some areas or hydrographic conditions may facilitate movements and migrations, for example by forming habitat corridors across unsuitable habitats or patches that constitute additional habitats. Connectivity can also be enhanced by 'stepping stones' – suitable habitat patches bridging an otherwise unsuitable area in a step-by-step process that acts over several generations (Coolen et al. 2020; Fowler et al. 2020). Artificial substrates, for example at offshore wind power farms, are known to be used as stepping stones for several hard bottom species, such as blue mussels (Coolen et al. 2020). Moreover, they may be used in efforts to restore or increase connectivity where linkages have been lost due to e.g. habitat degradation (Dafforn et al. 2015).

Coastal seascapes are commonly comprised of a heterogenous mosaic of habitat patches, which means that they are naturally quite fragmented landscapes (Pittman et al. 2021). How large a gap between habitat patches needs to be for constituting a barrier for movement varies depending on species, underlining the importance of scale in connectivity models. Anthropogenic disturbances may further fragment seascapes by for example coastal constructions, dredging or boating (Sundblad & Bergström 2014; Hansen et al. 2019). If such disturbances are located in areas where connectivity already is weak, e.g. in bottleneck locations, they may have a considerable negative impact.

2.5. Available software for estimating and measuring connectivity

How can the tools and methods that exist today be used to investigate which parts of the seascape are connected, which habitat patches are the most important, and identify critical distances between these? Seascape metrics may include sizes of patches, nearest neighbour distances (the distances between the closest patches), patch richness (the number of different patch types), habitat richness (the number of different habitat types), depth, and distance to land, etc. (Pittman et al. 2017). Mobility data and distribution and dispersal patterns of organisms and species can be derived from field surveys, tagging studies, or literature (Pittman et al. 2017). Then, computer generated models that quantify and map potential connectivity can be built by the use of an increasing number of software, of which many are widely applied in terrestrial ecology.

A majority of these software are based on **network analysis** which in turn builds on **graph theory**. Such programs are applied in 'resistance surface connectivity modelling', which classifies different habitat patches in a landscape or seascape based on how easily species can move across them (Wade et al. 2015). Different habitats are denoted a specific resistance, depending on the species in question, and if the habitat is facilitating or impeding dispersal (Wade et al. 2015). For example, if dispersal of bladderwrack is most frequent in shallow areas, these habitats will be given a low resistance. Deep areas, where dispersal is more difficult because large numbers of propagules may end up below the photic zone where they are unable to grow and spread forward, will be given high resistance. Areas with high probability of connectivity can be identified by mapping the resistance of the seascape.

Network analysis can answer habitat-related questions, such as which parts of the seascape are probably connected and which habitat patches are the most important, and estimate threshold values for distances among these (Pittman et al, 2017). Network analysis can give important information about metapopulations and habitats. For example, such analyses can help to estimate whether the protected areas are sufficient to secure healthy marine populations, or if areas need to be expanded. Below is a list of software used in this report:

CircuitScape is a connectivity modelling software that is extensively used within landscape ecology (Wade et al. 2015). It builds upon electrical circuit theory and is used for resistance-surface connectivity modelling (Wade et al. 2015), and can be used for predicting movement patterns and probabilities of dispersal of species, measuring the degree of connectivity or isolation of habitat patches and identifying key areas or corridors between patches (McRae et al. 2008). By using CircuitScape, it is possible to define areas in a seascape where species move relatively easily and areas where movements are reduced as well as identify bottlenecks for connectivity. CircuitScape should be used to study only species that are not affected by their surroundings but move in a more or less random way. The characteristics of the seascape drive the movements or spreading of such species.

Conefor is a modelling software that also builds upon network theory. It can be used within conservation planning, for example for quantifying the degree of importance of habitat patches and the links among these, as well as when estimating the effects of landscape changes (e.g., fragmentation) on connectivity. Conefor ranks patches where suitable conditions for connectivity are fulfilled based on an index which consists of 3 different metrics: intrahabitat connectivity (connectivity within a patch, which increases when the size of the patch increases), interhabitat connectivity (the links among habitat patches) and flux (a combination of both). In addition, also other available software were considered but not used in this report. Some of them are presented below.

Condatis is similar to CircuitScape in that it is also based upon electrical circuit theory (Hodgson et al. 2012). Condatis can be used for predicting long-term dispersal of species and identifying areas or habitats that are important from this perspective. It can also predict the speed of colonization into new habitats or areas. Condatis does not take the surrounding matrix into consideration, only the distance between habitats, and predicts the most rapid route depending on patch size and quality (Hodgson et al. 2012) By identifying potentially important areas for dispersal based on habitat maps, Condatis can be used to prioritize areas that may be considered for protection in the future.

Larval dispersal models and **kernel density estimation (KDE)** are additional methods commonly used to map and predict marine connectivity. These methods are not applied in this report, but hydrodynamic models from Kvarken will be used in discussions of potential trends in larval dispersal.

Zonation is a quantitative conservation and spatial prioritization tool, that makes it possible to include spatial models obtained from different connectivity softwares, e.g. the ones mentioned above into one multi-layer model (Moilanen et al. 2005). It is widely used within terrestrial research, but can be used also in marine environments (Virtanen et al. 2020). In short, Zonation generates a hierarchical prioritization model which takes different connectivity measurements (layers) into consideration (Virtanen et al. 2018). This enables the identification of the most valuable areas that should be prioritized within conservation initiatives (Virtanen et al. 2020). Also other prioritization tools are available, such as Marxan.

Regardless of which method and software is used, there is one aspect that is rarely considered because it is very difficult to estimate, and sometimes not even know. This aspect is rare and long-distance spreading events. This kind of spreading may drive the genetic variation of large seascapes, e.g., the whole Baltic Sea. Rare events of spreading can take place through vectors such as birds that eat aquatic vegetation and then transport spores, seeds or vegetative parts to a distant area. Transport via animals is called (endo)zoocory. Other alternative is that an individual is able to grow and spread for a certain time (year or years, one life cycle or several) in areas that normally are not suitable for that species.

2.6. Connectivity and climate change

The Baltic Sea is one of the major marine ecosystems most impacted by climate change (Belkin 2009). Predicted changes in the Gulf of Bothnia include decrease in salinity, reduction in ice cover and ice thickness and increase in water temperature, especially in the shallower areas. The ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia* describes these and other predicted changes in more detail. Species may be able to adapt to such changes by shifting their geographical range, but in highly fragmented or human-affected landscapes this can be difficult (Hodgson et al. 2016).

It is even more important to consider connectivity in marine conservation efforts than in terrestrial environments (Carr et al. 2017). This is mainly because the dispersal strategies of many marine species include a pelagic phase, where seeds, larvae or propagules are transported by water movements or currents over large distances (Carr et al. 2017). Different dispersal strategies, either passive or active, need to be taken into consideration in the design of successful marine protected areas (MPAs) (Félix-Hackradt et al. 2018; Berkström et al. 2019). To maintain resilient populations, protected areas need to either cover an area that is large enough to encompass dispersal distances or constitute of a network of protected areas that are located at distances that enable dispersal among them (Carr et al. 2017). Different types of connectivity also need to be considered depending on the goal of conservation. Short-range connectivity is important for species that disperse over short distances and inhabit highly fragmented areas. Long-range connectivity, on the other hand, is important for enabling range shifts and securing dispersal and genetic diversity over larger areas (Berkström et al. 2019). The size of suitable habitat patches is also critical for successful colonisation, because the larger an area is, the larger the probability that propagules will end up there (Hodgson et al. 2011). Thus, identifying connected habitats of high quality and sufficient size is important for the protection of marine environment.

In the Gulf of Bothnia, the present MPAs may not be able to protect valuable habitats or species if distribution ranges of species shift because of climate change. Therefore, defining and establishing more functional MPAs is needed to protect important habitats and to strengthen connectivity in the sea to meet climate change challenges. Connectivity-informed MPAs give underwater species more chances for finding suitable habitats also in the future (Carr et al. 2017). Establishing networks of MPAs and ensuring good possibilities for dispersal and other movements among these strengthens the resilience of the Baltic Sea against climate change.

2.7. Defining the aims and specifying methods to reach the aims

Currently, the majority of conservation efforts targeting connectivity mainly consider one aspect of connectivity, or connectivity that operates over one spatial scale (Rayfield et al. 2016). Moreover, few studies include both large-scale connectivity (long-range distance connections among habitat networks) and small-scale connectivity (small-range connections among habitat patches in networks) (but see Rayfield et al. 2016). It is possible to make predictions about key aspects of connectivity on different spatial and temporal scales by combining analysis tools based on circuit-based theory (CircuitScape) and network analysis or graph theory (Conefor). This report will adopt two approaches: a circuit theory -based approach will be applied to explain connectivity on a large spatiotemporal scale, and graph theory approach will be applied in analysing and quantifying network connectedness on a medium spatiotemporal scale.

In short, analyses of habitat patterns will be based on species distribution models – these will be key in identifying and mapping areas in the seascape where habitat requirements of the study species are met. Predicted connectivity of the species will be based on the probability that the locations meet these habitat requirements and that individuals can grow in and disperse from there and potentially use the locations as ‘stepping stones’. Also, the analyses will be based on structural connectivity and point out where the conditions for dispersal of the study species are good. Simulated dispersal patterns of the species will be based on the assumptions that i) species disperse passively, and ii) species move or disperse across the seascape without any previous knowledge of the habitats, i.e. they will choose routes with as little resistance as possible.

These different ‘pieces of the puzzle’ will provide important information for identifying seascapes with better and worse conditions for connectivity, both currently and in the future under the climate scenario RCP 8.5. In doing so, these results will highlight seascapes that should be prioritized in conservation efforts and reveals how well the current MPA network is protecting these seascapes and the connectivity of the study species. Depending on the results, recommendations will be presented on how to improve the MPA network for maintaining and facilitating ecological connectivity.

Within this context, the overall aim of this report is to evaluate the connectivity of habitats and the performance of the network of protected areas from a connectivity perspective. In practise, the aim is to understand how well the existing network of protected areas in the Gulf of Bothnia overlaps with areas that are valuable from a connectivity perspective, and how this might change in the future. This will be achieved by the identification of areas in the Gulf of Bothnia that are important for maintaining connectivity and therefore are valuable to protect, at present and in a hundred years ahead.

Additionally, the report will also identify seascapes that are more isolated and hence more vulnerable and would need to be considered within management plans in climate adaptation efforts. Future predictions are based on the worst-case climate scenario RCP 8.5 and nutrient scenario assuming the application of the BSAP. See the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia* for more information about the predictive models.

3. Methods

3.1. Seascapes and marine protected areas

The project area is located in the central Gulf of Bothnia (Fig. 3.). In this report, the study area is further divided into six seascapes, following the HELCOM classification on the Baltic sub-basins and the border between Finland and Sweden (adapted from HELCOM 2013b) (Fig. 3.).

Several marine protected areas (MPAs), including the UNESCO world heritage sites of Kvarken and Höga Kusten, HELCOM MPAs, Natura 2000 areas, national parks and nature reserves are located in the study area, both in Finnish and Swedish waters (Fig. 4). These areas have different degrees of protection. HELCOM MPAs do not have any legal protection, whereas the Natura 2000 areas, nature reserves and national parks are protected by law. Natura 2000 areas are implemented by the EU and are either managed according to the EUs Habitat Directive (Special Areas of Conservation) or EUs Birds Directive (Special Protected Areas). Nature reserves are the most common tool in Sweden to legally protect valuable natural environments. In Finland nature reserves have the highest degree of protection and are generally closed to the public.

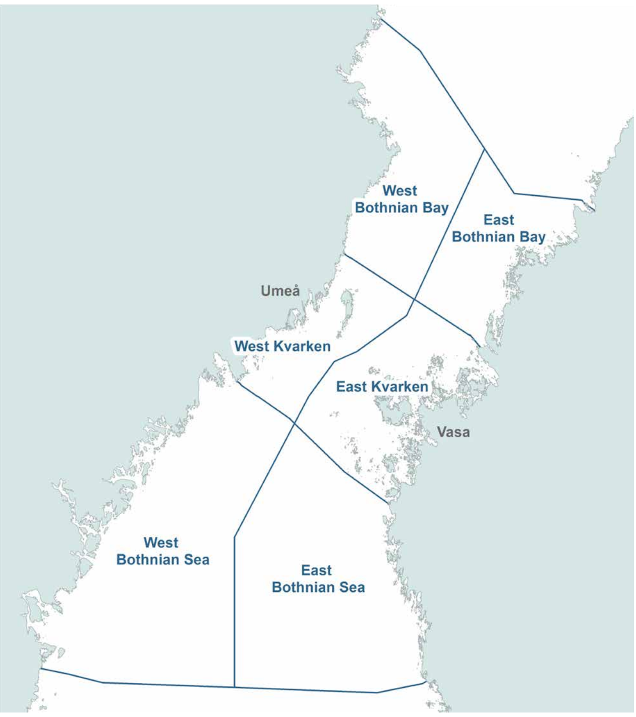


Figure 3. The central Gulf of Bothnia with the six seascapes: East Bothnian Bay, East Kvarken, East Bothnian Sea, West Bothnian Sea, West Kvarken and West Bothnian Bay. The classification is based on the sub-basin classification used by HELCOM (adapted from HELCOM 2013b) and the international border between Finland and Sweden.

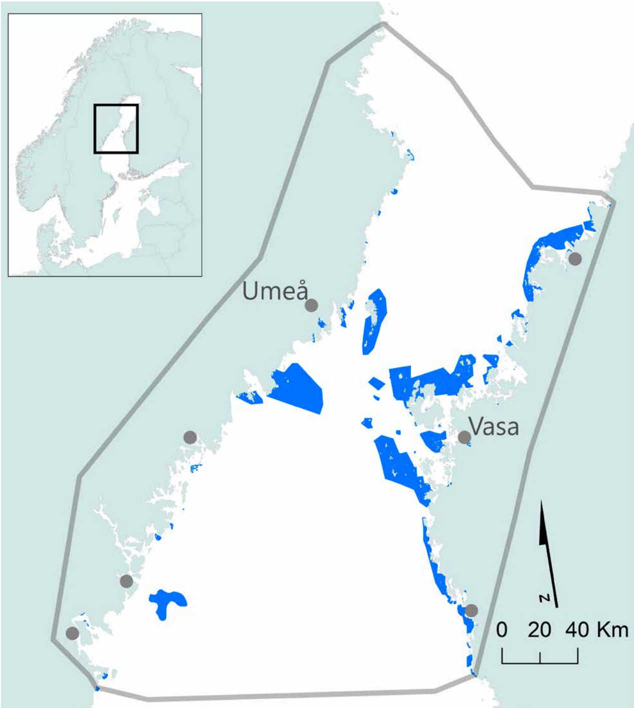


Figure 4. Marine protected areas (blue) inside the project area (grey border).

3.2. Study species

Connectivity is a species-specific concept (Wade et al. 2015). Features or conditions of a seascape which may offer connectivity for one species may constitute a barrier for another, and vice versa (Wade et al. 2015). It is also possible to perform generalisations when creating models and group species with similar movement patterns and habitat requirements (Hodgson et al. 2016).

Species distribution models were done for 12 species or species groups in this project. For the analysis of connectivity 5 of these were analysed in more detail. The selected species and species groups are the brown algae *Fucus vesiculosus* and *F. radicans* (hereafter referred to as *Fucus* spp.), the red alga *Furcellaria lumbricalis*, the blue mussel, pondweeds (*Potamogeton perfoliatus* and *Stuckenia pectinata*) and stoneworts (Charales). The remaining 7 species that were not analysed in detail are common and wide-spread in the project area and should therefore not have big problems regarding connectivity. In the following subsections, the dispersal strategies of the species included in this study are briefly summarized. For general information about the ecology of the species, see the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia*.

3.2.1. Aquatic mosses

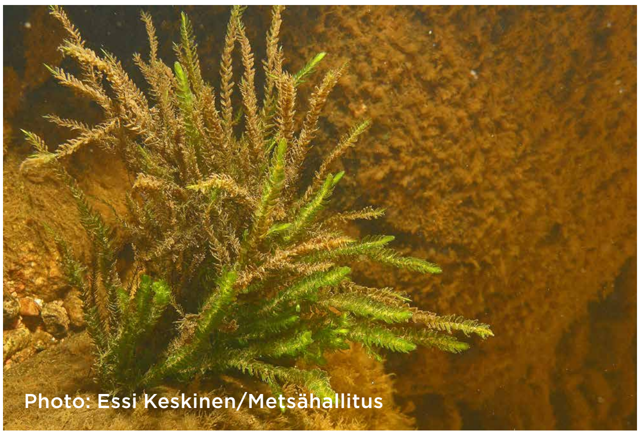


Photo: Essi Keskinen/Metsähallitus

Aquatic mosses are a group of habitat-forming freshwater plants (e.g. *Drepanocladus* spp., *Fissidens fontanus, Fontinalis dalecarlica*) that thrive in shallow, rocky areas with low salinity (Kautsky et al. 2017; Rinne et al. 2021). Dispersal occurs mainly through fragmentation, and thus this group is dependent on hydrodynamic conditions and the availability of substrate on which drifting fragments can attach (Korpelainen et al. 2013). Sexual reproduction and the development of spores is rare, but the spores are lighter than fragments and therefore may travel over larger distances (Korpelainen et al. 2013). Consequently, dispersal ranges are relatively short, but long-range dispersal by spores may happen occasionally (Korpelainen et al. 2013).

3.2.2. Baltic clam


Photo: Petra Pohjola/Metsähallitus

The Baltic clam (*Limecola balthica*, syn. *Macoma balthica*) is a widespread and often dominant species in macrobenthic communities in soft sediments in the Baltic Sea (Gogina et al. 2016). This species can disperse over large distances, mainly due to long pelagic larval phase (Beqcuet et al. 2013). Small genetic differences among subpopulations in the northern Baltic Sea indicate that connectivity is extensive and established over both small and large spatial scales (Wennerström et al. 2017).

3.2.3. Chironomids

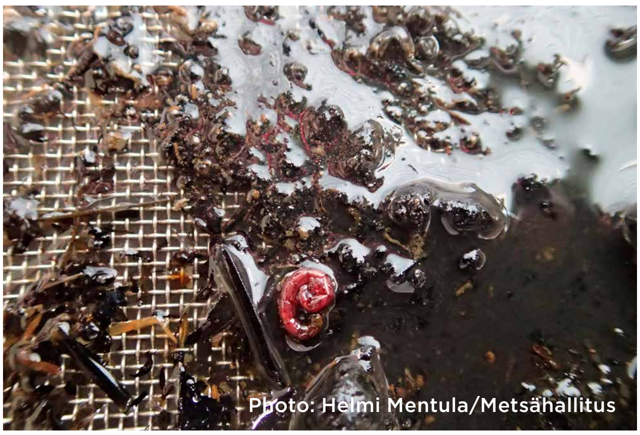


Photo: Helmi Mentula/Metsähallitus

Chironomid larvae are an important food source for many aquatic animals. The have a widespread distribution in soft sediment habitats, and can be found both in shallow and deeper areas. Because some species are tolerant of hypoxic conditions, they can be very abundant also in deeper areas where competition with other species is low. Because adults have relatively weak flying abilities, long range dispersal is probably influenced by water movements and by occasional events such as transportation by birds or on pieces of loose aquatic vegetation (Bitusik et al. 2017).

3.2.4. Filamentous annual algae

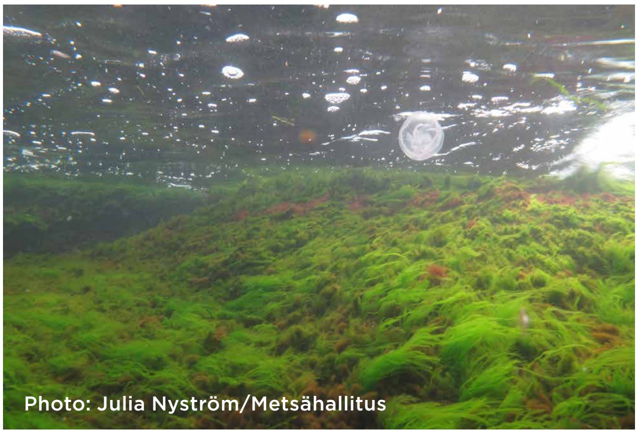


Photo: Julia Nyström/Metsähallitus

The filamentous algae in the Baltic Sea include various species of green, red and brown algae. These compose a common and extensive habitat in shallow areas on rocky substrate, but may also grow as epiphytes on e.g. *Fucus* spp. (Kraufvelin et al. 2007). Several environmental variables influence abundance and distribution of filamentous annual algae, such as nutrient concentrations, ice cover, turbidity, wave exposure, salinity and sea level fluctuations (Kiirikki & Lehvo, 1997; Kautsky et al. 2017). Dispersal occurs both by propagules and by vegetative fragments which are able to reattach when reaching a suitable habitat (Kiirikki & Lehvo, 1997; Bergström et al. 2003; Bergström 2005). Both strategies allow for dispersal over large geographical scales (Kiirikki & Lehvo, 1997; Bergström 2005). Detached filamentous algae may also create floating rafts (Berglund et al. 2003), from which algae can disperse further.

3.2.5. *Fucus* spp.


Photo: Juuso Haapaniemi

There are two species of *Fucus* present in the project area: *Fucus radicans*, which is endemic to the Baltic Sea, and *F. vesiculosus*, which has a more widespread distribution (Bergström et al. 2005; Kautsky et al. 2017). *Fucus radicans* mainly reproduces vegetatively and detached fragments have the ability to survive for long periods of time before reattaching, which enables dispersal across the Northern Baltic Sea (Tatarenkov et al. 2005; Ardehed et al. 2015). In contrast to the more competitive *F. vesiculosus, F. radicans* can tolerate lower salinity, which is suggested to be one of the reasons why *F. radicans* increases northwards at the expense of *F. vesiculosus* (Forslund et al. 2012). *Fucus vesiculosus* can reproduce either sexually, where fertilised eggs only travel short distances (~ few meters), or occasionally longer distances by detached fragments (Jonsson et al. 2018). Generally, population structure ranges between 1 – 10 km, the shorter distance being the most common (Tatarenkov et al. 2007; Jonsson et al. 2018).

3.2.6. *Furcellaria lumbricalis*


Photo: Julia Nyström/Metsähallitus

The red alga *Furcellaria lumbricalis* is often found associated with *F. vesiculosus*, growing on hard substrate beneath the canopy, or slightly deeper in the red algae belt (Kostamo et al. 2012). In the Norther Kvarken, salinity is suggested to be too low for this alga to reproduce sexually, so dispersal is restricted to vegetative propagules or fragments only (Kostamo et al. 2012). Similar to many other macroalgae, the distribution of *F. lumbricalis* is influenced by the availability of hard substrate, exposure, salinity and light conditions (Rinne et al. 2011).

3.2.7. *Marenzelleria* spp.

Photo: Metsähallitus

The introduced polychaetes *Marenzelleria* spp., originally from North America, were first documented in the Baltic Sea in 1985 (Bick & Burckhardt, 1989). Currently, they are abundant and widely distributed in soft sediment communities across the Baltic Sea. Three species are thought to occur in the area: *M. arctica, M. neglecta* and *M. viridis*, (Kauppi et al. 2015). Because the species are very similar and difficult to tell apart without the use of genetic methods (Kauppi et al. 2015), they will be referred to as *Marenzelleria* spp. All *Marenzelleria* species in the Baltic Sea have pelagic larvae which spend a rather long time in the water column (>1 month) (Kauppi et al. 2015). This has enabled them to disperse throughout the Baltic Sea, for example by currents (Kauppi et al. 2015). Adult worms are also able to migrate, but the spatial scale is not known (Kauppi et al. 2015; 2018).

3.2.8. *Monoporeia affinis*

Photo: Ari O. Laine

Dispersal of the amphipod *Monoporeia affinis* is probably restricted to relatively small spatial scales (< 1 km), even though this species is widespread through the Baltic Sea (Viitasalo et al. 2017). In some locations, *M. affinis* have been shown to have a rather restricted connectivity where even populations only a few kilometers apart may have limited exchange with each other (Guban et al. 2015). Similar to many amphipods, *M. affinis* lacks a pelagic larval stage and dispersal is mainly conducted by nocturnal migrations by adults, probably in the search for a mate or for suitable new habitats (Neiderman et al. 2003).

3.2.9. The blue mussel

Photo: Essi Keskinen/Metsähallitus

Dispersal of blue mussels is largely affected by currents, because they have a pelagic larval stage (Jonsson et al. 2021). The relatively long time that the larvae spend in the pelagic – up to 6 weeks – contributes to a widespread distribution in the Baltic Sea and dispersal distances up to 50 km (Kautsky

1982; Larsson et al. 2017; Berkström et al. 2019). However, the blue mussel populations in the Bothnian Sea and in the Baltic Proper are genetically different, suggesting that there is a dispersal barrier between them (Larsson et al. 2017). The barrier may partly depend on salinity gradient (Larsson et al. 2017). Blue mussels in the Bothnian Bay have probably shorter dispersal ranges and are more dependent on local recruitment than their relatives in the Baltic Proper (Johannesson et al. 2011; Larsson et al. 2017).

3.2.10. The common reed


Photo: Linda Jokinen Thai/Metsähallitus

The common reed (*Phragmites australis*) is common in shallow and sheltered areas in the project area. Long-range dispersal by seeds that are carried by currents or winds can reach up to 10 km (Fér & Hroudová 2009; Altartouri et al. 2015). Once established the common reed disperses vegetatively by the formation of rhizomes from which new individuals can grow (Altartouri et al. 2015). Because seeds can only survive in certain habitats (soft sediments that are not submerged) and in habitats with limited competition with other plants, vegetative and local dispersal is hypothesised to be the most common strategy (Altartouri et al. 2015).

3.2.11. Pondweeds

Rooted vascular plants dominate shallow bottoms with soft substrate in the Northern Baltic Sea (Kautsky et al. 2017). Pondweeds (*Potamogeton* spp.) can form dense and tall stands in sheltered bays, where they provide important habitat for fish and invertebrates (Hansen et al. 2011). Ice cover has a strong influence on the distribution of pondweeds, because it scours shallow areas clean of vegetation (Kaut-


Photo: Maja Wressel

sky et al. 2017). Salinity is also a restricting factor, because pondweeds thrive in freshwater or brackish environments (Kautsky et al. 2017). They disperse both by seeds transported by water movements and by clonal growth (King et al. 2002). Generally, dispersal ranges may not exceed 20 km (Berkström et al 2022), but occasional dispersal by birds may reach even 150-200 km (King et al. 2002).

3.2.12. Stoneworts

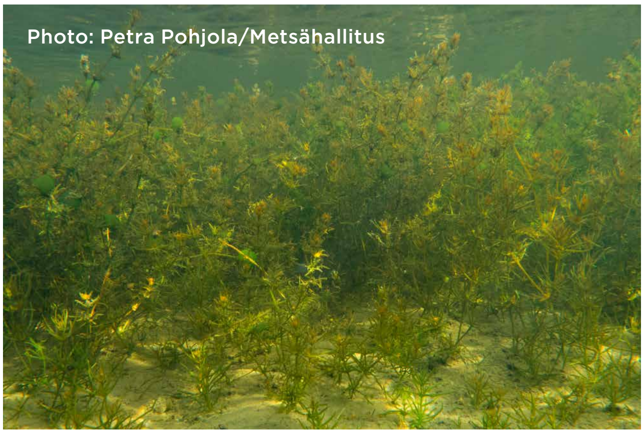


Photo: Petra Pohjola/Metsähallitus

Stoneworts, or charophytes, can be the dominant group in shallow soft-sediment coasts, where they may form dense stands that provide important habitats for other organisms (Kovtun et al. 2011; Kautsky et al. 2017). Wind and wave exposure, depth, substrate and salinity are strong predictors for their presence (Kautsky et al. 2017). Because stoneworts are sedentary, the connectivity for this group is constituted by the dispersion of propagules. Stoneworts generally have small and light propagules that can float with currents over large distances (Stenhardt & Selig, 2007).

3.3. Descriptive analyses

Potentially suitable areas for each of the study species and species groups in reference period (1976-2005) and in the future (2070-2099) were modelled using Boosted regression trees (BRT), a method of species distribution modelling (Elith et al. 2008). Modelling was based on field data on species presences and absences and modelled environmental conditions in the reference period and in the future, such as the salinity, water temperature, light availability and nutrients. In the future species distribution models it was assumed that climate will develop following the worst-case climate scenario, RCP 8.5, while future nutrient inputs into the sea were assumed to follow the goals of the Baltic Sea Action Plan. In other words, the future was assumed to be considerably warmer than the reference period, while nutrient levels were assumed to be lower. The environmental conditions used in the species distribution models were calculated from RCO-SCOBI, a three-dimensional physical-biogeochemical ocean circulation model of the Baltic Sea (e.g. Meier et al. 1999; Eilola et al. 2009; Saraiva et al. 2019) run by the Swedish Meteorological and Hydrological Institute (SMHI) and Finnish Meteorological institute (FMI). SMHI also run a model describing the currents in the sea under the present climate and in the future. More information on the chosen future scenarios, climate models, and species distribution models done in the project ECOnnect can be found in the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia*.

The area of the potentially suitable habitats in the six seascapes was calculated from both the reference period models and the future models. In addition, the absolute and proportional areas inside marine protected areas (MPAs) were calculated. The proportions of potentially suitable habitats inside protected areas in the reference period and in the future were compared to the protection objectives for the network of MPAs in the Gulf of Bothnia that have been set by the County Administrative Boards in Sweden (Länsstyrelserna 2021). Statistics about the areal distribution within the different seascapes and inside vs. outside the MPAs were calculated using ArcGIS and Excel.

The CircuitScape analysis was performed with the software CircuitScape (McRae et al. 2008). The resistance values described by Amos et al. 2012 were applied, giving barrier values of 10000 for the resistance matrix in areas deeper than 50 m. Then subsequentially lower values were given in the shallow depth intervals. The values imply that spreading is easier in the shallower areas.

The connectivity analyses were performed using several different software. The ArcGIS tool "*Conefor input*" was used to calculate the inputs for Conefor Sensinode 2.6 (Jenness 2016). Graph theory -based Conefor Sensinode 2.6 software (Saura & Torné, 2009) was used for the analysis of connectivity indices for the habitat patches and in the project area. ArcGIS and Excel were used for calculating the degree of spreading. The habitat network, or graph, was built using links of maximum of 2 km (Euclidean distance) between the habitat patches. This distance was defined to maintain the analysis clearly as a structural connectivity analysis. The chosen distance is also a medium distance that describes the seascape on a medium to large spatiotemporal scale. This way, the connectivity analysis can also give a metapopulation scale proxy. It is important to keep in mind that structural connectivity analysis yields information about conditions, not facts about connectivity. However, the results should be relevant for comparing different seascapes in terms of better or worse connectivity conditions between them.

The connectivity indices used in this report are Integral index of connectivity (IIC), Landscape coincidence probability (LCP), Harary index (H) and the degree of spreading. To get values of the importance of each habitat patch the IIC was used in the portioned fractions IIC-intra (Intra), IIC-flux (Flux) and IIC-connector (Connector).

The index IIC measures habitat availability based on the length of the shortest possible path between all pairs of nodes (measured as the number of links) and other properties of the nodes, such as patch area. IIC values are between 0 (all habitat lost) and 1 (entire landscape is connected), higher values indicating higher connectivity. Loss of a habitat patch or a non-redundant link lowers IIC. Similarly as IIC, also H increases with increasing connectivity.

The values of LCP are in the range from 0 to 1, higher values indicating higher connectivity. When areas of habitat patches are used as node attributes, the size of the study area is used as the maximum landscape attribute. In such case, if the whole study area is covered by the habitat, connectivity is naturally maximal, and consequently LCP gets a value of 1.

A landscape element, that can be for example a patch or a link, can contribute to habitat availability or connectivity in several ways. These can be studied through the portions of IIC called IIC-*intra*, IIC-*flux* and IIC-*connector*. These three components together sum up to dIICk, the total contribution of landscape element k, i.e. habitat patch, to the connectivity in the landscape d as measured with IIC. IIC-*Intra* describes the contribution of a patch to habitat connectivity or area. IIC-*Flux* is affected by both the area of a patch and its location in relation to other patches, because it describes the dispersal flow occurring through the patch. IIC-*Connector* measures the importance of a patch for the overall connectivity in the landscape considering only its location. The relative contribution of the different habitat patches on seascape-level connectivity can also be estimated with these indices. Here, the most important 25 % of patches of each study species were defined based on their values of IIC-*intra*, IIC-*flux* and IIC-*connector*. More information about the indices can be found in Saura & Rubio 2010.

We also propose a new index, namely the degree of spreading, as a proxy for how a species perceives the seascape. The principle is that it should be easier for a species to spread within its own habitat than in a non-habitat surrounding (the matrix, Fig. 5). Furthermore, the links between the habitat patches are the shortest possible, while also taking into account unfavorable areas. Because the unfavorable areas for marine species are land, the links represent the “water distance” between habitat patches. The distances are measures from the center of a habitat patch to the center of the next habitat patch. The new index, the degree of spreading, should be considered as a medium to large spatiotemporal connectivity index.

The degree of spreading in a case where all the links are in the sea considers the link to the nearest patch as well as the links between all patches. The degree of spreading, on the other hand, also takes into consideration the distance within a habitat patch, and is measured as percentage according to following function:

$$Degree\ of\ Spreading = \frac{LIH_{ij}}{TL_{ij}} \times 100$$

Where LIH_{ij} is the length inside a habitat patch for the link representing the nearest distance between the habitat patches *i* and *j*, and TL is the total length of the nearest link between the patches *i* and *j*.

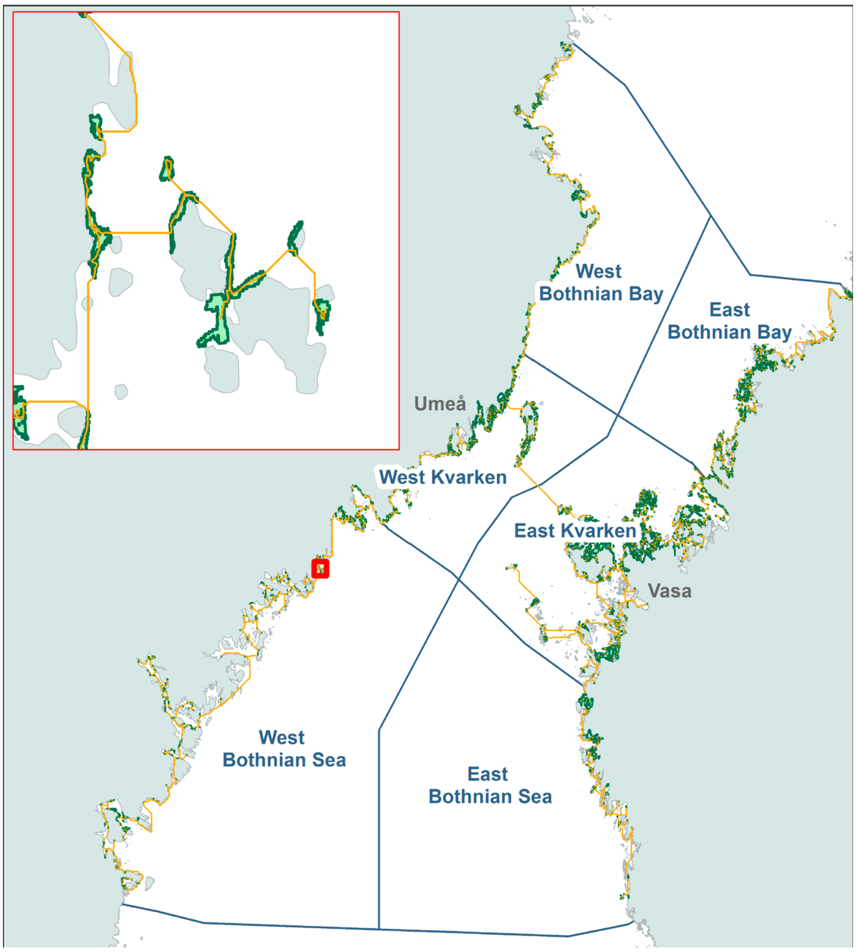


Figure 5. Illustration of links (orange line) between habitat patches (green areas) within the matrix (white). The degree of spreading is the proportion of the links inside the habitat patch. Example is from modelled areas of stoneworts in the reference period.

4. Results

4.1. Large-scale connectivity in the Gulf of Bothnia

Understanding connectivity in a large spatiotemporal scale requires understanding of the factors that influence growth and dispersal of the species. One such factor is the characteristics of the seascape, and one of the most relevant aspects, as showed in the species distribution models, is bathymetry. If a seascape is characterised by large shallow areas, the possibilities for growth and small-scale dispersal for most macrophyte species are better than in a seascape that is dominated by deep areas. To understand the spatiotemporal connectivity for species whose presence is limited by depth, the whole Gulf of Bothnia was analysed using the software CircuitScape. CircuitScape was set to consider depth and distance in the analysis.

The seascapes on the Finnish coast seem to have more favourable conditions for connectivity than those on the Swedish coast (Fig. 6). Furthermore, the results show that large-scale dispersal from south to north and vice versa is facilitated through the Finnish coast. The results also show Kvarken as a link and a potential way of dispersal between Sweden and Finland. The west coast of the Bothnian Sea can be defined as a naturally fragmented seascape. The Bothnian Bay has similar seascape characteristics that give similar possibilities for connectivity on both sides of the sea.

As only depth was used as a limiting factor in the CircuitScape analysis, the results apply for future as well as for today. The depth in the project area will not change much the next 100 years, because the land up-lift will counteract the global sea-level rise. The sea level rise is discussed in more detail in the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia*.

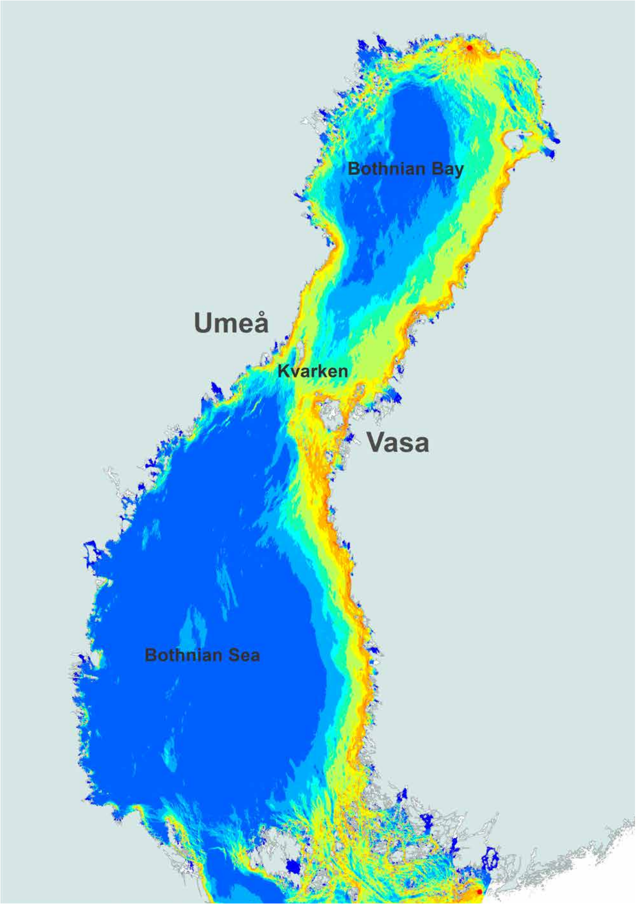


Figure 6. Connectivity on a large spatiotemporal scale illustrated by a CircuitScape-generated map showing potential areas for dispersal and dispersal routes depending on depth going from south to north in the Gulf of Bothnia. Blue colours denote worse possibilities for dispersal and orange and red better possibilities for dispersal.

Another aspect that affects connectivity on a large spatiotemporal scale is the sea currents. Surface currents, which are important for the dispersal of many marine species, may change in the future in the Gulf of Bothnia. During the summer months, visible changes are predicted to take place south of Kvarken on the Swedish coast (Fig. 7). The current models from SMHI suggest that the strong current that today follows the coast will move further away from the coast to a deeper part of the sea. This

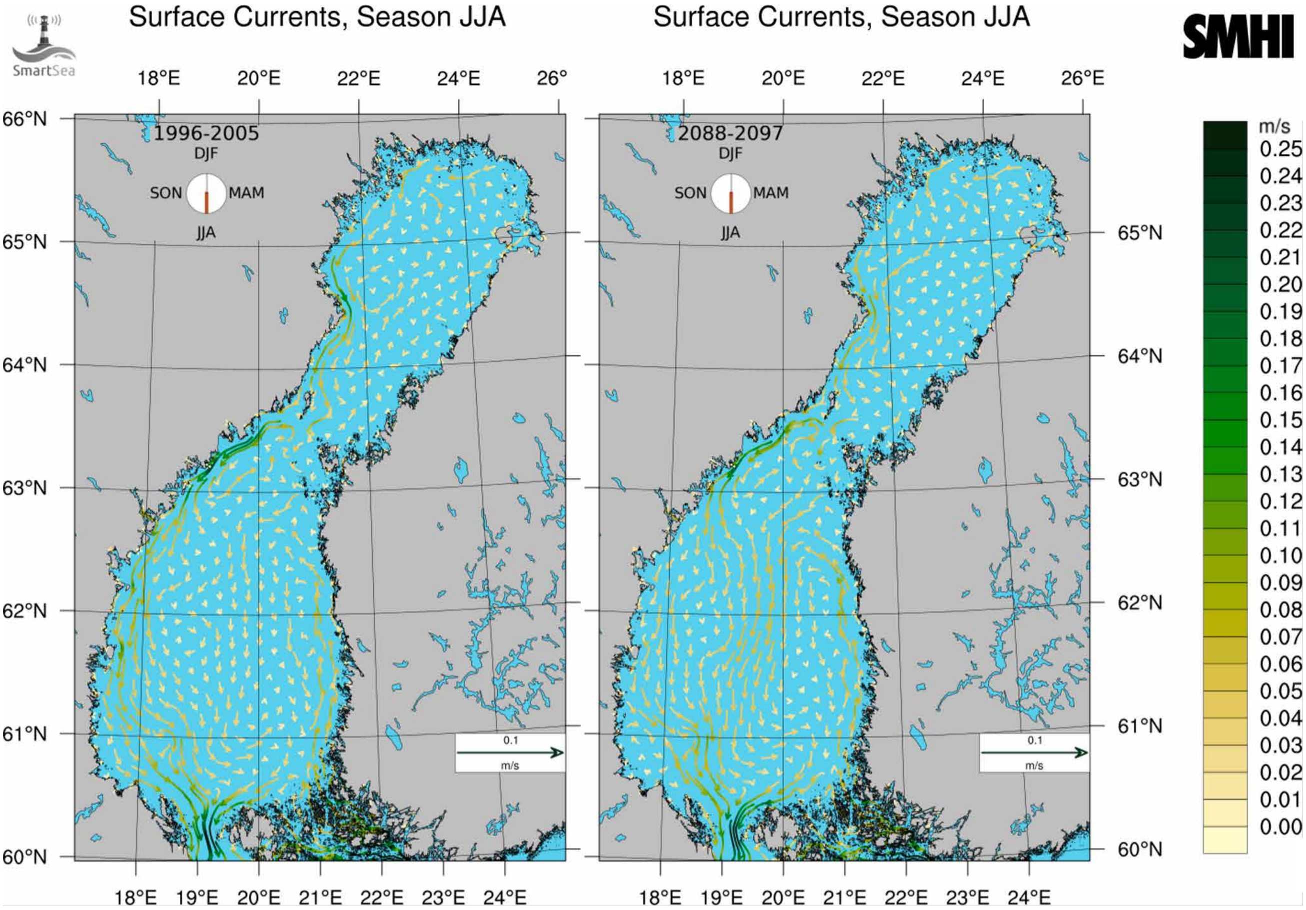


Figure 7. Surface currents in the summer months (Season JJA = June, July and August) in the Gulf of Bothnia in the period 1996-2005, left, and in the period 2088-2097, right. The maps are based on models of sea currents run by the SMHI. The directions of the currents are indicated with arrows and the velocity is indicated with colours, dark colours meaning stronger currents.

could mean that larvae, seeds and propagules of marine species may end up in deeper areas where they cannot find suitable habitats. This, together with the results of the CircuitScape (Fig. 6), indicates that the southern Swedish part of the project area may have poorer possibilities for spreading and thus poorer connectivity in the future.

4.2. Habitats in relation to protected areas

Modelled areas of suitable habitats for the different species and species groups in the different seascapes and inside protected areas in the reference period and in the future are presented in Table A1 in the Appendix. The predicted changes vary considerably between species and seascapes. Potential reasons for the changes in areas modelled suitable for each species are discussed in more detail in the ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia*. The species distribution models assume that the BSAP is applied, resulting in a better ecological state of the sea, but that at the same time the concentration of greenhouse gases in the atmosphere increases, leading to a remarkably warmer sea.

Several species are predicted to increase in the future, and because there is more unprotected than protected area in the seascape in general, also most of the increase tends to take place outside of the protected areas. As a result, the proportion of the total area predicted suitable inside current MPAs will decrease in the future for many species (Fig. 8). These species are therefore not under threat, even when the proportion of their potential occurrences located inside protected areas is predicted to decline. These species include annual filamentous algae, aquatic mosses, chironomid larvae, *Fucus* spp. (Fig. 9), and the red alga *Furcellaria lumbricalis*. These species are expected to benefit from the predicted thinning of ice and increased light availability in the future, expect for chironomid larvae, for which the main factor causing increase is temperature.

The polychaetes *Marenzelleria* spp. and the plant common reed are both very tolerant and abundant, and predicted to remain abundant or even slightly increase in the future. Most of their predicted increase could happen inside protected areas. As a result, both the absolute area and the proportion of total area inside MPAs will increase for both species, most notably in the Finnish coast. The same kind of pattern of both absolute and relative increase is seen in pondweeds, but in a much greater magnitude. The species distribution models suggest that areas suitable for pondweeds could expand greatly in the future, and especially inside MPAs. Therefore, also the proportion of their occurrences that are protected could increase remarkably.

In contrast, some species are predicted to decline in the future in some or all of the seascapes. If the decline will take place mostly outside of protected areas, then the proportion of the remaining occurrences inside protected areas will increase. This is the case for the Baltic clam and the blue mussel, which require saline water and may also have less food in the future if the availability of phytoplankton decreases. They are predicted to decline throughout the project area, but slightly more outside protected

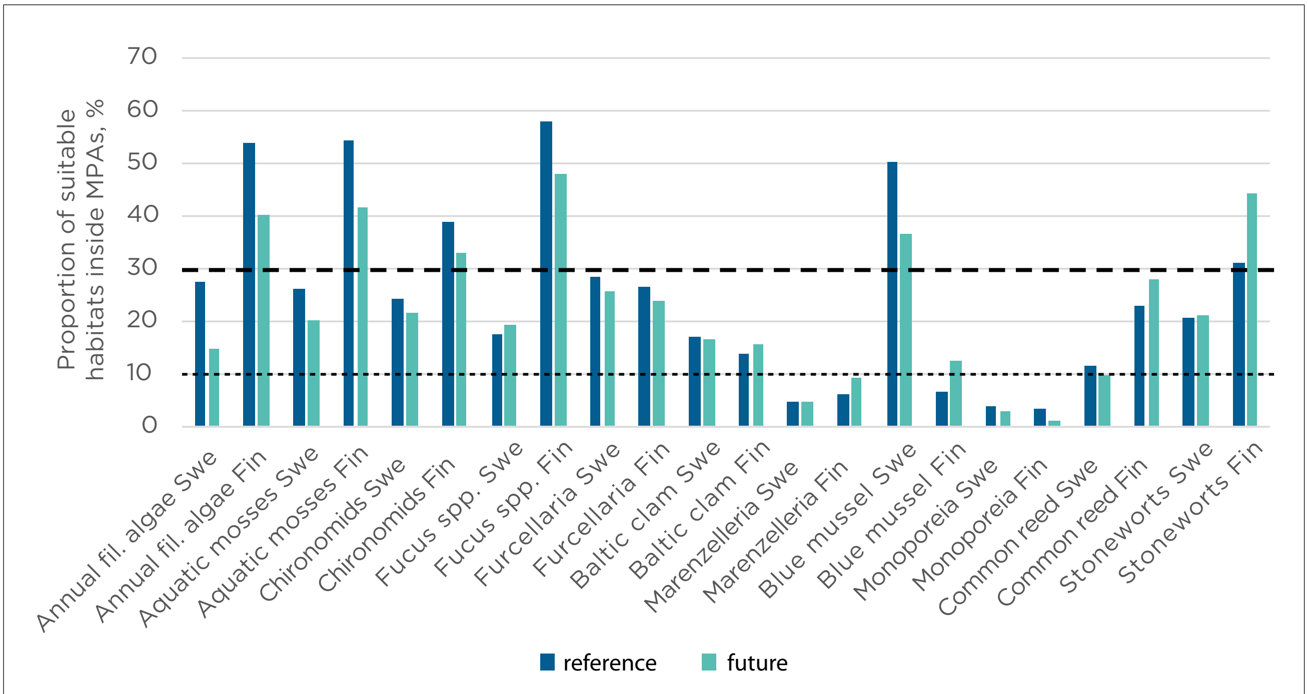


Figure 8. Proportion of potentially suitable habitats for the different study species inside marine protected areas (MPAs) in Sweden and in Finland in the reference period and in the future compared to the Aichi target (10 %, dotted line) and the EU Green deal (30 %, dashed line).

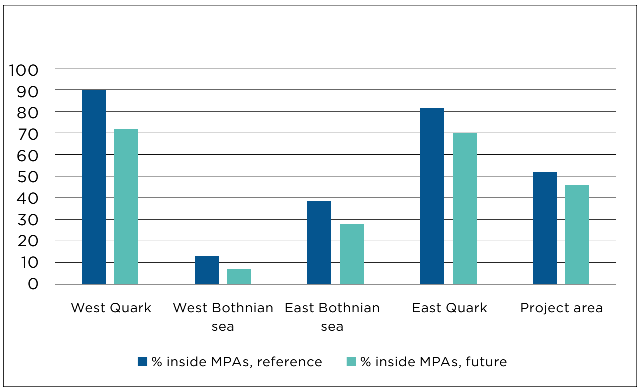


Figure 9. The proportion of habitats suitable for *Fucus* spp. inside marine protected areas in the reference period (1976-2005) and in the future (2070-2099) based on species distribution models.

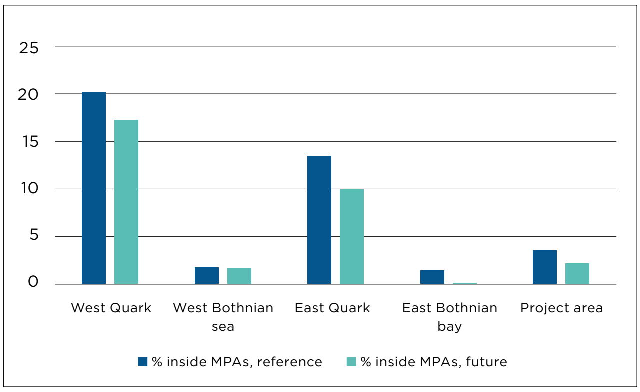


Figure 10. The proportion of habitats suitable for *Monoporeia affinis* inside marine protected areas in the reference period (1976-2005) and in the future (2070-2099) based on species distribution models.

areas than inside them in the Finnish coast, resulting in a small increase in the proportion of their occurrences inside Finnish MPAs. On the Swedish coast, in contrast, the blue mussel is predicted to decline especially in protected areas, resulting in a decline also in the proportion of potentially suitable habitats that are protected.

Monoporeia affinis is expected to decline throughout the project area, but even more inside protected areas than outside them. It is expected to suffer from increasing water temperature, which is predicted to be highest in shallow areas, where also most of the protected areas are located. As a result, the models suggest that both the absolute area of habitats predicted suitable for Monoporeia affinis and the proportion of them within MPAs could decline (Fig. 10).

Some species are predicted to show more complex spatial trends, declining in some areas while increasing in others. This is the case for stoneworts, which are predicted to slightly decline in Finnish coast outside protected areas, but increase inside protected areas, resulting in a remarkable increase in the proportion of protected occurrences.

Species that live mostly in deep areas tend to have a smaller proportion of their habitats under protection compared to species restricted to the photic zone. This is logical, as the protected areas are mostly in shallow areas, where diversity is highest, and the soft bottom organisms living in the deeper areas are generally less threatened. The Baltic clam, *Marenzelleria* spp. and *Monoporeia affinis* all have relatively low occurrence inside MPAs compared to most of the other study species (Fig. 8). Also the potentially suitable habitats for the blue mussel are mostly outside of protected areas in Finland, but in Sweden a remarkably higher proportion is protected. This is mostly due to the protected area in Vänta Litets Grund, where the blue mussel is abundant.

4.3. Habitats patch size in relation to protected areas

The size of a habitat patch affects the resilience of the species living in it. To understand fragmentation on a seascape level, the predicted changes on the five study species were analysed. Table 4.3.1 presents how much of the habitat patches is protected in three different size classes in the defined seascapes and how it may be affected by climate change in the future. The size of the patches, presented as classes, gives similar information as *largest patch index*, area of the largest patch in a seascape, (Pittman et al. 2004) or *patch area,* size of the patches, (Carroll & Peterson 2013).

The different patch sizes are well represented in the occurrences of pondweeds in Finland in general, but a comparison of the different seascapes in the Finnish coast reveals that the situation is not as good in the East Bothnian Bay as in the other Finnish seascapes. Based on the future species distribution models, climate change will result in a better protection of the largest patch sizes. The situation of

Table 4.3.1. Percentage of habitat patches of the different species and species groups inside MPAs for different patch size categories. - = 0 to 10 % inside MPAs; o = 10 to 30 % inside MPAs; + = 30 to 50 % inside MPAs and ++ = over 50 % inside MPAs. White background: reference period. Green background: future period.

	Pondweeds						Blue mussel						Stoneworts						Fucus spp.						Furcellaria					
	1 - 10 ha		10 - 100 ha		> 100 ha		1 - 10 ha		10 - 100 ha		> 100 ha		1 - 10 ha		10 - 100 ha		> 100 ha		1 - 10 ha		10 - 100 ha		> 100 ha		1 - 10 ha		10 - 100 ha		> 100 ha	
East Bothnian Bay	o	++	-	++	-	++							++	++	++	++	+	++												
East Bothnian Sea	+	+	o	o	-	++	o	o	-	-	-	-	+	++	+	++	-	-	++	o	+	+	++	++	++	o	+	+	++	++
East Kvarken	++	++	++	++	++	++	+	+	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++	++
Finland	++	++	++	++	o	++	o	o	o	o	o	o	++	++	++	++	++	++	++	+	++	++	++	++	++	+	++	++	++	++
West Bothnian Bay	-	-	-	-	-	-							-	-	-	-	-	-												
West Bothnian Sea	o	-	+	-	-	+	-	o	-	o	++	+	o	o	+	o	o	o	o	-	o	o	++	-	o	-	o	o	++	-
West Kvarken	+	++	o	++	-	++	+	++	+	++	o	-	++	++	+	+	+	++	++	++	++	++	++	++	++	++	++	++	++	++
Sweden	o	o	o	o	-	+	o	+	o	+	++	o	o	+	+	o	+	+	o	o	o	o	++	o	o	o	o	o	++	o
Project area	+	++	++	++	o	++	o	+	o	+	+	o	+	++	+	++	++	++	++	+	++	+	++	++	++	+	++	+	++	++

pondweeds is different in Sweden, where the MPA network does not protect most of the large patches in the reference period or in the future. In the West Kvarken, however, the larger patches are expected to be better covered by MPAs under the future climate.

The size class over 100 ha patches of blue mussels are well covered by protected areas in the East Kvarken. In the East Bothnian Sea and on the scale of the whole Finnish side of the project area, however, the size class 10-100 ha and over 100 ha patches are mostly not inside the MPAs. In Sweden most blue mussel patches are not inside MPAs except for the smaller patches in the West Kvarken and the biggest patches in the West Bothnian Sea. Potential habitat patches of stoneworts are generally well protected in Finland, but in the East Bothnian Sea the class over 100 ha patches are not protected. In Sweden the protection of habitat patches of stoneworts is less optimal as only the West Kvarken has patches in all size classes inside MPAs.

Fucus spp. and *F. lumbricalis* have similar level of protection of patches in size class over 100 ha inside MPAs. In the Finnish side more than half of them are inside MPAs. In the Swedish side the West Kvarken is an area where size class 10-100 ha patches of

Table 4.3.2. Relative change of habitat patches inside MPAs presented in three size classes. ↓ = more than 50 % reduction inside MPAs; ↘ = -50 to -10 % reduction inside MPAs → = -10 to 10 % change inside MPAs; ↗ = 10 to 50 % increase inside MPAs and ↑ = over 50 % increase inside MPAs.

	Pondweeds			Blue mussel			Stoneworts			Fucus spp.			Furcellaria		
	1 - 10 ha	10 - 100 ha	> 100 ha	1 - 10 ha	10 - 100 ha	> 100 ha	1 - 10 ha	10 - 100 ha	> 100 ha	1 - 10 ha	10 - 100 ha	> 100 ha	1 - 10 ha	10 - 100 ha	> 100 ha
East Bothnian Bay	↑	↑	↑				↗	↗	↗						
East Bothnian Sea	→	→	↑	→	→	→	↗	↗	→	↘	↘	↘	↘	↘	↘
East Kvarken	→	→	→	→	→	↗	→	↗	↗	↘	↘	→	↘	↘	→
Finland	→	→	↗	→	→	→	→	↗	↗	↘	↘	→	↘	↘	→
West Bothnian Bay	→	→	→				→	→	→						
West Bothnian Sea	→	↘	↗	↗	↗	↘	→	→	↘	→	→	↓	→	→	↓
West Kvarken	↗	↗	↑	↗	↗	↘	→	→	↗	↘	↘	→	↘	↘	→
Sweden	→	↘	↗	↗	↗	↘	→	→	→	→	→	↘	→	→	↘
Project area	→	→	↗	→	→	↘	→	→	↗	↘	↘	→	↘	↘	→

Table 4.4.1. Connectivity indices, H (Harary index), LCP (Landscape coincidence probability) and IIC (Integral index of connectivity) for the project area for the reference period (white) and for the future period (green).

	Stoneworts		Furcellaria		Blue mussel		Pondweeds		Fucus ssp.	
H	23027	43426	279	24046	30993	1549	4065	-	6160	13340
LCP	0,199	0,170	0,141	0,905	0,412	0,064	0,279	-	0,206	0,819
IIC	0,061	0,038	0,115	0,368	0,204	0,026	0,084	-	0,075	0,537

Table 4.5.1. The percentage of protection of the best 25 % of the patches that contribute most to habitat connectivity and availability in the landscape expressed as the *d*IIC*k* values partitioned *d*IICintra*k* (Intra), *d*IICflux*k* (Flux) and *d*IICconnect*k* (Connect). Values calculated for the reference period (white) period and the future period (green).

	Stoneworts						Furcellaria						Blue mussel						Pondweeds						Fucus spp.					
	Intra		Flux		Connect		Intra		Flux		Connect		Intra		Flux		Connect		Intra		Flux		Connect		Intra		Flux		Connect	
East Bothnian Bay	37	45	38	46	31	45													0	x	0	x	0	x						
East Bothnian Sea	24	37	9	50	0	15	33	17	37	15	18	19	7	100	9	100	11	0	30	x	21	x	25	x	33	17	35	22	39	11
East Kvarken	40	46	37	45	28	40	29	52	0	53	0	59	32	32	36	38	27	34	68	x	74	x	77	x	69	49	79	60	76	46
Finland	38	45	37	46	27	41	32	34	35	35	17	40	18	88	18	87	19	14	55	x	64	x	62	x	49	38	54	42	55	30
West Bothnian Bay	5	12	0	22	17	9													0	x	0	x	0	x						
West Bothnian Sea	23	21	44	26	11	16	0	18	0	83	0	8	5	21	50	31	3	21	27	x	38	x	18	x	14	7	0	83	10	4
West Kvarken	37	40	39	38	30	46	0	64	0	100	0	44	40	50	0	60	34	50	8	x	0	x	12	x	100	100	0	50	0	100
Sweden	24	27	37	32	19	27	0	25	0	83	0	17	24	34	5	43	23	36	18	x	31	x	14	x	23	14	0	83	10	9

both *Fucus* spp. and *F. lumbricalis* are well protected. In the West Bothnian Sea only the size class over 100 ha patches are well protected today, and even those are predicted to be located outside of MPAs in the future, when the climate change changes species distributions.

The protection of the large patches will improve for pondweeds and stoneworts in the future (Table 4.3.2). The protection of blue mussels will not change in Finland, but in Sweden the larger patches will mainly be outside of the MPAs while more of the smaller patches will be inside MPAs in the future. For *Fucus* spp. and *F. lumbricalis* the level of protection will decline. The climate change is predicted to increase their potential area of distribution, and because most of the increase will take place outside of MPAs, a smaller proportion of the large patches will be protected.

4.4. Connectivity of the study species

The connectivity in the project area varies between the different study species. The results from Conefor suggest that the connectivity in the future might decrease for stoneworts and blue musses (Table 4.4.1) while increasing for *Furcellaria lumbricalis* and *Fucus* spp. It was not possible to analyse the future connectivity of pondweeds due to computational challenges caused by the high number and complex shapes of areas predicted suitable for them in the future. However, because the species distribution models predict a significant increase in the areas potentially suitable for pondweeds in the future, the connectivity for pondweeds is also expected to increase in the future.

4.5. Patch contribution to connectivity in relation to protected areas

The protection of the habitat patches that are most important for the habitat network varies depending on the seascape and species (Table 4.5.1). In Finland the MPAs cover the most important habitat patches (in terms of the different indices of connectivity) better than in Sweden. The protection of the most important habitat patches is relatively better in the Kvarken area compared to the surrounding seascapes. On the scale of the whole project area the blue mussel is the only species for which only a very small proportion of the most important habitat patches are covered by MPAs. The areas potentially suitable for pondweeds are poorly protected in the Bothnian Bay and in Sweden. *Furcellaria lumbricalis* is poorly protected in Sweden. Stoneworts are relatively better protected if all the parts of connectivity (Intra, Flux and Connect) are considered.

Table 4.5.2. Relative changes of the most important habitat patches for the habitat network inside MPAs. ↓ = more than 50% reduction inside MPAs; ↘ = -50 to -10% reduction inside MPAs → = -10 to 10% change inside MPAs; ↗ = 10 to 50% increase inside MPAs and ↑ = over 50% increase inside MPAs. The variation in the protection of the best 25% of the patches that more contribute to habitat connectivity and availability in the landscape expressed as the *d*IIC*k* values partitioned to *d*IICintra*k* (Intra), *d*IICflux*k* (Flux) and *d*IICconnect*k* (Connect).

	Stoneworts			Blue mussel			Furcellaria			Fucus		
	Intra	Flux	Connect	Intra	Flux	Connect	Intra	Flux	Connect	Intra	Flux	Connect
East Bothnian Bay	→	→	↗									
East Bothnian Sea	↗	↗	↗	↑	↑	↘	↘	↘	→	↘	↘	↘
East Kvarken	→	→	↗	→	→	→	↗	↘	↑	↘	↘	↘
Finland	→	→	↗	↑	↑	→	→	↘	↗	↘	↘	↘
West Bothnian Bay	→	↗	→									
West Bothnian Sea	→	↘	→	↗	↘	↗	↗	↑	→	→	↑	→
West Kvarken	→	→	↗	→	↑	↗	↑	↑	↗	→	↗	↑
Sweden	→	→	→	→	↗	↗	↗	↑	↗	→	↑	→
Project area	→	↗	→	↑	↑	→	→	↗	↗	↘	↗	↘

Climate change will probably have different kinds of impacts on the different study species and seascapes (Table 4.5.2). In general, protection of the study species will be better in Sweden than in Finland if the climate will change as predicted under the climate scenario RCP 8.5. The main negative impacts will be on *Fucus* spp. and *F. lumbricalis* in Finland, even though these species are predicted to increase under the chosen future scenarios. The negative impact is caused by the spatial mismatch between modelled occurrence patches and the present MPAs. The complexity of the modelled pondweed distribution made it impossible to calculate results with the available computing power and time. It is not possible to do a subjective estimation of a probable output, but pondweeds are predicted to increase a lot and be very common in the future, which suggests a good connectivity. In such case, protection would not be as important as today for the connectivity for pondweeds because they will become very common in the project area. Then other aspects such representativity should have a higher priority.

4.6. The degree of spreading

The new connectivity index developed in this project, called the degree of spreading, is highest for the blue mussel in the reference period, but the decline predicted by the future species distribution models results in a decrease also in the degree of spreading. Blue mussels would then have to spread longer distances outside suitable habitats to reach all the habitat patches. Values under 50 % in the Table 4.6.1 probably represent naturally more fragmented seascapes and might need more attention to explore the conditions for connectivity. In the future, if the habitat patches suitable for the species in these areas will shrink, important parts of the habitat network become even more important. The species and seascapes that have a degree of spreading value below 50 percent are pondweeds in the East Bothnian Bay and in Sweden, stoneworts in the West Bothnian Sea and *Furcellaria lumbricalis* in the Kvarken area and in Sweden.

All the study species except for the blue mussel will get a higher degree of spreading in the future. However, because of uncertainties in the future species distribution models the increases in connectivity are not necessary as large as presented below (Table 4.6.1). There were also some problems with the analyses that may have some influence on the future values. This is because some of the habitat patches were very large and complex and therefore difficult to process.

4.7. The degree of spreading in relation to protected areas

The degree of spreading can be used as a proxy for conditions for connectivity and for studying how

Table 4.6.1. Degree of spreading for the reference period (white) and for the future period (green). The values are the percentage of the link between habitat patches that are inside habitat patches related to the whole link extent between two habitat patches. The links between habitat patches follow the water mask and are calculated from a geometrical centre of the habitat patch that have to be inside the habitat patch.

reference / future	Stoneworts		Pondweeds		Blue mussel		Furcellaria		Fucus	
East Bothnian Bay	57	78	9	97						
East Bothnian Sea	44	42	57	97	96	55	47	94	88	94
East Kvarken	75	80	55	97	96	67	26	97	86	97
Finland	70	77	52	97	96	60	60	95	87	95
West Bothnian Bay	45	68	34	97						
West Bothnian Sea	29	56	34	84	51	33	7	64	54	64
West Kvarken	70	84	22	98	77	38		54	40	54
Sweden	48	69	31	94	70	35	7	61	52	61
Project area	64	74	43	96	91	48	31	92	79	92

Table 4.7.1. The degree of spreading in the reference period (white) and the future period (green). The values are the percentage of the link between habitat patches that are inside habitat patches inside and outside the MPAs. The links between habitat patch follow the water mask.

reference / future	MPA	Stoneworts		Pondweeds		Blue mussel		Furcellaria		Fucus	
East Bothnian Bay	inside	59	78	3	96						
	outside	55	78	16	99						
East Bothnian Sea	inside	24	34	26	98	91	41	43	100	93	99
	outside	48	53	65	93	97	57	50	88	75	96
East Kvarken	inside	72	81	58	98	98	82	24	98	89	99
	outside	77	78	46	90	92	57	31	97	49	84
Finland	inside	70	77	53	97	97	71	37	98	91	99
	outside	71	76	51	96	96	57	47	91	69	93
West Bothnian Bay	inside	21	61	12	99						
	outside	46	68	35	97						
West Bothnian Sea	inside	55	82	52	98	92	58	0	69	65	52
	outside	24	51	32	78	39	28	8	64	52	67
West Kvarken	inside	69	82	14	97	72	49	0	61	41	44
	outside	71	86	29	98	84	27	0	33	0	10
Sweden	inside	63	81	27	97	74	52	0	62	53	46
	outside	43	65	32	93	66	28	8	60	51	61
Project area	inside	68	78	49	97	92	60	37	96	88	99
	outside	60	71	39	94	91	44	28	86	59	86

well the MPAs cover areas where species have good conditions for spreading. The Table 4.7.1 shows that *Furcellaria lumbricalis* has better conditions for spreading outside MPAs than inside MPAs in the project area. Pondweeds have only a small portion of the seascape with favorable conditions for spreading inside MPAs in the Bothnian Bay and in the Swedish sea zones. In other words, the areas where conditions for spreading are good for pondweeds are not covered by MPAs and therefore the areas with high connectivity are not protected.

5. Discussion

5.1. Connectivity on a large spatiotemporal scale

The conditions for connectivity vary in the project area on a large spatiotemporal scale. Figure 11 illustrates a summary of the natural conditions for connectivity on the scale of the six seascapes in the project area. The Kvarken area has the best natural conditions for connectivity within the project area and the West Bothnian Sea has the worst. This means that efforts to protect and conserve the existing habitat patches are very important for the resilience of species in the West Bothnian Sea. Based on the results of this study, the Kvarken area seems to be a naturally well connected and resilient seascape. In the management of the other seascapes, the Bothnian Bay and the East Bothnian Sea, focus should be on a combination of considering connectivity and also protecting larger areas. The areas that have the highest modelled occurrence probability of the studied species overlap in many places with the areas with high potential connectivity. This highlights the importance of the shallow parts of Kvarken for both species diversity and the maintenance of resilient metapopulations.

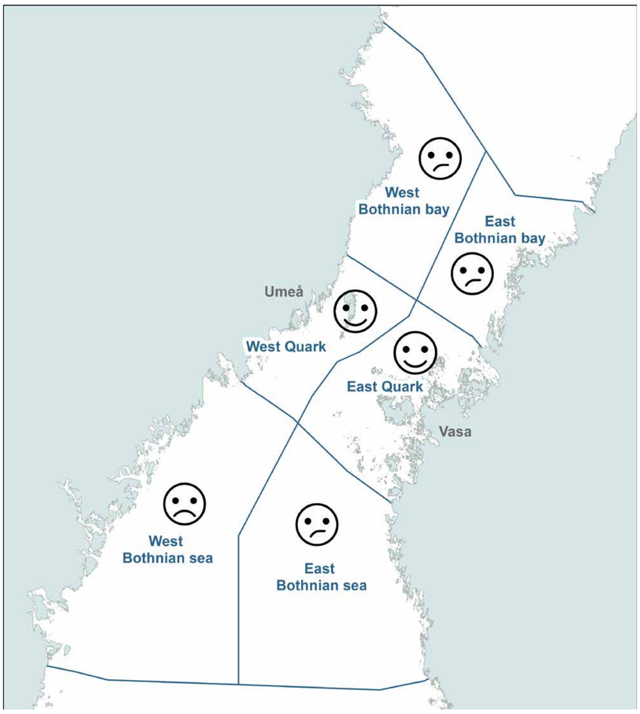


Figure 11. Compilation of the conditions for connectivity on a large spatiotemporal scale.

5.2. The degree of spreading

The different approaches to examine conditions for connectivity yield information on regional level and on medium to large temporal scale. The index results from the network analysis showed that the overall connectivity will increase for *Fucus* spp. and *Furcellaria lumbricalis*. Stoneworts will not have any considerable decrease of connectivity, whereas the blue mussel will have a decrease of connectivity as result of the climate change.

The degree of spreading gives a tool for finding seascapes that should be prioritized in the allocation of new MPAs so that they can be placed in seascapes where species have naturally better conditions for spreading and that are therefore probably more resilient. The values of degree of spreading inside versus outside MPAs can help in prioritizing seascapes and focusing the planning and allocation of new MAPs. The degree of spreading gives complementary information to the common network analysis by helping in identifying seascapes where spreading is easier. The index also gives spatial information about the possibilities to spread to all the connected habitat patches because the form and direction and the presence of land in relation to other habitat patches is considered. The results showed that for some species the modelled habitat patches are placed in a pattern that improves the spreading of the species across the seascape. In the project area all the studied species have at least 30 % of the links inside habitat patches. The analysis based on the future species distribution models suggests that the degree of spreading will increase for the studied species, but these results, as well as all future predictions, must be viewed with caution because of the uncertainties of the future models.

5.3. Species distribution and MPAs

The protection objectives set by the County Administrative Boards for the Gulf of Bothnia (Länsstyrelserna 2021) for most of the study species are currently not met. Analysis based on the species distribution models predict that meeting the objectives is also difficult under the projected future climate. It has to be kept in mind that the modelled species distributions are uncertain and specific to the used climate and nutrient scenarios. However, the modelled potentially suitable areas in the reference period and in the future serve as a useful proxy for species occurrences, and it is therefore interesting to compare the proportion of these areas inside MPAs now and in the future to the protection objectives. The results suggest that the soft bottom animals Baltic clam and chironomids are the only species for which the protection objectives are met in both countries, Finland and Sweden, and in both time periods, reference and future. These species have a low protection objective of 10 %, which is the same for all soft-bottom fauna, and they are common and resilient and have a high level of connectivity.

The protection objective for the blue mussel is set to 50 %, and based on the species distribution models, it seems like it could be already met in Sweden. However, this is not the case in reality, as it is estimated that the goal is not reached yet (Länsstyrelserna 2021). This difference demonstrates that the modelled potentially suitable habitats are not the same thing as realized species occurrences, and that the areas predicted suitable by the models are inevitably overestimated, because bottom substrate is not included in any of the models.

None of the plant or algae species seem to meet the protection objectives in the Swedish side of the project area at the moment. In the Finnish side, more than 50 % of the potentially suitable areas for *Fucus* spp. are located inside MPAs, meaning that the target might be reached already. In the future, this proportion will drop if *Fucus* spp. will increase, but that is hardly a concern, if Fucus spp. really would increase and the decrease in proportion of protected habitats would be caused by most of the increase taking place outside of protected areas. For pondweeds the low proportion of protected habitats compared to protection objective is probably caused by their very large modelled area of distribution. *Furcellaria lumbricalis* has almost an opposite case - it is not very abundant, but habitats potentially suitable for it are often modelled to be inside protected areas, and as the target for this species is also relatively low (30 %), the protection objective seems to be almost met. However, in the future, most of the predicted growth in areas suitable for *F. lumbricalis* takes place outside of protected areas, making it seem like the protection objective would be further away than in the reference period.

Finally, it has to be kept in mind that all these results are based on the modelled present and future species distributions and the network of MPAs that exist today. There will most likely be new MPAs in the coming years since the EU Green Deal aims at 30% protection of marina areas until 2030 (European Commission 2020), and if they are well placed, the proportion of protected occurrences of different species will be improved from what has been estimated here. Indeed, it is one of the aims of this project to provide information and predictions that could be used in efficient marine spatial planning and conservation.

5.4. Resilience

One of the aims of this report was to study how the large and cohesive areas important for population viability and connectivity are protected now and in the future. This aspect gives a proxy for how resilient the different areas are in the defined seascapes. The largest habitat patches of both *Fucus* spp. and *Furcellaria lumbricalis* are protected in the reference period, but the protection level decreases in the future based on the species distribution models. However, this is only because most of the predicted increase occurs outside of protected areas, leading to a decline in the proportion of protected patches. In other words, only the proportion declines, not the absolute number of protected large habitat patches. The proportion of protected large patches of pondweeds is low in the Bothnian Bay and the Bothnian Sea but might increase moderately in the future. In the Bothnian Sea the big areas of blue mussel are not well protected and under the future scenario RCP 8.5 the situation is not expected to improve. Stoneworts have a relatively good protection of the big cohesive areas in Finland and in the future the protection is expected to remain on a similar level. In Sweden the big cohesive areas of stoneworts are poorly protected in the reference period and in the future. The situation is worst in the West Bothnian Bay and the best is in the West Kvarken.

Including large and cohesive areas in the MPA network should be considered when planning coming MPAs. Efforts should be taken to find these areas, for example using the results of regional or local habitat models, and include them in the MPAs network. Due to the uncertainty of the models and especially due to the lack of information on bottom substrate also other methods could be used. Methods such as marine remote sensing based on satellite imagery can help to identify big cohesive areas with vegetation in shallow seascapes. Remote sensing on a more detailed scale, e.g. drone imagery, and field data can help to get the information necessary to differentiate species and identify these important areas (Rowan & Kalacska 2021). The results of this project can be used when identifying seascapes where connectivity is low and which would need more attention when future MPAs are allocated and prioritized.

The protection of the important habitat patches for connectivity as a partition of the IIC index in form of Intra (size), Flux (flow) and Connect (stepping stone character) gives a good idea of how the relative medium spatiotemporal scale connectivity is protected. The level of protection is low in the West Bothnian Sea and relatively higher in Kvarken, but there is also variation between the different species. In the future, under the chosen future scenario, the level of protection of the most important habitat patches seems to increase for all species and seascapes except for *Fucus* spp. in Finland.

The results from the analysis of the habitat patches important for connectivity can be used to prioritize the seascapes that have needs for improvement. For a smaller scale evaluation, better regional or local species distribution models are recommended as an input for better network analysis. The goal should be then to try to identify habitat patches that have relevant connectivity function, e.g. stepping stone or bottleneck habitat patches, to ensure that these are not threatened and evaluate possible protection efforts of them.

6. Conclusions

The project area has diverse seascapes with different characteristics from the vast shallow areas of the Kvarken archipelago to the deep and steep areas of the High Coast. The natural conditions for connectivity and level of protection vary as well. Nonetheless, some general conclusions can be made. The protection level of the studied species meets neither the Aichi target nor the EU Green Deal (European Commission 2020) in all of the parts of the project area. Parts of the project area can be described as a naturally fragmented seascape and need special attention to secure the existing connectivity. The West Bothnian Sea seems to be the most fragmented seascape and needs most attention regarding connectivity. The Bothnian Bay and the East Bothnian Sea have better conditions for connectivity but special attention on connectivity is still needed in the planning of new MPAs. Kvarken is the best part of the project area in terms of connectivity, and probably naturally more resilient than the other seascapes. Populations in the Kvarken area probably function as sources to populations in the surrounding seascapes in the project area. This characteristic should be taken in account in the planning of new MPAs and focus should be on protecting large areas with high biodiversity. The results of the different analyses give a more complex picture of how the conditions for connectivity and level of protection look like. The results can be used to prioritize and plan future MPAs in the project area. The methods used in this study can be applied to other areas and the results can be compared.

The goal of the project was to produce new material on how climate change might affect the project area in the next 100 years. There are no previous predictions on the effects of climate change on species distributions, ecosystem services or connectivity for the whole area. The produced material is meant to be used in climate adaptation and societal planning as well as by the public. Predictions of the effects of climate change on the sea can help in planning how to adapt to the possible changes and to help understand which areas might be especially important for species and ecosystems in the future, also from a conservation perspective. More information about the changes in environmental parameters and species distribution as well as on future changes in ecosystem services can be found in ECOnnect report *Future climate and species distribution models for the central Gulf of Bothnia* and ECOnnect report *Ecosystem services in the central Gulf of Bothnia*.

References

Amos, J.N., Bennett, A.F., Mac Nally, R., Newell, G., Pavlova, A., Radford, J.Q., Thomson, J.R., White, M. & Sunnucks, P. 2012. Predicting landscape-genetic consequences of habitat loss, fragmentation and mobility for multiple species of woodland birds. PLoS ONE, 7, e30888.

Alagador, D., Trivino, M., Cerdeira, J. O., Brás, R., Cabeza, M., & Araújo, M. B. 2012. Linking like with like: optimising connectivity between environmentally-similar habitats. Landscape Ecology 27, 291-301.

Altartouri, A., Nurminen, L., & Jolma, A. 2015. Spatial neighborhood effect and scale issues in the calibration and validation of a dynamic model of Phragmites australis distribution–A cellular automata and machine learning approach. Environmental Modelling & Software 71, 15-29.

Andersson A., Meier, H.E.M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., Eilola, K., Legrand, C., Figueroa, D., Paczkowska, J., Lindehoff, E., Tysklind, M. & Elmgren, R. 2015. Projected future climate change and Baltic Sea ecosystem management. AMBIO 44:345–356. doi: 10.1007/s13280-015-0654-8

Becquet, V., Lasota, R., Pante, E., Sokolowski, A., Wolowicz, M., & Garcia, P. 2013). Effects of fine-scale environmental heterogeneity on local genetic structure in Macoma balthica from the Gulf of Gdañsk (southern Baltic Sea). Hydrobiologia 714(1), 61-70.

Belkin, I. M. (2009). Rapid warming of large marine ecosystems. Progress in Oceanography 81(1-4), 207-213.

Berglund, J., Mattila, J., Rönnberg, O., Heikkilä, J., & Bonsdorff, E. 2003. Seasonal and inter-annual variation in occurrence and biomass of rooted macrophytes and drift algae in shallow bays. Estuarine, coastal and shelf science 56(5-6), 1167-1175.

Berglund, M., Jacobi, M. N., & Jonsson, P. R. 2012. Optimal selection of marine protected areas based on connectivity and habitat quality. Ecological Modelling 240, 105-112.

Bergström, L., & Bergström, U. 1999. Species diversity and distribution of aquatic macrophytes in the Northern Quark, Baltic Sea. Nordic Journal of Botany 19(3), 375-383.

Bergström, L., Bruno, E., Eklund, B., & Kautsky, L. 2003. Reproductive strategies of Ceramium tenuicorne near its inner limit in the brackish Baltic Sea. Botanica Marina 46(2).

Bergström L. 2005. Macroalgae in the Baltic Sea – responses to low salinity and nutrient enrichment in Ceramium and *Fucus*. Doctoral Thesis, Dept of Ecology and Environmental Science, Umeå University

Bergström, L., Tatarenkov, A., Johannesson, K., Jönsson, R. B., & Kautsky, L. 2005. Genetic and morphological identification of *Fucus radicans* sp. nov. (Fucales, Phaeophycae) in the brackish Baltic Sea 1. Journal of Phycology 41(5), 1025-1038.

Berkström C., Sacre E., & Bergström U. 2022. Ecological connectivity in marine protected areas in Swedish Baltic coastal waters - A coherence assessment. Aqua Reports: 2022:11. Sveriges lantbruksuniversitet, Institutionen för akvatiska resurser, Öregrund, Drottningholm, Lysekil.

Berkström C., Wennerström L. & Bergström U. 2019. Ekologisk konnektivitet i svenska vatten. En kunskapssammanställning. Aqua Reports: 2019:15. Sveriges lantbruksuniversitet, institutionen för akvatiska resurser, Öregrund, Drottningholm, Lysekil.

Berkström, C., Lindborg R., Thyresson, M. & Gullström, M. 2013. Assessing connectivity in a tropical embayment: Fish migrations and seascape ecology. Biological Conservation 166:43–53. doi: 10.1016/j.biocon.2013.06.013

Bick, A., & Burckhardt, R. 1989. Erstnachweis von *Marenzelleria viridis* (Polychaeta, Spionidae) für den Ostseeraum, mit einem Bestimmungsschlüssel der Spioniden der Ostsee. Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologisches Museum und Institut für Spezielle Zoologie (Berlin), 65(2), 237-247.

Bitušík, P., Svitok, M., Novikmec, M., Trnková, K., & Hamerlík, L. 2017. A unique way of passive dispersal of aquatic invertebrates by wind: Chironomid larvae are traveling in fragments of aquatic mosses. Limnologica 63, 119-121.

Breilin, O., Kotilainen, A., Nenonen, K. & Rasanen, M. 2005. The unique moraine morphology, stratotypes and ongoing geological processes at the Kvarken Archipelago on the land uplift area in the western coast of Finland. Special paper of the Geological Survey of Finland 40, 97.

Carr, M.H., Robinson, S.P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacker, E.J. & Williams, M. 2017. The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. Aquatic Conservation: Marine and Freshwater Ecosystems 27, 6–29. doi: 10.1002/aqc.2800

Carroll JM, Peterson BJ. 2013. Ecological trade-offs in seascape ecology: Bay scallop survival and growth across a seagrass seascape. Landscape Ecology 28: 1401–1413.

Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W.J. Gutowski, T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A.J. Weaver & M. Wehner, 2013: Long-term Climate Change: Projections, Commitments and Irreversibility. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Coolen, J.W.P., Boon, A.R., Crooijmans, R., Pelt, H., Kleissen, F., Gerla, D., Beermann, J., Birchenough, S.N.R., Becking, L.E. & Luttikhuizen, P.C. 2020. Marine stepping-stones: Connectivity of *Mytilus edulis* populations between offshore energy installations. Molecular Ecology 29, 686–703. doi: 10.1111/mec.15364

Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M. & Johnston, E.L. 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. Frontiers in Ecology and the Environment 13, 82–90. doi: 10.1890/140050

Danley, B. & Widmark, C. 2016. Evaluating conceptual definitions of ecosystem services and their implications. Ecological Economics 7.

Donaldi, S., Bergström L., Berglund J.M.B., Bäck, A., Mikkola, R., Saarinen, A. & Bergström U. 2020. Perch and pike recruitment in coastal bays limited by stickleback predation and environmental forcing. Estuarine, Coastal and Shelf Science. 246.1-11

Eilola, K., Meier, HEM., & Almroth, E. 2009. On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. J. Mar. Syst. 75, 163–184. doi: 10.1016/j.jmarsys.2008.08.009.

Elith, J., Leathwick, JR. & Hastie, T. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77, 802–813.

European Commission (2020). EU Biodiversity Strategy for 2030 - Bringing nature back into our lives. Brussels, 20.5.2020

Félix-Hackradt, F. C., Hackradt, C. W., Treviño-Otón, J., Pérez-Ruzafa, Á. & García-Charton, J. A. 2018. Effect of marine protected areas on distinct fish life-history stages. Marine environmental research 140, 200-209

Fér, T., & Hroudova, Z. 2009. Genetic diversity and dispersal of Phragmites australis in a small river system. Aquatic Botany 90(2), 165-171.

Fischer J., Lindenmayer, D.B. & Fazey, I. 2004. Appreciating Ecological Complexity: Habitat Contours as a Conceptual Landscape Model. Conservation Biology 18:1245–1253. doi: 10.1111/j.1523-1739.2004.00263.x

Floeter, S.R. & Gasparini, J.L. 2001. Brazilian endemic reef fishes. Coral Reefs 19, 292–292.

Florin, A.-B., Sundblad, G. & Bergström, U. 2009. Characterisation of juvenile flatfish habitats in the Baltic Sea. Estuarine, Coastal and Shelf Science 82, 294–300. doi: 10.1016/j.ecss.2009.01.012

Forman, R.T.T. 1995. Some general principles of landscape and regional ecology. Landscape Ecology 10, 133–142. doi: 10.1007/BF00133027

Forslund, H., Eriksson, O., & Kautsky, L. 2012. Grazing and geographic range of the Baltic seaweed *Fucus radicans* (Phaeophyceae). Marine Biology Research 8(4), 322-330.

Fowler, A.M., Jørgensen, A.-M., Coolen, J.W.P., Jones, D.O.B., Svendsen, J.C., Brabant, R., Rumes, B. & Degraer, S. 2020. The ecology of infrastructure decommissioning in the North Sea: what we need to know and how to achieve it. ICES Journal of Marine Science 77:1109–1126. doi: 10.1093/icesjms/fsz143

Franklin, A. B., Noon, B. R., & George, T. L. 2002. What is habitat fragmentation? Studies in avian biology 25, 20-29.

Franklin, J.F., & Lindenmayer, D.B. 2009. Importance of matrix habitats in maintaining biological diversity. Proceedings of the National Academy of Sciences 106:349–350. doi: 10.1073/pnas.0812016105

Gaggiotti, O.E. 1996. Population Genetic Models of Source–Sink Metapopulations. Theoretical Population Biology 50:178–208. doi: 10.1006/tpbi.1996.0028

Gogina, M., Nygård, H., Blomqvist, M., Daunys, D., Josefson, A. B., Kotta, J., Maximov A., Warzocha J., Yermakov V., Gräwe U. & Zettler, M. L. 2016. The Baltic Sea scale inventory of benthic faunal communities. ICES Journal of Marine Science 73(4), 1196-1213.

Guban, P., Wennerström, L., Elfwing, T., Sundelin, B., & Laikre, L. 2015. Genetic diversity in Monoporeia affinis at polluted and reference sites of the Baltic Bothnian Bay. Marine pollution bulletin 93(1-2), 245-249.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., & Townshend, J.R. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052. doi: 10.1126/sciadv.1500052

Hansen, J. P., Wikström, S. A., Axemar, H., & Kautsky, L. 2011. Distribution differences and active habitat choices of invertebrates between macrophytes of different morphological complexity. Aquatic Ecology 45(1), 11-22

Hansen, J.P., Sundblad, G., Bergström, U., Austin, Å.N., Donadi, S., Eriksson, B.K., & Eklöf, J.S. 2019. Recreational boating degrades vegetation important for fish recruitment. Ambio 48:539–551. doi: 10.1007/s13280-018-1088-x

Hanski, I. 1998. Metapopulation dynamics. Nature 396, 41–49. doi: 10.1038/23876

Hanski, I., & Simberloff, D. 1997. The Metapopulation Approach, Its History, Conceptual Domain, and Application to Conservation. In: Metapopulation Biology. Elsevier, pp 5–26.

Heckwolf, M.J., Peterson, A., Jänes, H., Horne, P., Künne, J., Liversage, K., Sajeva, M., Reusch, T.B.H., & Kotta, J. 2021. From ecosystems to socio-economic benefits: A systematic review of coastal ecosystem services in the Baltic Sea. Science of The Total Environment 755:142565. doi: 10.1016/j.scitotenv.2020.142565

HELCOM & Baltic Earth. 2021. Climate Change in the Baltic Sea. 2021 Fact Sheet. Baltic Sea Environment Proceedings n°180. HELCOM/Baltic Earth 2021.

HELCOM. 2020. First draft of the updated BSAP. Retrieved 5.3.2021 from: https://helcom.fi/first-draft-of-the-updated-baltic-sea-action-plan-is-unveiled-to-helcom-decision-makers-at-hod-59-2020/

HELCOM. 2018a. HELCOM Thematic assessment of biodiversity 2011-2016. Baltic Sea Environment Proceedings No. 158. Retrieved 21.4.2021 from: http://stateofthebalticsea.helcom.fi/wp-content/uploads/2019/09/BSEP158-Biodiversity.pdf

HELCOM. 2018b. Implementation of the Baltic Sea Action Plan 2018: Three years left to reach good environmental status. Retrieved 5.3.2021 from: https://helcom.fi/wp-content/uploads/2019/06/Implementation-of-the-BSAP-2018.pdf

HELCOM. 2017. First version of the 'State of the Baltic Sea' report - June 2017 - to be updated in 2018. Retrieved 5.3.2021 from: http://stateofthebalticsea.helcom.fi/wp-content/uploads/2017/07/HELCOM_State-of-the-Baltic-Sea_First-version-2017.pdf

HELCOM. 2013a. Climate change in the Baltic Sea area: HELCOM thematic assessment in 2013. Balt. Sea Environ. Proc. No. 137

HELCOM. 2013b. HELCOM Monitoring and Assessment Strategy. 2013 HELCOM Ministerial Declaration. Retrieved 5.3.2022 from: https://helcom.fi/wp-content/uploads/2020/02/Monitoring-and-assessment-strategy.pdf

HELCOM. 2009. Biodiversity in the Baltic Sea – An integrated thematic assessment on biodiversity and nature conservation in the Baltic Sea. Balt. Sea Environ. Proc. No. 116B. Retrieved 2.3.2021 from: https://helcom.fi/wp-content/uploads/2019/08/BSEP116B.pdf

Heller, N.E. & Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142(1),14-32.

Hiddink, J.G. & Coleby, C. 2012. What is the effect of climate change on marine fish biodiversity in an area of low connectivity, the Baltic Sea?: Effect of climate change on fish biodiversity. Global Ecology and Biogeography 21:637–646. doi: 10.1111/j.1466-8238.2011.00696.x

Hodgson, J.A., Thomas, C.D., Wintle, B.A. & Moilanen, A. 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology 46:964–969. doi: 10.1111/j.1365-2664.2009.01695.x

Hodgson, J. A., Thomas, C. D., Dytham, C., Travis, J. M., & Cornell, S. J. 2012. The speed of range shifts in fragmented landscapes. PloS one, 7(10), e47141.

Hodgson, J.A., Wallis, D.W., Krishna, R. & Cornell, S.J. 2016. How to manipulate landscapes to improve the potential for range expansion. Methods in Ecology and Evolution 7, 1558–1566. doi: 10.1111/2041-210X.12614

Hyytiäinen, K., Bauer, B., Bly Joyce, K., Ehrnsten, E., Eilola, K., Gustafsson, B.G., Meier, H.E.M., Norkko, A., Saraiva, S., Tomczak, M. & Zandersen, M. 2021. Provision of aquatic ecosystem services as a consequence of societal changes: The case of the Baltic Sea. Population Ecology 63, 61–74. doi: 10.1002/1438-390X.12033

Jaatinen, K., Westerbom, M., Norkko, A., Mustonen, O., Koons, D. N. 2020. Detrimental impacts of climate change may be exacerbated by density-dependent population regulation in blue mussels. Journal of Animal Ecology, 00:1-12. DOI: 10.1111/1365-2656.13377

Jackson, E.L., Santos-Corujo, R.O. & Pittman S.J. 2017. Seascape Patch Dynamics. In: Seascape Ecology. eds: S.J. Pittman. John Wiley & Sons Ltd

Jenness, J. 2016. Conefor Inputs. http://www.jennessent.com/arcgis/conefor_inputs.htm. Accessed 28.4.2022

Johannesson, K., Smolarz, K., Grahn, M., & André, C. 2011. The future of Baltic Sea populations: local extinction or evolutionary rescue? Ambio 40(2), 179-190.

Jonsson, P. R., Kotta, J., Andersson, H. C., Herkül, K., Virtanen, E., Sandman, A. N., & Johannesson, K. 2018. High climate velocity and population fragmentation may constrain climate-driven range shift of the key habitat former *Fucus vesiculosus*. Diversity and Distributions 24(7), 892-905.

Jonsson, P. R., Hammar, L., Wåhlström, I., Pålsson, J., Hume, D., Almroth-Rosell, E., & Mattsson, M. 2021. Combining seascape connectivity with cumulative impact assessment in support of ecosystem-based marine spatial planning. Journal of Applied Ecology 58(3), 576-586.

Korpelainen, H., von Cräutlein, M., Kostamo, K., & Virtanen, V. 2013. Spatial genetic structure of aquatic bryophytes in a connected lake system. Plant Biology 15(3), 514-521.

Kauppi, L., Norkko, A., & Norkko, J. 2015. Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. Biological invasions 17(7), 2055-2074.

Kauppi, L., Norkko, A., & Norkko, J. 2018. Seasonal population dynamics of the invasive polychaete genus *Marenzelleria* spp. in contrasting soft-sediment habitats. Journal of Sea Research 131, 46-60

Kautsky, H., Martin, G., & Snoeijs-Leijonmalm, P. 2017. The phytobenthic zone. In Biological oceanography of the Baltic Sea (pp. 387-455). Springer, Dordrecht.

Kautsky, N. 1982. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic Mytilus edulis population. Marine Biology 68(2), 143-160.

Kautsky, L. & Kautsky, N. 2000. The Baltic Sea, including Bothnian Sea and Bothnian Bay. Chapter 8. In: Sheppar, C. Seas at the millennium: an environmental evaluation. Elsevier Science Amsterdam 1-3, 121-133.

Kiirikki, M., & Lehvo, A. 1999. Life strategies of filamentous algae in the northern Baltic Proper. Sarsia 82(3), 259-267.

King, R. A., Gornall, R. J., Preston, C. D., & Croft, J. M. 2002. Population differentiation of Potamogeton pectinatus in the Baltic Sea with reference to waterfowl dispersal. Molecular Ecology 11(10), 1947-1956

Korpelainen, H., von Cräutlein, M., Kostamo, K., & Virtanen, V. 2013. Spatial genetic structure of aquatic bryophytes in a connected lake system. Plant Biology 15(3), 514-521.

Kostamo, K., Korpelainen, H., & Olsson, S. 2012. Comparative study on the population genetics of the red algae *Furcellaria lumbricalis* occupying different salinity conditions. Marine Biology 159(3), 561-571.

Kotilainen, A. T., Kaskela, A. M., Bäck, S., & Leinikki, J. 2012. Submarine De Geer moraines in the Kvarken Archipelago, the Baltic Sea. In: *Seafloor Geomorphology as Benthic Habitat* (pp. 289-298). Elsevier.

Kovtun, A., Torn, K., Martin, G., Kullas, T., Kotta, J., & Suursaar, Ü. 2011. Influence of abiotic environmental conditions on spatial distribution of charophytes in the coastal waters of West Estonian Archipelago, Baltic Sea. Journal of Coastal Research, 412-416.

Kratzer, S., Brockmann, C., & Moore, G. 2008. Using MERIS full resolution data to monitor coastal waters — A case study from Himmerfjärden, a fjord-like bay in the northwestern Baltic Sea. Remote Sensing of Environment 112, 2284–2300. doi: 10.1016/j.rse.2007.10.006

Kraufvelin, P., Ruuskanen, A. T., Nappu, N., & Kiirikki, M. 2007. Winter colonisation and succession of filamentous macroalgae on artificial substrates and possible relationships to *Fucus vesiculosus* settlement in early summer. Estuarine, Coastal and Shelf Science 72(4), 665-674.

Krosby, M., Tewksbury, J., Haddad, N. M., & Hoekstra, J. 2010. Ecological connectivity for a changing climate. Conservation Biology 24(6), 1686-1689.

Lappalainen, J., Kurvinen, L., Kuismanen, L. 2020. Suomen ekologisesti merkittävät vedenlaiset mariluontoalueet (EMMA) – Finlands ekologiskt betydelsefulla marina undervattensmiljöer (EMMA). Suomen Ympäristökeskuksen rapporteja. 8. Suomen ympäristökeskus, Merikeskus.

Larsson, J., Lind, E. E., Corell, H., Grahn, M., Smolarz, K., & Lönn, M. 2017. Regional genetic differentiation in the blue mussel from the Baltic Sea area. Estuarine, Coastal and Shelf Science 195, 98-109.

Lehtomäki, J., & Moilanen, A. 2013. Methods and workflow for spatial conservation prioritization using Zonation. Environmental Modelling & Software 47, 128-137.

Leppäranta, M. & Myrberg, K. 2009. Physical Ocenaography of the Baltic Sea. Chapter 1. Springer-Praxis books in geophysical sciences, Springer, Berlin.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press.

Levins, R. 1969. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. Bulletin of the Entomological Society of America 15:237–240. doi: 10.1093/besa/15.3.237

Länsstyrelserna 2021. Plan för marint områdesskydd i Bottniska viken Regionala mål och prioriteringar.

Mackenzie, B.R., Gislason, H., Möllmann, C. & Köster, F.W. 2007. Impact of 21st century climate change on the Baltic Sea fish community and fisheries. Global Change Biol 13:1348–1367. doi: 10.1111/j.1365-2486.2007.01369.x

McRae, B.H., Dickson, B.G., Keitt, T.H., & Shah, V.B. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89, 2712–2724. doi: 10.1890/07-1861.1

Meier, H. E. M., Kniebusch, M., Dieterich, C., Gröger, M., Zorita, E., Elmgren, R., Myrberg, K., Ahola, M., Bartosova, A., Bonsdorff, E., Börgel, F., Capell, R., Carlén, I., Carlund, T., Carstensen, J., Christensen, O. B., Dierschke, V., Frauen, C., Frederiksen, M., Gaget, E., Galatius, A., Haapala, J. J., Halkka, A., Hugelius, G., Hünicke, B., Jaagus, J., Jüssi, M., Käyhkö, J., Kirchner, N., Kjellström, E., Kulinski, K., Lehmann, A., Lindström, G., May, W., Miller, P., Mohrholz, V., Müller-Karulis, B., Pavón-Jordán, D., Quante, M., Reckermann, M., Rutgersson, A., Savchuk, O. P., Stendel, M., Tuomi, L., Viitasalo, M., Weisse, R., and Zhang, W. 2021. Climate Change in the Baltic Sea Region: A Summary, Earth Syst. Dynam. Discuss. [preprint], https://doi.org/10.5194/esd-2021-67, in review.

Meier, H. E. M., Hordoir, R., Andersson, H.C., Dieterich, C., Eilola, K., Gustafsson, B.G., Höglund, A & Schimanke, S. 2012. Modeling the combined impact of changing climate andchanging nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961–2099. Climate Dynamics 39, 2421–2441.

Meier, H. E. M., Döscher, R., Coward, A. C., Nycander, J., & Döös, K. 1999. RCO - Rossby Centre Regional Ocean ClimateModel: Model Description (version1.0) and First Results From the Hindcast Period 1992/93. Reports Oceanography No. 26, SMHI, Norrköping.

Metzger, J.-P., & Décamps, H. 1997. The structural connectivity threshold: An hypothesis in conservation biology at the landscape scale. Acta Oecologica 18:1–12. doi: 10.1016/S1146-609X(97)80075-6

Moilanen, A., Franco, A. M., Early, R. I., Fox, R., Wintle, B., & Thomas, C. D. 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings of the Royal Society B: Biological Sciences 272(1575), 1885-1891.

Mooney, H., Larigauderie, A., Cesario, M., Elmquist, T., Hoegh-Guldberg, O., Lavorel, S., Mace, G.M., Palmer, M., Scholes, R., & Yahara, T. 2009. Biodiversity, climate change, and ecosystem services. Current Opinion in Environmental Sustainability 1:46–54. doi: 10.1016/j.cosust.2009.07.006

MPA FAC, 2017. Harnessing Ecological Spatial Connectivity for Effective Marine Protected Areas and Resilient Marine Ecosystems: SCIENTIFIC SYNTHESIS AND ACTION AGENDA Harnessing Ecological. Marine Protected Areas Federal Advisory Committee (MPA FAC). www.marineprotectedareas.noaa.gov/fac

Navenhand, J.N. 2012. How will ocean acidification affect Baltic Sea evosystems? An assessment of plausible impacts on key functional groups. AMBIO 41, 637-644.

Palumbi, S.R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. Ecological Applications 13, 146–158. doi: 10.1890/1051-0761(2003)013[0146:PGDCAT]2.0.CO;2

Peterson G., Allen, C.R. & Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1(1), 6-18.

Pittman SJ, McAlpine CA, Pittman KM (2004) Linking fish and prawns to their environment: a hierarchical landscape approach. Marine Ecology Progress Series 283: 233–254.

Pittman, S. (ed) 2017. Seascape ecology: taking landscape ecology into the sea. Wiley Blackwell, Hoboken, NJ.

Pittman, J.S., Davis B. & Santos-Corujo, O.S. 2017. Animal Movement through the Seascape: Intergrating Movement Ecology with Seascape Ecology. In: Seascape Ecology. eds: S.J. Pittman. John Wiley & Sons Ltd, Hoboken, NJ.

Pittman, S., Kneib, R., & Simenstad, C. 2011. Practicing coastal seascape ecology. Mar Ecol Prog Ser 427:187–190. doi: 10.3354/meps09139

Pittman, S., Yates, K., Bouchet, P., Alvarez-Berastegui, D., Andréfouët, S., Bell, S., Berkström, C., Boström, C., Brown, C., Connolly, R., Devillers, R., Eggleston, D., Gilby, B., Gullström, M., Halpern, B., Hidalgo, M., Holstein, D., Hovel, K., Huettmann, F., Jackson, E., James, W., Kellner, J., Kot, C., Lecours, V., Lepczyk, C., Nagelkerken, I., Nelson, J., Olds, A., Santos, R., Scales, K., Schneider, D., Schilling, H., Simenstad, C., Suthers, I., Treml, E., Wedding, L., Yates, P., & Young, M. 2021. Seascape ecology: identifying research priorities for an emerging ocean sustainability science. Mar Ecol Prog Ser 663:1–29. doi: 10.3354/meps13661

Poutanen, M. & Steffen, H. 2014. Land uplift at Kvarken Archipelago /High Coast UNESCO world heritage area. Geophysica 50(2), 49-64.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., & Brashares, J.S. 2008. Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci USA 105:20770. doi: 10.1073/pnas.0806080105

Pulliam, H.R., & Danielson B.J. 1991. Sources, Sinks, and Habitat Selection: A Landscape Perspective on Population Dynamics. The American Naturalist 137:S50–S66. doi: 10.1086/285139

Rayfield, B., Pelletier, D., Dumitru, M., Cardille, J.A., & Gonzalez, A. 2016. Multipurpose habitat networks for short-range and long-range connectivity: a new method combining graph and circuit connectivity. Methods in Ecology and Evolution 7, 222–231. doi: 10.1111/2041-210X.12470

Rinkineva, L. & Bader, P. 1998. Chapter 2.3 Den marina miljön in Kvarkens natur. Kvarkenrådets publikationer 10.

Rinne, H., Boström, M., Björklund, C., & Sahla, M. 2021. Functionality of HELCOM HUB classification in describing variation in rocky shore communities of the northern Baltic Sea. Estuarine, Coastal and Shelf Science 249, 107044.

Rinne, H., Salovius-Laurén, S., & Mattila, J. 2011. The occurrence and depth penetration of macroalgae along environmental gradients in the northern Baltic Sea. Estuarine, Coastal and Shelf Science 94(2), 182-191.

Roberts, C.M. 1997. Connectivity and Management of Caribbean Coral Reefs. Science 278, 1454–1457. doi: 10.1126/science.278.5342.1454

Rosenberg, D.K., Noon, B.R., & Meslow, E.C. 1997. Biological Corridors: Form, Function, and Efficacy. BioScience 47(10), 677-687.

Rowan, G.S.L. & Kalacska, M. A. 2021. Review of Remote Sensing of Submerged Aquatic Vegetation for Non-Specialists. Remote Sensing 13, 623. https://doi.org/10.3390/rs13040623

Saraiva, S., Meier, H. E. M., Andersson, H., Höglund, A., Dieterich, C., Gröger, M., Hordoir, R., Eilola, K. 2019. Uncertainties in Projections of the Baltic Sea Ecosystem Driven by an Ensemble of Global Climate Models. Frontiers in Earth Sciense 6, 244. doi: 10.3389/feart.2018.00244

Saura, S. & L. Pascual-Hortal. 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. Landscape and Urban Planning 83 (2-3), 91-103.

Saura, S. & Rubio, L. 2010. A common currency for the different way in which patches and links con contribute to habitat availability and connectivity in the landscape. Ecography 33, 523-537. doi: 10.1111/j.1600-0587.2009.05760.x

Saura, S. & J. Torné. 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software 24, 135-139.

SeaGIS2.0. https://seagis.cartesia.se/SMART/profile/28705a12-8b6f-46f0-a3b7-5aaf1613347f/f7a41b8b-409a-478d-aef4-cf3987f378e5/d8391aa2-3ff8-46cf-ac66-51ba4916eaef?language=sv. Accessed 26.4.2022.

Snickars, M., Sundblad, G., Sandström, A., Ljunggren, L., Bergström, U., Johansson, G., & Mattila, J. 2010. Habitat selectivity of substrate-spawning fish: modelling requirements for the Eurasian perch Perca fluviatilis. Mar Ecol Prog Ser 398, 235–243. doi: 10.3354/meps08313

Snickars, M., Weigel, B., & Bonsdorff, E. 2015. Impact of eutrophication and climate change on fish and zoobenthos in coastal waters of the Baltic Sea. Marine Biology 162, 141–151. doi: 10.1007/s00227-014-2579-3

Steinhardt, T., & Selig, U. 2007) Spatial distribution patterns and relationship between recent vegetation and diaspore bank of a brackish coastal lagoon on the southern Baltic Sea. Estuarine, Coastal and Shelf Science 74(1-2), 205-214.

Sundblad, G., Bergström, U. 2014. Shoreline development and degradation of coastal fish reproduction habitats. AMBIO 43, 1020–1028. doi: 10.1007/s13280-014-0522-y

Takolander, A., Cabeza, M., Leskinen, E. 2017. Climate change can cause complex responses in Baltic Sea macroalgae: a systematic review. Journal of Sea Research 123, 16-29.

Tatarenkov, A., Bergström, L., Jönsson, R. B., Serrão, E. A., Kautsky, L., & Johannesson, K. 2005. Intriguing asexual life in marginal populations of the brown seaweed *Fucus vesiculosus*. Molecular ecology 14(2), 647-651.

Tatarenkov, A., Jönsson, R. B., Kautsky, L., & Johannesson, K. 2007. Genetic structure in populations of *Fucus vesiculosus* (Phaeophyceae) over spatial scales from 10 m to 800 km. Journal of phycology 43(4), 675-685

Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. 1993. Connectivity is a vital element of landscape structure. Oikos 68(3), 571-573.

The Convention on Biological Diversity. 2021. Ecologically or Biologically Significant Marine Areas (EBSA). Retrieved 15.10.2021 from https://www.cbd.int/ebsa/.

Thiele, J., Buchholz, S., & Schirmel, J. 2018. Using resistance distance from circuit theory to model dispersal through habitat corridors. Journal of Plant Ecology 11, 385–393. doi: 10.1093/jpe/rtx004

Treml, E.A., & Kool, J. 2017. Networks for Quantifying and Analysing Seascape Connectivity. In: Seascape Ecology. eds: S.J. Pittman. John Wiley & Sons Ltd, Hoboken, NJTurner, M.G. 1989. Landscape Ecology: The Effect of Pattern on Process. Annual Review of Ecology and Systematics 20, 29.

Turner, M.G. 2005. Landscape Ecology in North America: Past, Present, and Future. Ecology 86, 1967–1974. doi: 10.1890/04-0890

UNESCO. 2021. United Nations Educational, Scientific and Cultural Organization. World Heritage Convention. High Coast / Kvarken Archipelago. Retrieved 31.5.2021 from: https://whc.unesco.org/en/list/898/

Ulrich, C., Hemmer-Hansen, J., Boje, J., Christensen, A., Hüssy, K., Sun, H., & Clausen, L.W. 2017. Variability and connectivity of plaice populations from the Eastern North Sea to the Baltic Sea, part II. Biological evidence of population mixing. Journal of Sea Research 120:13–23. doi: 10.1016/j.seares.2016.11.002

Viitasalo, M. & Bonsdorff, E. 2021. Global climate change and the Baltic Sea ecosystem: direct and indirect effects on species, communities and ecosystem functioning. Earth System Dynamics 13, 711–747.

Viitasalo, M., Kostamo, K., Hallanaro, E. L., Viljanmaa, W., Kiviluoto, S., Ekebom, J. & Blankett, P. 2017. Meren aarteet: löytöretki Suomen vedenalaiseen meriluontoon. Gaudeamus, 518.

Virtanen, E. A., Viitasalo, M., Lappalainen, J., & Moilanen, A. 2018. Evaluation, gap analysis, and potential expansion of the Finnish marine protected area network. Frontiers in Marine Science 5, 402.

Virtanen, E. A., Moilanen, A., & Viitasalo, M. 2020. Marine connectivity in spatial conservation planning: analogues from the terrestrial realm. Landscape Ecology 35(5), 1021-1034.

von Storch, H., Omstedt, A., Pawlak, J. & Reckermann, M. 2015. Introduction and Summary. Chapter 1. In: Second assessment of climate change for the Baltic Sea basin. The BACC II Author Team. Springer International Publishing, 1-22.

Wade, A.A., McKelvey, K.S., & Schwartz, M.K. 2015. Resistance-surface-based wildlife conservation connectivity modeling: Summary of efforts in the United States and guide for practitioners. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO

Waldeck, P. & Larsson, K. 2013. Effects of winter water temperature on mass loss in Baltic blue mussels: Implications for foraging sea ducks. Journal of Experimental Marine Biology and Ecology 444, 24-30.

Wennerström, L., Jansson, E., & Laikre, L. 2017. Baltic Sea genetic biodiversity: Current knowledge relating to conservation management. Aquatic Conservation: Marine and Freshwater Ecosystems 27(6), 1069-1090.

Westerbom, M., Kilpi, M., & Mustonen, O. 2002. Blue mussels, Mytilus edulis, at the edge of the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea. Marine Biology 140, 991–999.

Wikström, S. A. & Kautsky, L. 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuarine, Coastal and Shelf Science 72(1-2), 168-176.

Appendix

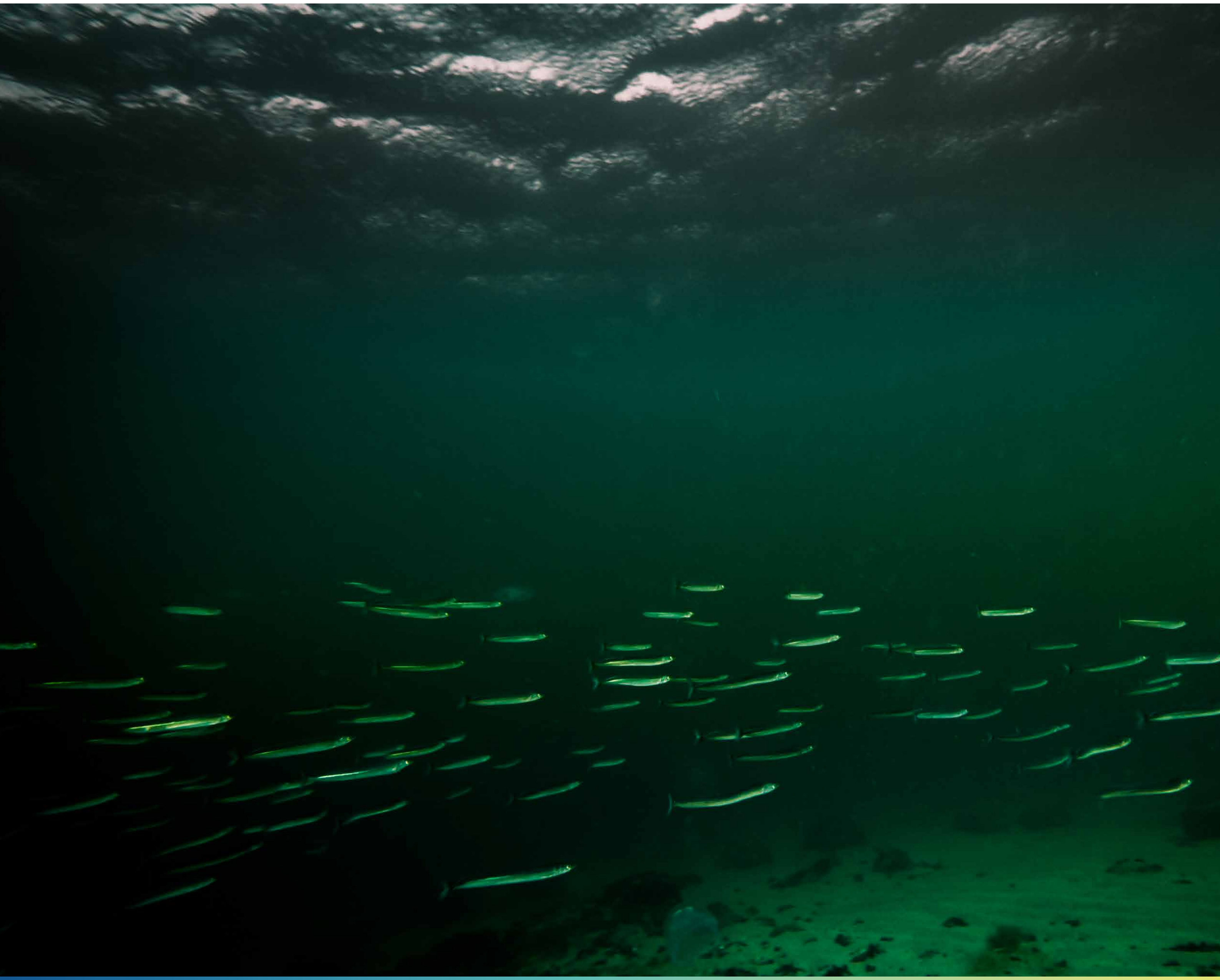
Table A1. Modelled areas of potentially suitable habitats for the study species in the reference period (1976-2005) and in the future (2070-2099) in the different sub-basins, in Sweden and Finland, and in the project area as a whole.

WBB=West Bothnian Bay, WK=West Kvarken, WBS=West Bothnian Sea, EBS=East Bothnian Sea, EK=East Kvarken, EBB=East Bothnian Bay. See Fig. 3 in the report for the sub-basins and the project area boundaries and section 3.2 in the report for the description of the study species.

Species	Time period	Measure and unit	WBB	WK	WBS	EBS	EK	EBB	Sweden	Finland	Project area
Filamentous annual algae	Reference	Area, km²	133	196	103	173	186	6	432	366	797
		Area inside MPAs, km²	6	93	19	55	137	4	118	196	314
		Area inside MPAs, %	5	47	18	32	74	70	27	54	39
	Future	Area, km²	345	157	206	864	1589	147	708	2600	3308
		Area inside MPAs, km²	9	67	28	175	803	68	104	1046	1151
		Area inside MPAs, %	3	43	14	20	51	46	15	40	35
Aquatic mosses	Reference	Area, km²	44	83	102	229	297	13	229	539	768
		Area inside MPAs, km²	0,4	35	24	97	190	6	60	292	351
		Area inside MPAs, %	1	43	24	42	64	41	26	54	46
	Future	Area, km²	298	384	293	607	1743	556	975	2906	3881
		Area inside MPAs, km²	10	151	36	154	811	239	196	1204	1400
		Area inside MPAs, %	3	39	12	25	47	43	20	41	36
Stoneworts	Reference	Area, km²	35	64	41	29	207	63	140	299	439
		Area inside MPAs, km²	1	23	5	3	72	18	29	93	122
		Area inside MPAs, %	4	35	12	9	35	29	21	31	28
	Future	Area, km²	33	59	53	15	170	69	146	254	400
		Area inside MPAs, km²	2	22	6	4	79	29	31	112	143
		Area inside MPAs, %	5	38	12	26	46	42	21	44	36

Species	Time period	Measure and unit	WBB	WK	WBS	EBS	EK	EBB	Sweden	Finland	Project area
Chironomid larvae	Reference	Area, km²	174	306	219	854	2100	591	699	3545	4245
		Area inside MPAs, km²	7	132	30	153	963	263	168	1380	1548
		Area inside MPAs, %	4	43	14	18	46	45	24	39	36
	Future	Area, km²	458	635	404	1387	2893	804	1497	5084	6581
		Area inside MPAs, km²	12	261	46	191	1137	335	318	1662	1981
		Area inside MPAs, %	3	41	11	14	39	42	21	33	30
Fucus spp.	Reference	Area, km²		3	43	168	132		46	301	347
		Area inside MPAs, km²		2	6	66	108		8	174	182
		Area inside MPAs, %		90	13	39	82		17	58	53
	Future	Area, km²		13	58	494	440		70	934	1004
		Area inside MPAs, km²		9	4	139	311		13	449	463
		Area inside MPAs, %		72	8	28	71		19	48	46
Red alga Furcellaria lumbricalis	Reference	Area, km²		9	29	322	107		37	429	466
		Area inside MPAs, km²		6	4	73	40		11	113	124
		Area inside MPAs, %		73	15	23	38		28	26	26
	Future	Area, km²		24	63	967	609		87	1576	1662
		Area inside MPAs, km²		14	9	118	257		22	375	397
		Area inside MPAs, %		58	13	12	42		26	24	24
Baltic clam	Reference	Area, km²		1852	1787	2717	3477	125	3638	6319	9957
		Area inside MPAs, km²		407	211	132	743	0,2	618	875	1493
		Area inside MPAs, %		22	12	5	21	0,2	17	14	15
	Future	Area, km²		1415	1567	2084	2303	17	2982	4404	7386
		Area inside MPAs, km²		326	160	86	600	6	486	692	1178
		Area inside MPAs, %		23	10	4	26	36	16	16	16
Marenzelleria	Reference	Area, km²	4729	3093	12032	9862	3887	3762	19854	17511	37364
		Area inside MPAs, km²	6	658	209	92	682	231	873	1005	1879
		Area inside MPAs, %	0,1	21	2	1	18	6	4	6	5
	Future	Area, km²	5263	3198	12136	10202	4908	4058	20598	19167	39765
		Area inside MPAs, km²	6	690	219	191	1187	345	915	1723	2638
		Area inside MPAs, %	0,1	22	2	2	24	9	4	9	7

Species	Time period	Measure and unit	WBB	WK	WBS	EBS	EK	EBB	Sweden	Finland	Project area
Monoporeia affinis	Reference	Area, km²	5582	2899	11917	8935	3230	3420	20399	15585	35984
		Area inside MPAs, km²	9	582	194	2	433	48	785	482	1267
		Area inside MPAs, %	0,2	20	2	0,02	13	1	4	3	4
	Future	Area, km²	4955	2142	11655	8397	1226	2881	18752	12503	31256
		Area inside MPAs, km²	1	369	180	3	121	1	550	125	675
		Area inside MPAs, %	0,03	17	2	0,04	10	0,02	3	1	2
The blue mussel	Reference	Area, km²		91	146	865	230		237	1095	1332
		Area inside MPAs, km²		24	95	10	58		120	68	187
		Area inside MPAs, %		27	65	1	25		50	6	14
	Future	Area, km²		15	21	35	17		36	52	88
		Area inside MPAs, km²		7	6	1	6		13	6	20
		Area inside MPAs, %		48	28	2	34		37	12	22
The common reed	Reference	Area, km²	8	7	22	38	143	32	37	213	250
		Area inside MPAs, km²	0,4	2	1	7	35	7	4	49	53
		Area inside MPAs, %	5	34	7	18	25	21	11	23	21
	Future	Area, km²	10	9	34	60	120	39	52	219	272
		Area inside MPAs, km²	0,5	3	2	15	38	8	5	61	66
		Area inside MPAs, %	5	30	6	24	31	22	10	28	24
Pondweeds	Reference	Area, km²	11	13	24	31	24	2	48	57	105
		Area inside MPAs, km²	0,3	3	4	2	14	0,3	7	16	24
		Area inside MPAs, %	3	25	15	7	56	17	15	29	22
	Future	Area, km²	139	181	140	363	945	330	460	1638	2097
		Area inside MPAs, km²	6	75	19	117	404	120	100	641	741
		Area inside MPAs, %	4	41	14	32	43	36	22	39	35



EUROPEAN UNION

Interreg
Botnia-Atlantica
European Regional Development Fund