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What will the sea look like in 2120?

Future climate and species distribution models for the central Gulf of Bothnia

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ECONNECT 2120

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What will the sea look like in 2120?

Future climate and species distribution models for the central Gulf of Bothnia

Interreg Botnia-Atlantica
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Foreword

Climate change is the greatest environmental crisis of our time. 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. In the ECOnnect project we have studied 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). In this report, we present the current state of the marine environment and discuss possible changes to future environmental parameters and species distribution. The other two reports concentrate on identifying the present ecosystem services in the area and how these might change in the future, and evaluating existing and future networks of protected areas from a connectivity perspective.

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

BALTEX	The Baltic Sea Experiment
BSAP	The HELCOM Baltic Sea Action Plan
EMMA	Finnish ecologically significant marine underwater areas
FMI	Finnish Meteorological Institute
GCMs	General circulation models
GHG	Greenhouse gas
MAI	Maximum allowable input of nutrients, indicating the maximum level of inputs of water and airborne nitrogen and phosphorus to the Baltic Sea sub-basins to reach good environmental status of the Baltic Sea (in BSAP)
MPA	Marine protected area
NICs	Nutrient Input Ceilings in BSAP
RCO-SCOBI	Physical-biogeochemical ocean circulation model RCO-SCOBI
RCP8.5	Representative concentration pathway 8.5, the worst-case climate scenario
SDMs	Species distribution models
SMHI	Swedish Meteorological and Hydrological Institute
VIF	Variance inflation factor value

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 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.

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).

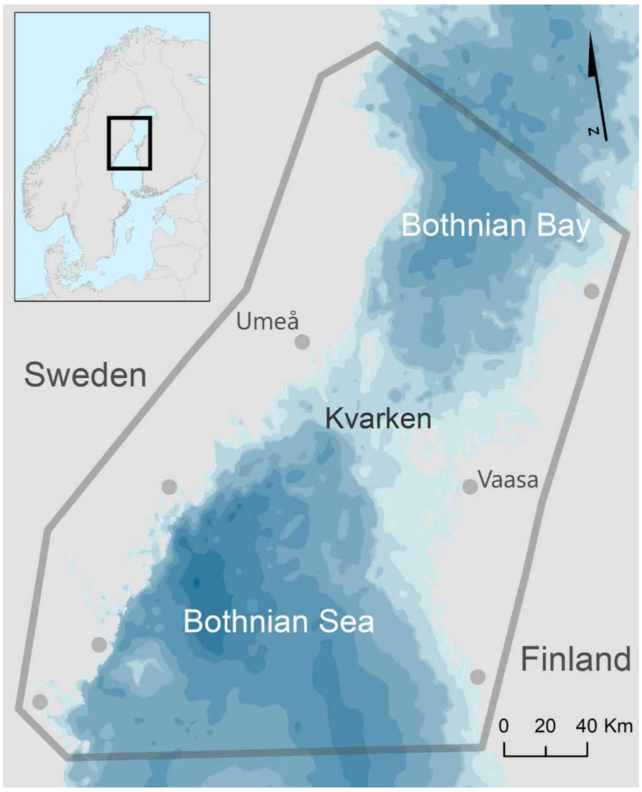


Figure 1. The ECOnnect project area is situated in the Gulf of Bothnia in the northern Baltic Sea.

Within this central part of the Gulf of Bothnia lies Kvarken. Kvarken is a shallow transitional area separating the Bothnian Sea (BS) from the Bothnian Bay (BB). 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 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, a lot of stress is put on the species. This stress can result in the smaller size of the species, for example, compared to areas where the species are not 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 the water balance, and because run-off is the greatest factor affecting salinity there are large uncertainties as to 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 will be further discussed in section 2. 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 to 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 some shell-building species, for example, 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 CO2 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).

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 2013e; von Storch et al. 2015; HELCOM & Baltic Earth 2021).

2. Sea level changes in the project area in the future

Jani Särkkä, the Finnish Meteorological Institute (FMI)

The coast of the Gulf of Bothnia is affected by the land uplift, where the Earth's crust is rising after having been under the weight of the Fennoscandian glacier. The thickest parts of the glacier were in the Kvarken area, where the land uplift is highest (9 mm/year). Due to the land uplift, the mean sea level relative to the land has declined by several hundred meters.

Up to 1900, the relative mean sea level declined at a steady rate. After 1900, the global mean sea level rise has counteracted the land uplift, slowing down the rate of the relative mean sea level change. During past hundred years, the relative mean sea level in the Gulf of Bothnia has decreased by 30–70 cm, as the land uplift has exceeded the effect of the global mean sea level rise. The global mean sea level rises are due to the thermal expansion of seawater and melting of mountain glaciers and the ice sheets in Greenland and the Antarctic with the warming climate.

The global mean sea level rise is expected to accelerate due to climate change. However, there is some uncertainty in the projections due to the unknown response of the West Antarctic ice sheet to the warming climate. Global mean sea level rise exceeding one meter by the year 2100 is possible if the West Antarctic marine ice sheet collapses. In most scenarios the rate of mean sea level rise is smaller than the land uplift rate, so that the accelerating mean sea level rise slows down the local decline in the relative mean sea level. If the more extreme mean sea level rise scenarios come true, the mean sea level rise would exceed the land uplift after 2050 in the Gulf of Bothnia, leading to the submerging of the coastline.

The short-term sea level changes are caused by the wind, air pressure and internal oscillations of the Baltic Sea. Sea levels in the Gulf of Bothnia have been recorded with tide gauges from the early 20th century. In the ECOnnect project area, the highest observed sea levels were detected during two extreme events. In January 1984, measured with respect to the mean sea level, the sea level reached 139 cm at Jakobstad, 144 cm at Vasa, 148 cm at Kaskö, 148 cm at Furuögrund, and 127 cm at Spikarna. In February 2002, the sea level reached 142 cm at Ratan and 131 cm at Skagsudde. In the climate scenarios, there are no clear indications of stronger winds or more frequent storms in the future in the Baltic Sea region that would lead to higher sea level extremes. Due to the large variability in sea level in the Baltic Sea, higher extremes exceeding those recorded are possible in the present climate if the atmospheric conditions affecting the sea level (such as the minimum low pressure value and track of the low pressure systems) are optimal.

The changing mean sea level also affects extreme values and flooding probabilities in the coastal areas. It is important to consider the expected changes when estimating flooding risks and planning the coastal infrastructure. The future probabilities of coastal floods in Finland have been estimated by Pellikka et al. (2018). They combined 14 different mean sea level rise scenarios, where several greenhouse gas scenarios (RCP4.5, RCP8.5, and some older scenarios) were used to estimate the range of projected mean sea levels in the future. In addition, they considered land uplift and changes in the wind climate and made combined distributions for the exceedance probabilities of sea levels in 2050 and in 2100 on the Finnish coast.

The results for the Finnish coast in the ECOnnect project area can be applied also to the Swedish coast, as the only major difference in the factors affecting the relative mean sea level rise in the area are the land uplift rates, being 1 mm/year higher on the Swedish coast. For the mean sea level rise between 2000 and 2100 in the ECOnnect project area, considering the results by Pellikka et al. (2018) for the Finnish coast, and the different land uplift rate on the Swedish coast, we find that the numbers differ at most by 10 cm for different locations (Table 1).

Most of the sea level rise scenarios predict that sea level will continue to decline in the central Gulf of Bothnia, because land uplift will compensate for the global rise in sea level. Thus, it is considered likely that sea level will continue to decline in the Gulf of Bothnia also in the future, but more slowly than in the past. The predicted mean net change in sea level from 2000 to 2100 in the area is -30 cm, but the predictions vary from an even lower sea level, -70 cm, to a rise in sea level of + 20 cm (95 % confidence level). This means that in an extreme case, if the Antarctic ice sheet collapses, global mean sea level will rise so much that the land uplift in the Gulf of Bothnia is not enough to compensate the change, and as a result, sea level would rise also here. Even in that case, the rise would be considerably smaller (about 20 cm) than the global sea level rise (more than 1 m), thanks to the continuing land uplift, which is unaffected by the climate change.

Table 1. Mean sea level change (cm) between 2000–2100 in the coastlines of Finland and Sweden of the ECOnnect project area with confidence intervals.

City	Low (5 %)	Average	High (95 %)
Jakobstad	-72	-29	23
Vaasa	-74	-31	21
Kaskinen	-66	-22	33
Skellefteå	-82	-39	13
Umeå	-84	-41	11
Härnösand	-74	-31	21

When building near the coastline, it is important to prepare for rare coastal flooding events. Under the decline of the relative mean sea level, the flooding risks will be reduced. As the uncertainties in the mean sea level scenarios increase by 2100, one should prepare for rising mean sea levels, even if there is a small probability of occurrence. In the method by Pellikka et al. (2018), flooding risks estimated in 2100 include both high short-term sea level extremes with the most likely mean sea level rise, and lower short-term extremes with less likely mean sea level rises. As an example, for the extreme sea levels, the sea level with a return frequency of one hundred years in Vasa is 169 cm in 2010, 155 cm in 2050, and 180 cm in 2100. Comparing 2010 to 2050, the exceedance level is lower due to relative mean sea level decline, but between 2050 to 2100 the level increases due to widening uncertainty in the relative mean sea level rise by 2100.

3. Future scenarios

Climate models and species distribution models (SDMs) can help us to understand what the future could look like. It is easier to adapt to the consequences of climate change if we know what effects it could have on the environment. Climate models represent the complex and complicated reality of the climate system, and include input data describing the atmosphere, ocean, sea ice, land, vegetation, carbon cycling, etc. (McGuffie & Henderson-Sellers 2014). SDMs provide estimates of habitat suitability for different species and communities in ecosystems. This is especially helpful in marine environments where species are more difficult to monitor and access than on land (Reiss et al. 2011), for example.

In this project, SDMs are used to predict changes in species distribution in response to climate change, which can help to identify species at risk (Slavich et al. 2014). However, it is important to remember that models only provide estimations with notable inherent uncertainty, and they should be utilized with that in mind. There are some issues when using SDMs to predict future species distributions in a changing climate, but SDMs are nevertheless a widely used tool for estimating the impact of climate change on species (Gusian & Thuiller 2005; Littel et al. 2011; Porfirio 2014; Simon-Nutbrown et al. 2020). A description of the species studied in this project can be found in section 4.

Different kinds of climate models are used when predicting the future climate, most notably general circulation models (GCMs) and regional climate models (RCMs) (von Storch et al. 2015). GCMs describe the climate based on grid points with a resolution of about 100–300km. However, many important processes such as precipitation and cloud formation happen on a much smaller scale. Thus, the GCMs are downscaled with RCMs which can better describe local climates (von Storch et al. 2015). A more detailed description of climate modelling can be found in Wibig et al. 2015 and Saraiva et al. 2019a, for example.

Climate models include a lot of uncertainty related to the accuracy and amount of input data, future changes in atmospheric greenhouse gas (GHG) concentrations, aerosols, and land use change, among other sources (von Storch et al. 2015). Changes in GHG concentrations, aerosols, and land use are difficult to predict and that is why different climate scenarios are based on projections for the future development of the world's economy and population. These climate scenarios are then used within climate models for predicting the future climate (von Storch et al. 2015). The climate scenario used within this project was created by the Intergovernmental Panel on Climate Change (IPCC) in 2013. The scenarios used in this work are further discussed in the next section, 3.1. Other aspect that further increases the uncertainty of climate models is that large-scale atmospheric circulation patterns are chaotic in nature and thus difficult to foresee. There are also natural variations in the climate which are unrelated to human influences. Improving GHG scenarios or the models themselves would not eliminate these uncertainties (von Storch et al. 2015).

3.1. What kind of future are we looking at?

The climate models used in this project were 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 one of four climate scenarios created by the IPCC (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 (HELCOM 2020).

In the Fifth Assessment Report (AR5), the IPCC presented four new climate scenarios called Representative Concentration Pathways (RCPs) (Cubasch et al. 2013). The RCPs are identified by the radiative forcing (in W/m^2) in the year 2100 relative to pre-industrial levels. Radiative forcing measures how the energy balance of the Earth's atmosphere changes. RCP8.5, which was used in this project, is the worst-case scenario where radiative forcing would reach 8.3 W m^{-2} in 2100 (Collins et al. 2013). For comparison, the radiative forcing in 2020 was 3.2 W m^{-2} (NOAA 2021). This increase in GHG emissions could be translated into a global warming that would exceed 4 °C by 2100 (Collins et al. 2013). This equals to a mean temperature increase of almost 6 °C by 2100 in Sweden and Finland (SMHI 2021; Ruosteenoja et al. 2016) as the northern hemisphere is warming up faster than the southern hemisphere (Friedman et al. 2013; Meier et al. 2021). The other three climate scenarios are called RCP2.6, RCP4.5, and RCP6.0 and in these scenarios the effect of climate change is expected to be milder (IPCC 2019). In 2021, the IPCC published the Sixth Assessment Report (AR6) where new climate scenarios were presented (IPCC 2021). In this project, the focus is on the RCP8.5 scenario due to time restrictions.

The BSAP was adopted in 2007 with the goal to achieve a good environmental status in the Baltic Sea by 2021. As it was found that this goal was not going to be reached, in 2018 the HELCOM Ministers decided to update the plan in 2021 (HELCOM 2020). The updated plan builds on the original plan maintaining all actions previously agreed on whilst including measures to address new or earlier unaddressed challenges such as climate change, pharmaceuticals, and marine litter (HELCOM 2020). The BSAP has four focus areas: biodiversity, hazardous substances and litter (added in the updated plan), maritime activities, and eutrophication (HELCOM 2020, 2018b). In the ECOnnect's future scenario models the nutrient reduction targets come from the original BSAP, according to which the nutrient loads from rivers, land and atmosphere were to be reduced to the maximum allowable input (MAI). In the new updated BSAP from 2021 (HELCOM 2021a) the MAI targets are roughly the same as in the original but in the new plan there is more focus put on the reduction of inputs from diffuse sources as most of the point sources of the original plan have already been addressed. Also, in the updated BSAP there are some changes made in the Nutrient Input Ceilings (NICs), which define maximum inputs via water and air to achieve good status with respect to eutrophication for Baltic Sea sub-basins for each country. The NICs are calculated as shares of MAI. So, for the Bothnian Sea and Bothnian Bay, even as the MAI have stayed the same in the updated plan, the new emphasis in achieving them has changed the NICs and thus the nutrient reduction targets have increased slightly (more information is found in HELCOM 2021b). The reason for not using the new BSAP in the models is that the models have been produced before the new BSAP was adopted. Although there are changes in NICs in the new plan, it is important to note that the MAI targets are nearly the same in both plans. Therefore, the original BSAP can also be considered as valid to be used in the models. The main outcome of both of these plans, if achieved, is still equally low total nutrient inputs to the sea in the future.

The results from the project were based on the assumptions that concentrations of greenhouse gases in the atmosphere would continue to increase in the future following RCP8.5, but that the Baltic Sea would reach a good environmental status concerning eutrophication. This means that nutrient inputs would be reduced to the level that the Baltic Sea can handle, and eutrophication would not threaten the sea anymore.

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 achieve 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 enough 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 marine ecosystems and human well-being are intertwined. In contrast, the eutrophication of the Baltic Sea has been taken seriously for a while, and inputs of nitrogen and phosphorus decreased by 22 % and 24 %, respectively, in the period 1995-2014 (HELCOM 2018b). Therefore, it seems possible to achieve the goals of the (new) BSAP in the future. Nevertheless, much of the work against eutrophication and other environmental stressors remains to be done. We also wanted to show how important it is to reduce nutrient input to lessen stress on the marine environment to avoid cumulative effects of eutrophication and climate change. Eutrophication mitigation and the impacts of climate change are coupled, after all, because climate-change-induced leaking of phosphorus from the soil and runoff from rivers may increase nutrient inputs and counteract mitigation measures.

4. Materials and methods

4.1. Climate models

Environmental conditions in both the reference period and in the future were based on the RCO-SCOBI three-dimensional physical-biogeochemical ocean circulation model of the Baltic Sea (e.g. Meier et al. 1999; Eilola et al. 2009; Saraiva et al. 2019a) run by the FMI and SMHI to the year 2099. RCO-SCOBI was driven by forcing from three general circulation models: MPI-ESM-LR (Max-Planck Institute Earth System Model), hereafter called model A, EC-EARTH (European Countries Earth System Model), hereafter called model B, and HadGEM2-ES (Hadley Center Global Environmental Model), hereafter called model D, following the naming of the models used in Saraiva et al. 2019a. Model D was only run until the year 2097, whereas the others were run until the end of 2099. Even though the initial goal of the ECOnnect project was to model what the sea might look like in 2120, the climate models could only be run until the end of 2099. The reason for this is that the underlying forcing data, CMIP5, is not available further than that. Further details on the RCO-SCOBI model as well as the general circulation models are beyond the scope of this report but can be found for example in Saraiva et al. 2019a. The modelling setup is based on work done in a previous project, SmartSea, where projections were run until 2059 (SmartSea 2022).

The models were run with climate scenario RCP8.5 and a nutrient reduction scheme that follows the Baltic Sea Action Plan (BSAP) (Fig. 2). The salinity, temperature, nutrients, and other environmental variables (discussed in Chapter 4.3) were calculated as means of the values predicted by the models A, B and D. Multiple models (A, B and D) were used, because no model is clearly better than the others, yet they differ (e.g. Wilcke & Bärring 2016; Saraiva et al. 2019a). The advantage of using multiple models is that uncertainty can be accounted for better than by a single model. Furthermore, by using the means of the three models, the result is just one future salinity and one future *Fucus* spp. distribution, for example, instead of three different alternative future abiotic conditions and species distributions that would be the result of using the three models separately.

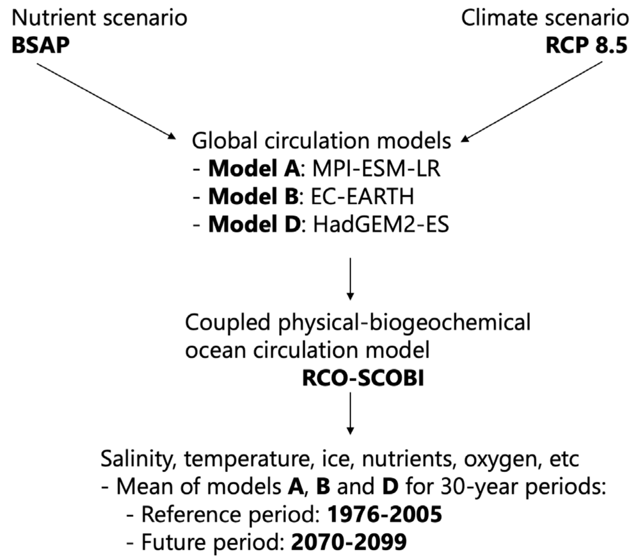


Figure 2. From climate and nutrient scenarios to modelled growing season conditions in the reference period and in the future. The workflow is simplified to only include the components and phases mentioned in this report.

4.2. Species data

A total of 12 species or species groups were included in this study, as presented below. A thorough list of the taxa included in the larger species groups, such as aquatic mosses and chironomids, can be found in Table A1 in the Appendix. These 12 study species and species groups were selected based on their ecological importance and ability to provide ecosystem services in the central Gulf of Bothnia. Additionally, the estimated sensitivity to changes in salinity and temperature were considered when selecting the species. The chosen species and species groups are also characteristic of HUB-biotopes (HELCOM Underwater biotope and habitat classification system biotopes), but the models and the underlying data are not strictly speaking HUBs, as dominance hierarchies were not considered. In other words, we calculated 10 % or higher coverage of *Fucus* spp. as a *Fucus* spp. presence, regardless of whether some other species had a higher coverage.

Species data was gathered from Finnish and Swedish underwater inventory databases, and the data included observations mostly based on drop-videos and diving transects. Finnish macrophyte data was based on the VELMU inventories (The Finnish Inventory Programme for the Underwater Marine Environment) and Finnish zoobenthos data was obtained from the Hertta database (Finnish Environment Institute). In addition, 60 Van Veen zoobenthos samples were taken in summer 2019 to cover previously sparsely sampled areas. Swedish inventory data was gathered from the SMHI Shark database and was complemented with additional smaller data sets that the County administrative boards of Västerbotten and Västernorrland had stored, for example including diving or snorkelling transects in Martrans from previous projects. In total, the inventory data was comprised of over 1 300 soft bottom infauna samples, over 35 000 vegetation observation points (often also including blue mussels), and over 1 000 hard bottom blue mussel points, mostly Kautsky samples, that sometimes also had data on vegetation (Table 2). For the common reed only, satellite images were also used to create 500 additional presence points, as the reeds were rarely observed in vegetation surveys that typically are not carried out in the shallowest areas with dense reed belts.

The values of the raw data, i.e. the abundance of macrophytes and blue mussels and density of zoobenthos, were transformed to presences and absences for modelling. Species-specific thresholds based on quantiles of observed densities were used for zoobenthos, and fixed coverages of 10 and 25 % for macrophytes. For example, only bottom samples with 48 Baltic clams or more were considered as presences and samples with 0–47 clams as absences. This was done to focus the modelling on the densest populations, or in other words, the most suitable habitats. The thresholds in Table 2 (below) are presented for the lower density models. For most species and species groups, two versions of the models were made, one for a lower (25% quantile or 10 % coverage) and one for a higher (75% quantile or 25 % coverage) density or coverage. The data on blue mussels included two data types, which were merged: bottom fauna samples, where their density was measured, and vegetation surveys, where their abundance was evaluated as the percentual coverage.

Table 2. Thresholds for presence-absence conversion and resulting numbers of samples classified as presences or absences, and the total sample sizes for the study species and species groups.

Species or species group	Threshold for presence	Presences	Absences	Total	Prevalence (presences / total sample)
Baltic clam	48 ind/m^2	491	820	1311	0.37
Monoporeia affinis	39 ind/m^2	481	815	1296	0.37
Chironomids	43 ind/m^2	473	838	1311	0.36
Marenzelleria spp.	61 ind/m^2	604	707	1311	0.46
Blue mussel	500 ind/m^2 or 5 %	847	27324	28189	0.03
Fucus spp.	10 %	2558	30963	33521	0.076
Pondweeds	25 %	1746	33263	35009	0.049
Aquatic mosses	1 %	1569	33397	34966	0.045
Furcellaria lumbricalis	1 %	1347	30649	31996	0.042
Common reed	25 %	587	34063	34650	0.017
Stoneworts	10 %	3239	31770	35009	0.093
Filamentous annual algae	25 %	5129	29863	34992	0.15

Study species and species groups

Twelve different species and species groups notable in the Kvarken area were used in the species distribution modelling where the effects of climate change on the future species distribution were studied. The study species were selected based on their ecological importance, and ability to form habitats and provide ecosystem services. Climate change is expected to have an effect especially on salinity and temperature in the Baltic Sea, so notable species susceptible to changes in these variables were also chosen for examination. Major losses in the distribution area of these species in the future could mean an impaired ability for the area to provide vital ecosystem services. Furthermore, changes in the distribution and dominance between species might shift the ecosystems' service provision into a new equilibrium.

***Fucus* spp.**
Blåstång & smaltång
Rakkohauru & itämerenhauru
(HELCOM HUB C1)

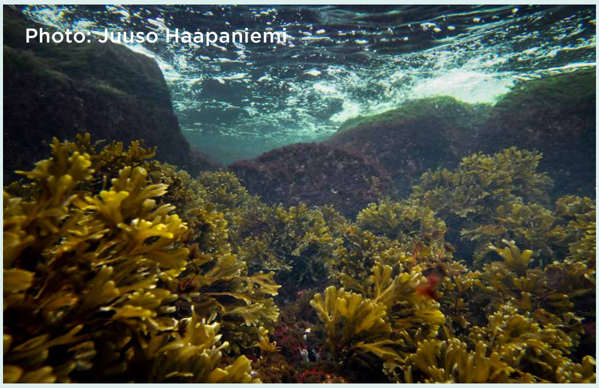


Photo: Juuso Haapaniemi

Two species of *Fucus* occur in the northern Baltic Sea, *Fucus vesiculosus* (bladderwrack) and *Fucus* radicans (narrow wrack). *Fucus* spp. are brown macroalgae of marine origin that grow on hard substrates like rocks and stony bottoms in areas where the salinity exceeds 3–4 ‰ (Kontula & Raunio 2018; Rugiu 2018). *Fucus* spp. can also occur to a lesser extent as an unattached form on soft bottoms in sheltered bays, in which case it is considered a distinct habitat type (HELCOM HUB Q1). The Kvarken area is the northernmost area of occurrence for both species due to the salinity gradient which drops below tolerance for the species in the Bothnian Bay. The two species are morphologically similar, but *F. radicans* tolerates less saline waters than *F. vesiculosus*. Under favourable conditions, *Fucus* spp. can form dense and uniform belts to depths of ca. 0.5–5 meters, and in clear water areas the species can be found up to a depth of 10 meters. Of these morphologically very similar species, *F. radicans* occurs mainly in the Kvarken area on the Finnish coast and Kvarken and Bothnian Sea on the Swedish coast, while *F. vesiculosus* is a common habitat provider in all Swedish and Finnish sea areas south of Kvarken (e.g. Schagerström 2015). As large and perennial species, *Fucus* spp. act as one of the most important key species in the Baltic Sea. They form a habitat for a multitude of organisms and foster biodiversity (e.g. Wikström & Kautsky 2007). Amidst them live many invertebrate species (i.a. *Idotea balthica*, *Jaera* spp., *Gammarus* spp., *Cerastoderma glaucum*), smaller macroalgae (i.a. *Cladophora* spp., *Ceramium* spp.) and several fish species (i.a. the sea stickleback *Spinachia spinachia*, European eelpout *Zoarces viviparus*, and Syngnathidae). *Fucus* spp. also provide an important spawning site, nursery habitat and feeding grounds for fish (Aneer 1989; HELCOM 2013a). Additionally, *Fucus* spp. play an important role in binding nutrients from the water and providing a carbon stock (e.g. Heckwolf et al. 2021). Eutrophication and climate change are the greatest threats to *Fucus* spp. (Kontula & Raunio 2018).

Red alga *Furcellaria lumbricalis*
Kräkel/ gaffeltång
Haarukkalevä
(HELCOM HUB C2)


Photo: Julia Nyström/Metsähallitus

Furcellaria lumbricalis is a common and robust red alga species inhabiting most of the Baltic Sea (HELCOM 2013c). It is of marine origin and due to the drop in the salinity gradient below suitable for the species, its northernmost occurrence is limited to the Kvarken area (Kostamo 2008; Kontula & Raunio 2018). *F. lumbricalis* inhabits stony and rocky bottom surfaces both in the *Fucus* belt and deeper in the red algal belt among other red algae species most commonly at depths of ca. 3–8 meters. However, in clear waters it may be found up to a depth of 15 meters. Especially in the deeper water, perennial *F. lumbricalis* forms an important and diverse habitat where sessile invertebrates (i.a. the blue mussel *Mytilus trossulus x edulis*) and various other macroalgae species occur (i.a. *Battersia arctica, Cladophora rupestris, Polysiphonia* spp.). Many small invertebrate species (i.a. *Jaera* spp. & *Idotea balthica*; Kotta et al. 2000; Saarinen et al. 2018) find shelter and food within the *F. lumbricalis* branches and small fish species and fish juveniles can hide amongst the shrub-like growths (e.g. Olsson & Korpelainen 2013). Mixed communities of *Fucus* spp. and *F. lumbricalis* also provide a spawning habitat, for example for Baltic herring (*Clupea harengus membras*) near open and stony shores (Kontula & Raunio 2018). *F. lumbricalis* thrives in clear water and eutrophication with the following increased water turbidity has pushed the species into shallower waters in the past decades. Additionally, climate change, excess sedimentation and an increase in filamentous algae impose threats to the species (Kontula & Raunio 2018).

Filamentous annual algae
Ettåriga trådalger
Yksivuotiset rihmalevät
(HELCOM HUB S1)

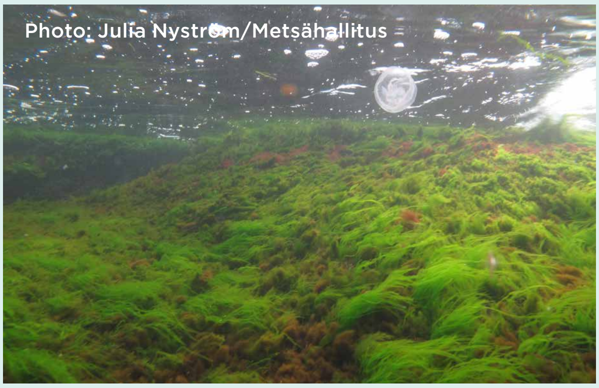


Photo: Julia Nyström/Metsähallitus

Several species of filamentous annual green, brown and red algae form a habitat on hard rocky and stony bottoms from the surface to depths of ca. 3–4 meters (Kontula & Raunio 2018). Some of the common species are *Cladophora glomerata, Dictyosiphon foeniculaceus, Ectocarpus siliculosus, Pylaiella littoralis* and *Ulva* spp., and occasionally also filamentous annual red algae (i.a. *Ceramium* spp.) occur in the community. The biotope formed by filamentous annual algae is very common throughout the entire Baltic Sea, although in areas with very low salinity the species diversity is lower as most of the species are originally marine (VELMU 2020). Filamentous algae form extensive fur-like growths that can cover rocky surfaces entirely. In deeper water, the filamentous algae belt changes to *Fucus* spp., even though filamentous annual algae also occur generally among and as epiphytes in the *Fucus* spp. belt (Kontula & Raunio 2018). Filamentous algae provide an important habitat with shelter and food for several invertebrate species (Zander et al. 2015; Kraufvelin & Salovius 2004). The rich invertebrate fauna found amidst filamentous algae further benefit various fish species that feed amongst the growth (Zander et al. 2015). Filamentous annual algae have benefited from increased nutrient concentrations in the Baltic Sea and as epiphytes they can suppress the *Fucus* spp. by preventing light from entering the *Fucus* thalli (Kontula & Raunio 2018). In the spring, rapidly growing filamentous algae also occupy new areas effectively, impairing the chances of *Fucus* spp. to spread to new places.

Aquatic mosses
Akvatiska mossor
Vesisammalet
(HELCOM HUB D)


Photo: Essi Keskinen/Metsähallitus

Aquatic mosses are one of the specialties of the Baltic Sea, as water mosses are usually found only in fresh waters (Kontula & Raunio 2018). Particularly in the low-saline Bothnian Bay as well as in Kvarken, aquatic mosses form diverse plant communities on rocky bottoms. In the Bothnian Bay, where *Fucus* spp. do not occur due to the low salinity, aquatic mosses act as a similar habitat-forming species fostering biodiversity in rocky surfaces. They provide a habitat, shelter and food for invertebrate species, and on shallower bottoms the mosses occurring with *Phragmites australis* are a preferred habitat for pike (*Esox lucius*) larvae (Kallasvuo et al. 2011). Water mosses grow mainly in rather open shores at depths of 3–6 meters. Light attenuation strongly regulates their growth depth, and the habitat typically occurs in patches. Several species of aquatic mosses are found in the Baltic Sea: *Fontinalis* spp., *Fissidens fontanus* and *Oxyrrhynchium speciosum* being the most common (VELMU 2020). The species diversity of aquatic mosses increases from the open sea towards estuaries. Aquatic moss species in the Baltic Sea have been historically poorly known, and even in recent years species previously unseen in the northern Baltic Sea have been identified in the Bothnian Bay (Bergdahl et al. 2020). As perennial species, aquatic mosses give an addition to the important carbon and nutrient sequestration that vascular plants and algae provide in the Baltic Sea. Excess sedimentation and an increased spreading of filamentous algae pose threats to the aquatic moss species (Kontula & Raunio 2018).

Stoneworts
Kransalger
Näkinpartaiset
(HELCOM HUB B4)

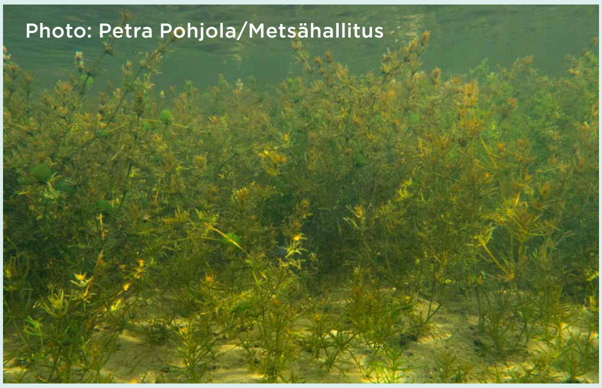


Photo: Petra Pohjola/Metsähallitus

Charales is an order of freshwater and brackish water green algae commonly known as stoneworts that in appearance resemble vascular plants more than algae (Schubert & Blindow 2003). Several species from four different genera *Chara, Nitella, Nitellopsis* and *Tolypella* inhabit Swedish and Finnish coastal waters. Stoneworts form meadow habitats both in sheltered areas such as bays and flads on muddy bottoms, as well as in more open areas on sandy bottoms (Kontula & Raunio 2018; HELCOM 2013d). Larger species thrive in sheltered areas and the meadows they form are taller and more layered than the meadows on open shores. Stonewort meadows provide an important habitat for invertebrates and fish species offering shelter and food. Especially in sheltered areas, tall stonewort growths act as a spawning habitat for fish and provide a valuable nursery habitat for fish fry (Viitasalo et al. 2017; Kontula & Raunio 2018). Dense and wide stonewort meadows stabilize the soil, bind nutrients very effectively from the water, and improve water quality (Blindow et al. 2002; Appelgren & Mattila 2005). Additionally, stonewort species can produce compounds that limit the production of planktonic algae and cyanobacteria (Berger & Schagerl 2003). The species are sensitive to excess sedimentation, increased filamentous algae spreading, high turbidity and excessive marine traffic (Kontula & Raunio 2018).

Pondweeds
Nateväxter
Vidat
(HELCOM HUB B1)

Photo: Maja Wressel

Several species of pondweeds occur in the Baltic Sea, yet the most abundant and widespread are the species *Stuckenia pectinata* and *Potamogeton perfoliatus* (Mossberg & Stenberg 2012). These species are found widely both in freshwater and brackish water environments and as adaptable species they occur virtually in the whole Baltic Sea (GBIF 2021a). Sandy and muddy bottom substrates are ideal for both species to grow and on suitable conditions they can form very wide-spread and uniform stands (Kontula & Raunio 2018). In addition, both species grow tall and thus the pondweed communities provide an important habitat for other species. Amidst them several invertebrate species and fish find shelter and food (Hansen et al. 2011; Hansen 2010) and they also act as spawning grounds for fish, such as Baltic herring (Kääriä et al. 1997; Rajasilta et al. 1993) and perch (*Perca fluviatilis*; Snickars et al. 2010). Other aquatic plants also prosper amongst pondweeds increasing plant biodiversity in the stands. Perennial pondweeds stabilize sediment and prevent erosion (Zhang et al. 2020), enhance the functioning of microbial communities in the sediment (Caffrey & Kemp 1990), reduce turbidity and have an effect on the chemical quality of water by nutrient sequestration (e.g. Austin et al. 2017). Possible future threats for the species include heavy eutrophication and water transport which can destroy the tall stands and cause excess turbidity which is harmful to the species (Kontula & Raunio 2018).

The Common reed
Bladvass
Järviruoko
(HELCOM HUB A1)

Photo: Linda Jokinen Thai/Metsähallitus

The common reed, *Phragmites australis*, is a widespread wetland grass growing up to 4 meters and forming extensive and uniform stands on shorelines in the Baltic Sea (Hämet-Ahti et al. 1998). It thrives on various bottom substrates and environmental conditions but requires rather sheltered shores to grow (Kontula & Raunio 2018). The common reeds is a grass adapted primarily to fresh water but tolerates a brackish water environment well. Many species of birds live and breed amongst reed habitats such as warblers *Acrocephalus* spp., water rails *Rallus aquaticus* and Eurasian bitterns *Botaurus stellaris*. The common reed also provides shelter and food for various fish species, frogs and bats and the reeds are especially important as spawning sites and nursery habitats for fish species (e.g. perch, Snickars et al. 2010; pike, Kallasvuo et al. 2011). The invertebrate species diversity is high in common reed stands (Ikonen & Hagelberg 2007). Eutrophication and the decline in traditional cattle pasturage on shores has favoured the common reed which nowadays forms denser stands and has also spread to new areas (Niemelä 2012). This has adversely affected especially the biodiversity of coastal meadows. The common reed plays a role in shoreline nutrient cycling (Struyf et al. 2007; Paavilainen 2005; Karstens 2016), nitrogen sequestration and the control of erosion (Karstens 2016).

The Blue mussel
Blåmussla
Sinisimpukka
(HELCOM HUB E1)

The blue mussel, *Mytilus trossulus x edulis*, is one of the most important key species living in the Baltic Sea. It inhabits rocky and stony bottoms particularly in the outer archipelagos and offshore reefs, thriving in areas where currents are strong, and the effect of the waves is deep (Viitasalo et al. 2017). As originally a marine species, blue mussels require salinity levels over 4‰, and to form dense and extensive habitats an even higher salinity of at least 5‰ is required. The Kvarken area is the northernmost area of occurrence for the species in the Baltic Sea. The Baltic Sea blue mussel is a hybrid of two marine species *M. trossulus* & *M. edulis* (Waldeck & Larsson 2013) and it grows smaller than its marine relatives, only ca. 1–4 cm in length (Kontula & Raunio 2018). The species forms habitats especially below *Fucus* spp. and red algae belts at depths of ca. 8–12 meters but under favourable conditions also on shallower or deeper bottoms (Westerbom & Jattu 2006; Viitasalo et al. 2017). Blue mussels are often also found in mixed communities with other hard-bottom species, especially with red algae. Blue mussels create and maintain new habitats for many other species and provide them with shelter and food (e.g. Zander et al. 2015; Kautsky 1981). Over 40 species of macroinvertebrates (including amphipods, isopods, gastropods; Viitasalo et al. 2017) have been observed in the blue mussel communities. Blue mussels are an important food source for several birds (i.a. common eider *Somateria mollissima*, long-tailed duck *Clangula hyemalis*) and fish species (i.a. European flounder *Platichthys flesus*, and European eelpout; Kautsky 1981; Kontula & Raunio 2018). The mussels filtrate phytoplankton and other micro-organisms from the water for food and in the process clear and purify the water (Viitasalo et al. 2017). The filtration capacity of the species is enormous, and they accumulate large amounts of both nutrients and pollutants (Kautsky & Kautsky 2000). Climate change (increasing temperatures and decreasing salinity), eutrophication-related factors (sedimentation & filamentous algae spreading), competition with invasive barnacles *Amphibalanus improvisus*, and chemical pollutants pose threats to blue mussels in the future (Kontula & Raunio 2018).

The Baltic clam
Östersjömussla
Liejusimpukka
(HELCOM HUB L1)

The most widespread species of bivalve molluscs in the Baltic Sea, the Baltic clam *Limecola balthica*, inhabits sandy and muddy bottom sediments up to 190 meters in depth (Viitasalo et al. 2017; Kontula & Raunio 2018). Most abundantly the species occurs at a depth range of 2–5 meters. This marine species has a high tolerance for low salinity levels enduring brackish water down to 3‰ salinity. Thus, the range of occurrence exceeds the Kvarken area for the species and it can be found also in the southern parts of Bothnian Bay. The Baltic clam is highly adaptable to various environmental conditions and although it is a rather small species growing only ca. 2 cm long, it is one of the most important benthic invertebrate species in the Baltic Sea. It is often the dominant species in terms of biomass in the benthic communities and on the most suitable bottom conditions thousands of individuals can occur in one square meter (e.g. Viitasalo et al. 2017; Laine 2003). The Baltic clam is a burrowing organism extending only its siphons to the sediment surface. They move actively within the sediment enhancing the transfer of oxygen deeper into the substrate and, as a result, the ability of the sediment to bind phosphorus. As a deposit-feeder, Baltic clams decompose organic matter and play a role in biogeochemical processes at the sediment–water interface (Heilskov et al. 2006; Michaud et al. 2006). The clam is also an important food source for many species of fish and birds (Mustamäki et al. 2014; Lappalainen et al. 2004; Ejdung & Bonsdorff 1992). Possible future threats to the species include anoxic bottom conditions, which have already narrowed the depth distribution of the species in some areas (Kontula & Raunio 2018).

Amphipod *Monoporeia affinis*
Vitmärla Valkokatka
(HELCOM HUB N1)

The amphipod species *Monoporeia affinis* is an integral part of the benthic community of the deep and soft bottoms of the Baltic Sea (Viitasalo et al. 2017). It is originally a freshwater species and a glacial relict left in the Baltic Sea after the last glaciation, and it tolerates seawater up to 18‰ salinity (HELCOM 2013b). The distribution of the species covers almost the entire Baltic Sea, apart from the most southern areas. *M. affinis* is a cold water species living on soft bottoms from the depth of about 10 meters down to as much as 200 meters, although in the northern areas of the Baltic Sea it is also found in shallower waters (HELCOM 2013b). The species actively burrows in the sediment and feeds on plankton sinking to the bottom and other detrital material. The burrowing behaviour of the species mixes the sediment effectively and this has an important role in oxygenizing the top layer of the sediment and further binding phosphorus to the sediment. *M. affinis* is sensitive to hypoxic bottom conditions and thus it has disappeared from some of its distribution areas affected by low oxygen concentrations (Kontula & Raunio 2018). *M. affinis* is most abundant in the northern Baltic Sea and especially in the Gulf of Bothnia, where bottom oxygen conditions are good. Under favourable conditions, as many as 10 000 individuals can occur in one square meter (Donner et al. 1987; Bonsdorff et al. 2003; Viitasalo et al. 2017). The species is an important food source for other invertebrates (for example the isopod *Saduria entomon*) and for fish (i.a. Baltic herring, smelt *Osmerus eperlanus*, and whitefish *Coregonus lavaretus*; Hägerstrand et al. 2018; Donner et al. 1987; Englund et al. 2008).

Chironomid larvae
Fjädermyggslarv
Surviaissääskien toukat
(HELCOM HUB P)

Chironomids are nonbiting midges with a global distribution and high species diversity (GBIF 2021b). Adults are small flying insects that often swarm above waters and coastal vegetation and their larvae live burrowed in the bottom sediment both in freshwater and brackish water environments (Viitasalo et al. 2017; Kontula & Raunio 2018). The larvae of most chironomid species are very small in size, although individuals of some of the largest species can grow up to 3 cm in length. Depending on the species, chironomid larvae have various feeding habits. Within the sediment, dead organic matter provides a common food source while some larvae are predators or parasites (Kahanpää & Salmela 2021). In shallow coastal waters chironomid larvae occur in mixed communities with other benthic organism such as polychaetes (bristle worms), clams (i.a. *Limecola balthica*) and other aquatic insects and their larvae (Kontula & Raunio 2018). In the deeper parts and in hypoxic areas they become more dominant in the benthic communities and thousands of individuals can occur in a square meter (Viitasalo et al. 2017). The colouring of the larvae varies by species from green and yellow to red. In the deeper areas, red coloured larvae especially occur as they contain a haemoglobin-like substance that effectively binds oxygen and helps the red larvae survive in low oxygen conditions. Chironomid larvae are an important food source for various fish species such as perch (Mustamäki et al. 2014; Lappalainen et al. 2001), European flounder (Uzars et al. 2003) and whitefish (Hägerstrand et al. 2018). High numbers of chironomid larvae affect the decomposition of organic matter in the sediment (Andersen & Skovgaard 1991) and play a role in nutrient recycling and translocation (e.g. Vanni 2002). Eutrophication in the Baltic Sea has most likely increased the areas of chironomid-larvae-dominated habitats (Kontula & Raunio 2018).

Polychaete *Marenzelleria* spp.
Nordamerikansk havsborstmask
Liejuputkimadot
(HELCOM HUB M3)

Photo: Metsähallitus

Marenzelleria spp. are alien bristle worm species that originally arrived in the Baltic Sea most probably in ships' ballast water and now they occupy soft bottom sediments throughout the entire Baltic Sea (Katajisto et al. 2021). Three very similar species of *Marenzelleria* are found in the northern Baltic Sea in Finnish and Swedish waters: *M. viridis, M. neglecta* and *M. arctia*. The species *M. viridis* and *M. neglecta* are originally native to North America, and *M. Arctia* is originally from the Arctic Ocean, evidently the estuaries of the great rivers of Russia (Katajisto et al. 2021). Polychaete *Marenzelleria* are rather delicate in structure, and although they can grow to about 10 cm in length, worms of only a few centimetres or less are much more common. *Marenzelleria* spp. have become very successful in the Baltic Sea (HELCOM 2012) and they occupy soft sediments both in shallower and in deeper waters, and especially in the deeper waters they may occur in high numbers in the sediment (Zettler et al. 2002; Kauppi et al. 2015). *Marenzelleria* spp. burrow in the bottom sediment feeding on dead organic matter and in the process form deep and wide tube tunnels, which promote the transport of oxygen into the sediment and further binds phosphorus. It has been feared that the alien *Marenzelleria* spp. would displace the natural soft-bottom invertebrate species of the Baltic Sea, but there is no clear research evidence to support this (Katajisto et al. 2021).

4.3. Modelling

Species distribution modelling is a modelling technique where the combination of environmental conditions suitable for a species is inferred from inventory data and generalized over to areas where inventories have not been made. In other words, the aim is to predict where a species might occur based on environmental conditions. The suitable range of environmental conditions is defined based on field observations that serve as input data. As a result, sparce point data on presences and absences is transformed into a map that shows predicted occurrence probability for a species.

Here, we used inventory data on the 12 study species and combined that with 11 environmental variables describing local conditions by extracting the value of each environmental variable at the inventory location. Two of the environmental variables, depth and sea floor exposure, were based on maps produced for the project area in an earlier project (SeaGIS2.0). In addition, the distance to the coast was calculated as a new variable for this project, and the 8 remaining variables were based on physical and biogeochemical models from the FMI and SMHI. The 8 variables based on the FMI and SMHI models for sea water characteristics were salinity, temperature, ice thickness, vertical light attenuation, and the concentrations of oxygen, nitrate (NO_3), ammonium (NH_4), and phosphate (PO_4).

To study how species might be affected by climate change, two sets of species distribution models were created and compared: reference period models and future models (Fig. 3). The reference period was defined as the 30-year period from 1976 to 2005, and the future period as the 30-year period from 2070 to 2099. The timing of the reference period originates from the CMIP5 forcing data underlying the climate models and could not be changed. However, environmental conditions in the Gulf of Bothnia, such as nutrient levels, have not changed drastically between the reference period and the actual present day, about 2004–2020, from which the majority of the species data is taken. Therefore, the temporal mismatch between the data collection and the modelled environmental conditions does not have any significant effect on the reliability of the modelling process.

For both time periods, the reference and the future, the mean growing season (May–September) values were calculated for all the environmental variables based on the FMI and SMHI's models, except for the ice thickness, for which the months from December to April were used. Nutrient concentrations in both the surface water layer (0–3 m) and the bottom water layer were calculated. The other variables were only calculated for either the surface (ice thickness) or bottom (salinity, temperature, and oxygen). The same depth, sea floor exposure, and distance to coast were used for both time periods, so these three variables were assumed not to change between the reference period and future.

The species distribution models were made using boosted regression trees (BRT) modelling. BRT is an advanced additive regression modelling method, which combines regression-tree-based statistical approach and boosting, which is the practice of utilizing a large number of relatively simple regression tree models (Elith et al. 2008). As a result, BRT models have several advantages, including the modelling of nonlinear responses and the ability to handle different classes of predictors and interactions between them, and importantly, high predictive performance (Elith et al. 2008). The BRT models were run in the programming environment R (R Core team 2019) using functions of R packages called 'gbm' (Greenwell et al. 2019) and 'dismo' (Hijmans et al. 2017). R packages can be described as toolboxes that provide tools (i.e., functions) for different purposes, such as for species distribution modelling in this case. The values for the tree complexity and learning rate were selected so that the models had the lowest possible deviance and a minimum of 1000 trees. A bag fraction of 0.75 was used in all models. 70 % of the observations were used to train the models and 30 % were used to evaluate the model performance. See Table 2 for the sample sizes.

All explanatory variables were initially included in the models, unless they had overly high variance inflation factor values (VIFs), in which case they were left out. In practice, this means that we avoided including very correlated variables, even though BRT does handle correlated variables well. However, the key variables salinity, temperature, nitrate and phosphate were always included in the initial models, even if they had a high VIF. The final variables in each model (Table A2) were selected from the initial

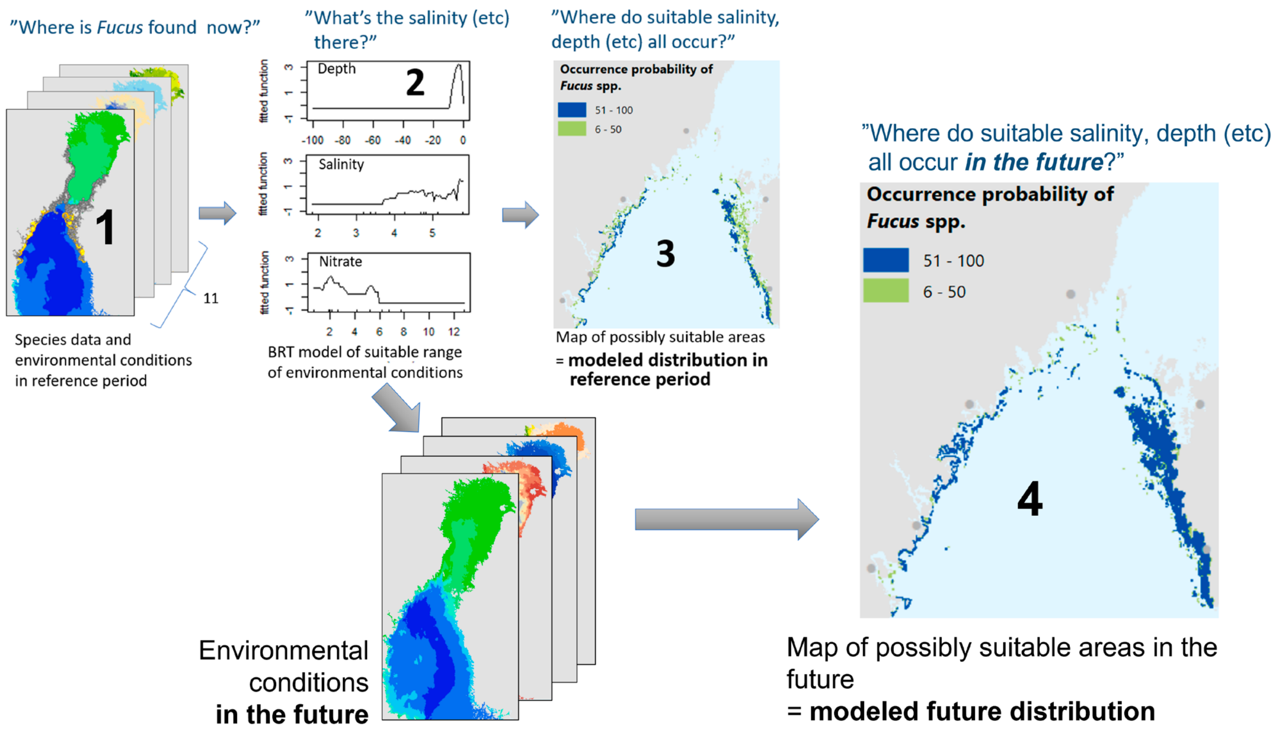


Figure 3. Illustration of the key steps in species distribution modelling using *Fucus* spp. as an example. 1) Species observation data, both presences and absences, is layered on top of environmental data, for example salinity. 2) From the data, the BRT modelling process infers the response of the species concerning the different environmental variables, for example, that *Fucus* spp. is more likely to be found at the sampled locations with higher salinity. 3) The responses inferred in step 2 are generalized over the maps of environmental variables to find areas where conditions resemble conditions in the places where *Fucus* spp. was found. 4) Step 3 is repeated using modelled future conditions.

ones with the function gbm.simplify so that only variables that improved the model performance were included and those that did not improve it were left out.

Species distribution modelling was done separately for each species, and only environmental variables were used as predictors. In other words, the models do not take species interactions into account.

Another shortcoming is that the bottom substrate was not included in the environmental variables, because sufficiently good maps covering the whole study area were not available. As a result, the models tend to overestimate the area suitable for the modelled species, as competition, for example between *Fucus* spp. and filamentous algae, and the availability of the right kind of bottom are not taken into account.

5. Results

5.1. Changes in environmental variables

According to the climate models, the mean growing season conditions in the Gulf of Bothnia in the future will be substantially different from the past. By comparing modelled mean conditions in the reference period (1976–2005) to the modelled mean conditions in the future period (2070–2099), we found that the predicted effects of climate change on the marine environment were in line with several previous studies (reviewed in Helcom & Baltic Earth 2021; Meier et al. 2021), naturally especially those that have used the same RCO-SCOBI ocean circulation model (Saraiva et al. 2019a, b). Throughout this section as well as the whole report, the reader is advised to keep in mind the inherent uncertainty in future predictions and especially climate models, as well as the choice of scenarios used, in this case RCP8.5 and the BSAP. The greatest changes will concern sea ice and water temperature, which are directly affected by the increasing air temperature.

Sea ice will be thinner in future winters. On average, more than 80 % of the ice thickness will be lost in the project area by 2099 (Fig. 4). This is a result of several simultaneous and connected changes. The open sea will not freeze every winter and the duration of ice cover will be shorter, and when there is ice, it will be on average considerably thinner than in

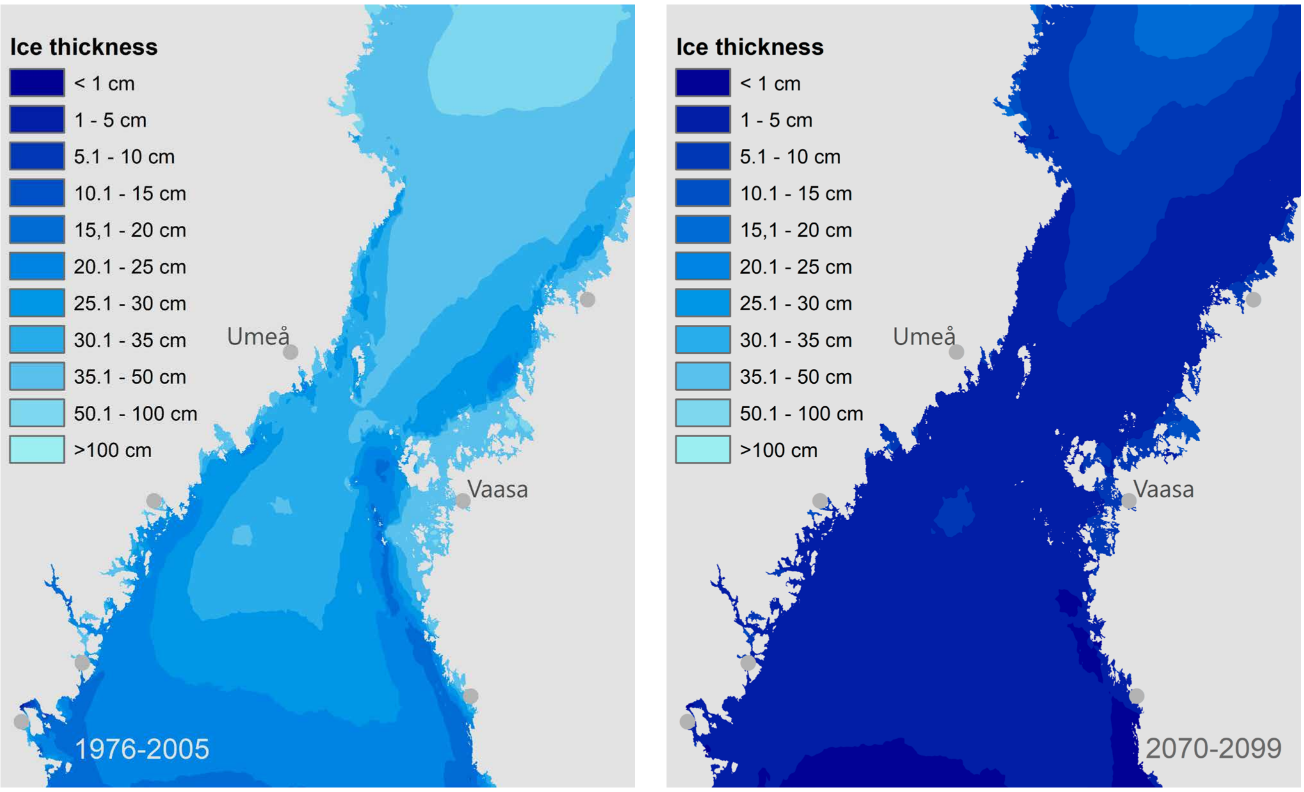


Figure 4. Modelled mean ice thickness during winters in the reference period (left) and in the future period (right).

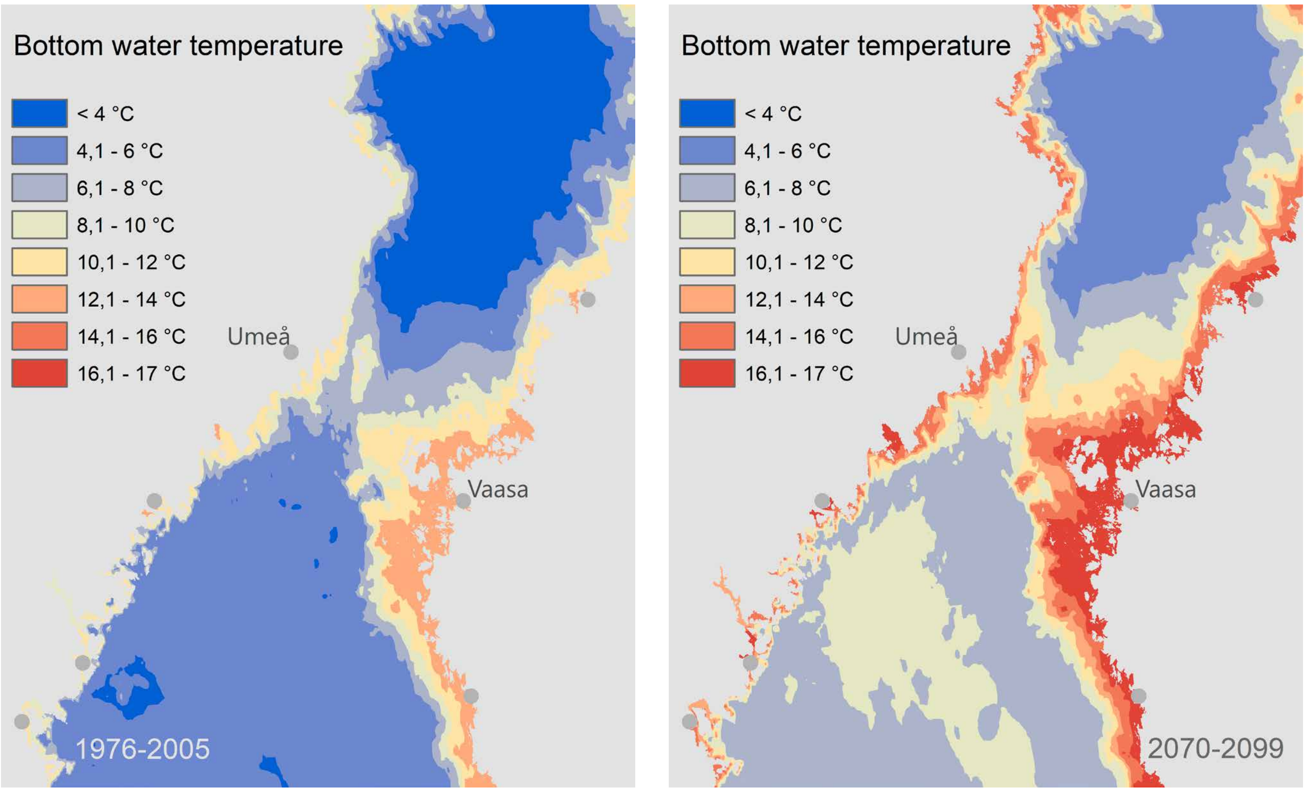


Figure 5. The temperature in the bottom water layer during the growing season (May–September) is expected to increase by 3 °C on average from the reference period (left) to the future (right).

the reference period. All these changes will lead to a drastic decline in the mean conditions. However, the sea ice will not be totally lost, but winters with thin, short-lived, or missing ice cover will be more common.

The mean **bottom water temperature** during the growing season in the project area will increase on average by 3°C. This change will be even greater in shallow areas, and in contrast smaller in deeper waters (Fig. 5). In general, predictions for the future (water) temperature are considered more reliable and precise than predictions for other environmental variables such as the salinity that are not directly but only indirectly affected by increasing GHG concentrations. Changes in the sea ice and water temperature are of a much higher certainty, compared to other environmental factors.

The **salinity** is considered the most important abiotic factor shaping the distributions of both freshwater and marine species in the project area, and especially in the Kvarken region. Therefore, future changes in salinity are especially interesting and important. Unfortunately, salinity is the most uncertain variable. Salinity is difficult to model, as it is affected by complex physics through several intertwined processes. The projected mean decline in the bottom salinity in the project area is -0.52‰, or -10%, compared to the reference period (Fig. 6.). This projected change is considerably smaller than some earlier models have suggested (e.g. Meier et al. 2006). More recent studies (reviewed in Helcom & Baltic Earth 2021; Meier et al. 2021), however, predict the salinity to decline only a little and also show remarkable variation between models, even concluding that it is uncertain whether the salinity will increase or decrease. These most recent reviews also emphasize the high uncertainty of and low confidence in any future projections for salinity.

As we have in this work chosen to look into a future where the nutrient input has been reduced as outlined in the BSAP, the models predict a remarkable decline in the phosphate (PO_4) concentration in the sea water. The **phosphate concentration** will drop by approximately 80% in the project area. As a result, primary production will also decline, which

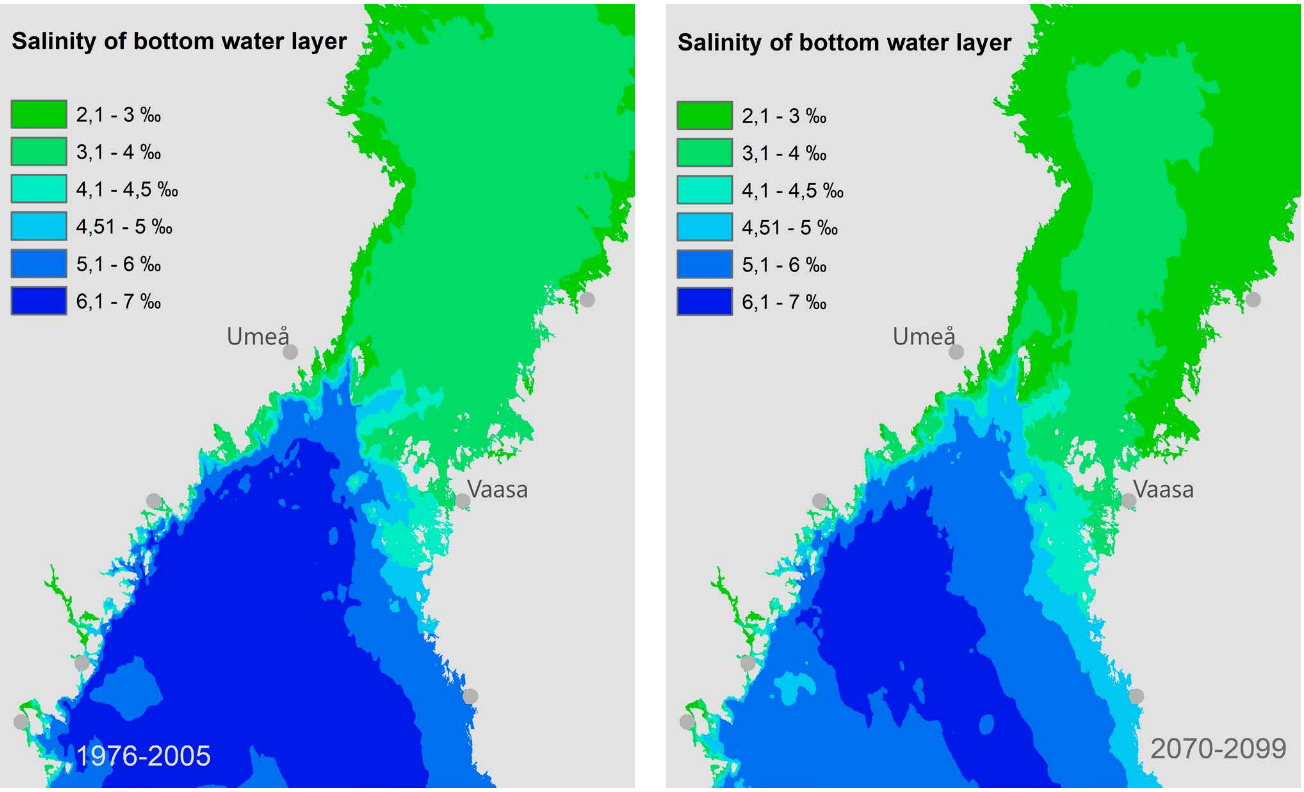


Figure 6. Based on the climate models, the salinity in the future (right) will be on average 0.5 permille units lower than in the reference period (left).

will lead to an increase in **nitrate (NO_3) concentration** due to less consumption by phytoplankton. The increasing nitrate concentration in the sea water during the growing season therefore does not imply an increased input from the land (as the nutrient scenario used was BSAP) but an increased accumulation of nitrates in the water instead of biomass due to the phosphorous-limited primary production. For this reason, the greater nitrate concentration in the future compared to the reference period is not a sign of a worse chemical or ecological state of the sea. Even though the nutrient levels have been reasonably low in the Bothnian Sea and Bothnian Bay for a long time, increased nutrient levels have been detected due to the inflow of nutrient rich waters from the heavily eutrophicated Baltic Proper and Archipelago Sea into the Gulf of Bothnia (Rolff & Elfwing 2015). The reasons for this phenomenon are not yet well understood, but the consequences are, unfortunately, easier to foresee. If the nutrient intrusion from the southern sea areas into the Gulf of Bothnia continues or grows, the nutrient levels may increase and the ecological state may decline even further, because the nutrient levels in the Archipelago Sea and Baltic proper are at the moment much higher than in the Gulf of Bothnia. However, the updated new BSAP (HELCOM 2021a) has small nutrient reduction targets for Finland and Sweden for the Bothnian Sea and Bothnian Bay, and if these are achieved with the BSAP nutrient reduction targets for the southern nutrient rich waters, the total combined effect for the water quality of Bothnian Sea and Bothnian Bay will be positive.

According to the models assuming the BSAP, the **oxygen concentration** in the bottom water layer will mostly remain on roughly the same level, but regionally oxygen concentrations may either decline or increase in the future. The biogeochemical models suggest a slightly higher oxygen concentration in the future in the deeper areas near the Swedish coast in Västernorrland, for example east from the island of Norra Ulvön. In contrast, shallow areas that will be much warmer will have less oxygen, but not so little as to be threatened by hypoxia. Overall, during an average growing season, oxygen will not be an issue in the future, if the BSAP is successfully implemented.

5.2. Changes in present and future species distributions

In this chapter the modelled present and future distributions of important underwater species are shown. BRT modelling was used to assess the probability of occurrence in the central Gulf of Bothnia with the future scenario RCP8.5 and the assumption that the targets of the BSAP will be met. The relative influences of different environmental variables in each model, as well as statistics of the model performance, are presented in Table A2 in the Appendix.

5.2.1. *Fucus* spp. *(F. vesiculosus & F. radicans)*

The species distribution models that were run with environmental conditions for the reference period (1976–2005) and future period (2070–2099) suggest that the areas potentially suitable for *Fucus* spp. may increase significantly in the future (Fig. 7). This is mainly because of thinner or missing ice. Shallow rocky shores that are now scraped by ice every winter, and are therefore suitable for only annual algae, will become available also for perennial algae, such as *Fucus* spp. This, together with the improving chemical state of the Baltic Sea and hence increasing light availability, increases the depth range where *Fucus* spp. can grow. As a result, *Fucus* spp. could grow in both shallower and deeper areas in the future. The decreasing Secchi depth in the past 50 years has caused a remarkable reduction in areas suitable for *Fucus* spp. communities (Sahla et al. 2020), so the projected increase in the future can be seen as a recovery rather than pure colonization of new areas. Mild winters in the Baltic Sea have already been shown to result in denser *Fucus* spp. growth near the surface (Kiirikki & Ruuskanen 1996).

Fucus spp. are marine species that require a minimum of approximately 3–4‰ salinity, depending on the species, and possibly also locally adapted genotype (Rugiu 2018). Based on the models used in this study, the salinity will decline so little that it will not have a significant impact on *Fucus* spp. as a group. However, the decreasing salinity will inhibit *Fucus* spp. from colonizing new areas further north, even

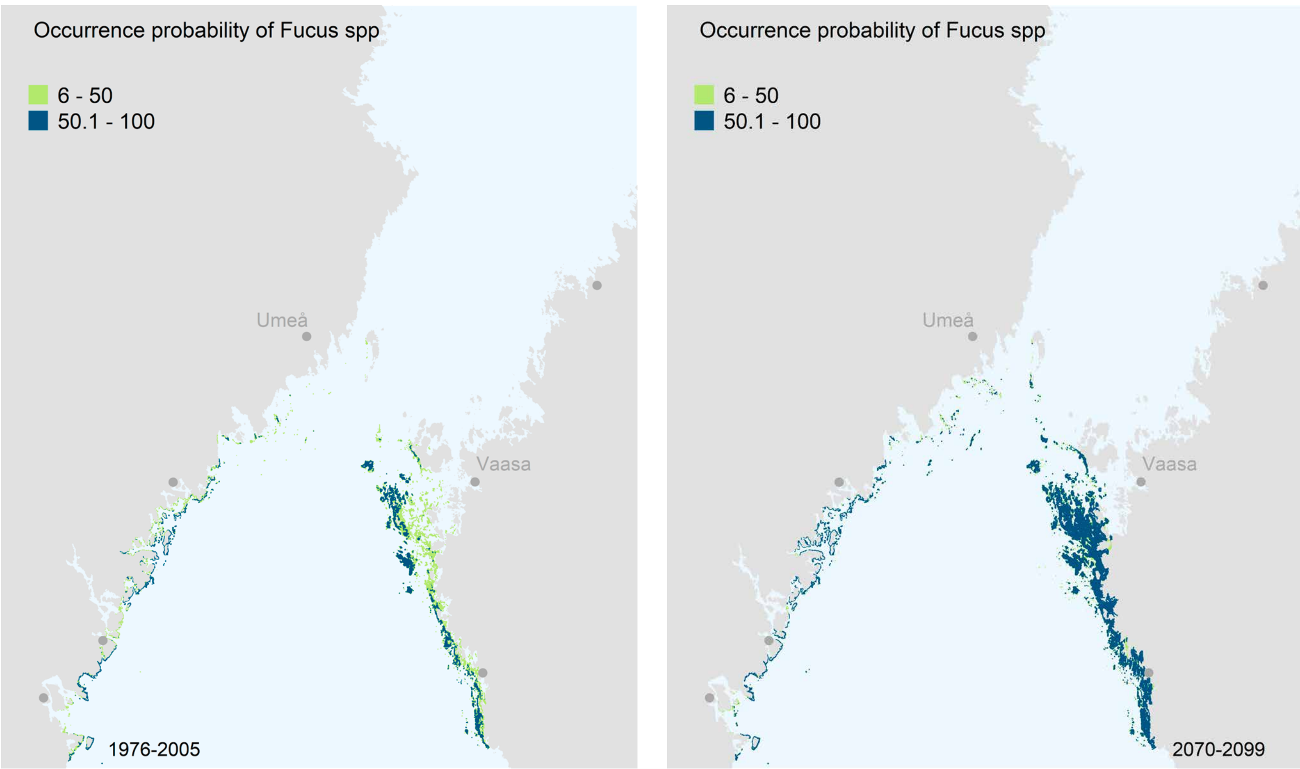


Figure 7. Modelled suitable areas for *Fucus* spp. in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature, light availability and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models are only suitable if there is a hard substrate to which *Fucus* spp. can attach themselves.

when other environmental conditions become more favourable. Additionally, in the northernmost parts of the area of distribution *F. radicans* is expected to replace *F. vesiculosus*, which requires higher salinity. Several previous studies using species distribution modelling have predicted *Fucus* spp. to withdraw south, but the magnitude of the change depends on the climate scenario used (e.g. Jonsson 2018; Kotta et al. 2019; Saari 2021; Viitasalo & Bonsdorff 2021). Our climate models predict a smaller change in salinity than was used in most of the previous studies, which explains most of the differences in predicted future *Fucus* spp. distribution. Additionally, including or excluding the effect of ice determines whether *Fucus* spp. are predicted to increase or decrease in the future.

The increasing water temperature can have both positive and negative effects on *Fucus* spp. Higher temperature decreases survival and reproductive success but can promote growth (Takolander et al. 2017a; Rugiu 2018). Even if the mean temperature during the growing season remains tolerable for *Fucus* spp., heat waves may become detrimental to them. Therefore, the shallow areas that might be suitable for *Fucus* spp. in the future because of thinner or missing ice might not be suitable after all if the temperature rises too high.

Additionally, with the decreasing nutrient levels (assuming that the BSAP is applied), filamentous algae are expected to lose their competitive advantage over *Fucus* spp., which will further improve the growth conditions for *Fucus* spp. in the future. As the suffocation of *Fucus* spp. growths by filamentous algae will ease, *Fucus* spp. can also better compete with filamentous algae for the new, mostly ice-free habitats (Wallentinus 1979; Kiirikki 1996).

The seemingly vast suitable areas in Southern Kvarken in the future are probably an overestimation, because the bottom substrate is not included in the models. As a result, the modelled suitable areas are only suitable if there is hard substrate such as rock or large stones to which the algae can attach. Moreover, ice conditions will continue to vary between winters, and harsh winters with thick ice will continue to occasionally limit *Fucus* spp. occurrence near shallow rocky shores. The mean conditions will be more favourable, but mean conditions, by definition, will not prevail all the time. Therefore, as with all the models, we conclude it is likely that the models indicate the right direction of change, but the actual values and areas depicted on the maps should be viewed cautiously. *Fucus* spp. will probably thrive in the future, and in many places may grow at a broader range of depths, thanks to clearer waters with more light availability as well as mostly ice free shores.

5.2.2. Perennial red alga *(Furcellaria lumbricalis)*

The marine red alga *Furcellaria lumbricalis* will be slightly negatively affected by the declining salinity, and higher water temperatures on top of the decline in salinity may lead to local declines in some near-coastal waters. However, the overall occurrence probability of *F. lumbricalis* will increase especially on the Finnish side of the project area (Fig. 8). Reducing eutrophication as outlined in the BSAP will result in clearer waters and therefore increased light availability. Better light availability will probably make the deeper parts of the region with high enough salinity even more favourable for the species. *F. lumbricalis* prefers deeper waters, because like many other red algae, it is adapted to the light conditions prevailing in deep areas. This adaptation gives them a competitive advantage over other algae. Eutrophication and the following increased water turbidity has pushed the species to shallower waters (e.g. Kontula & Raunio 2018), but the species could spread back to deeper water again in the future, just like *Fucus* spp., as discussed above. The same is expected to happen on the Swedish side of the project area, even though it cannot be seen on the map. This is because the Swedish coastline deepens so rapidly that a similar clear and extensive movement of species into deeper waters cannot be seen at this resolution.

In deeper waters there is less competition with other species compared to shallower depths so this can further benefit *F. lumbricalis* in the future. Our models may fail to a certain extent to take into account the effects of the increasing temperature on *F. lumbricalis*. In deeper waters the increase in temperature can be beneficial to *F. lumbricalis* but in shallower depths the temperatures may rise so high that it becomes detrimental to the species. Torn et al. (2020) predicted that the increasing temperature will be more detrimental to *F. lumbricalis* than declining salinity, resulting in a significant reduction in its distribution. Furthermore, Pajusalu et al. (2016) measured the net photosynthetic rate to be the

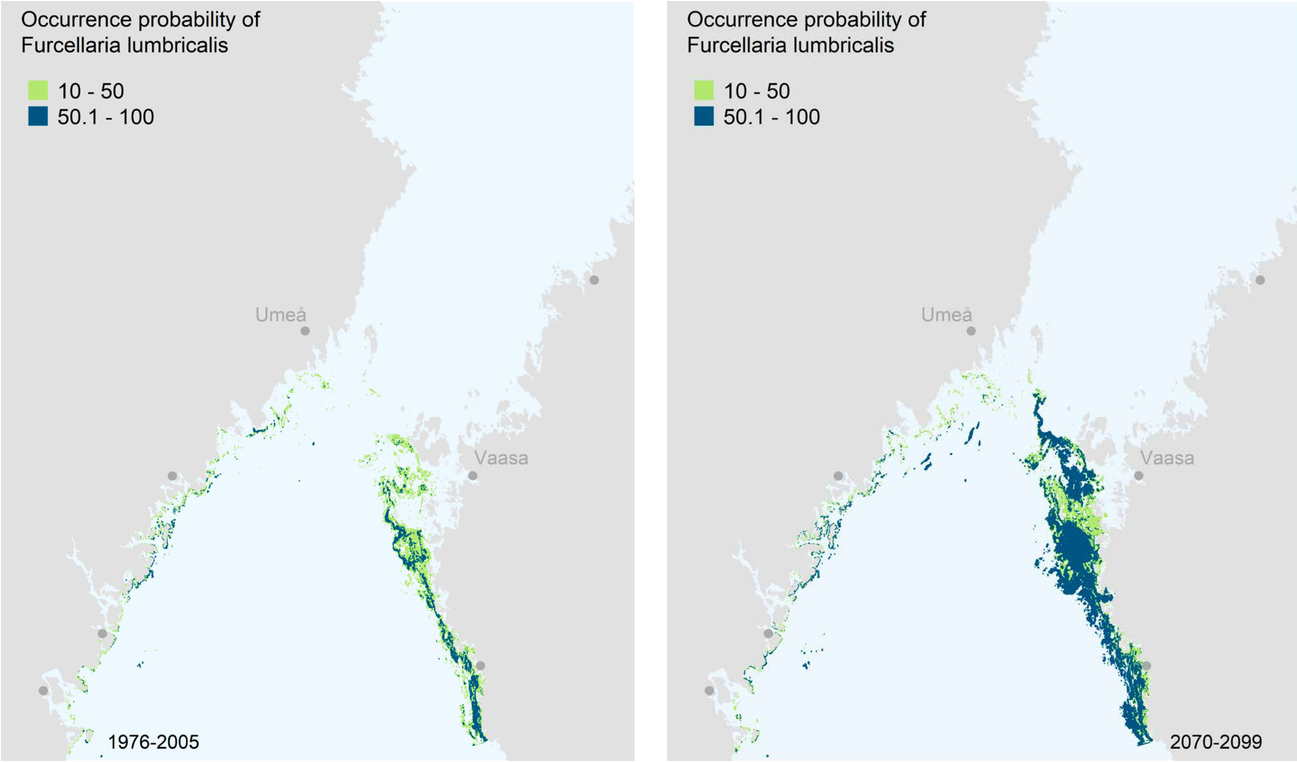
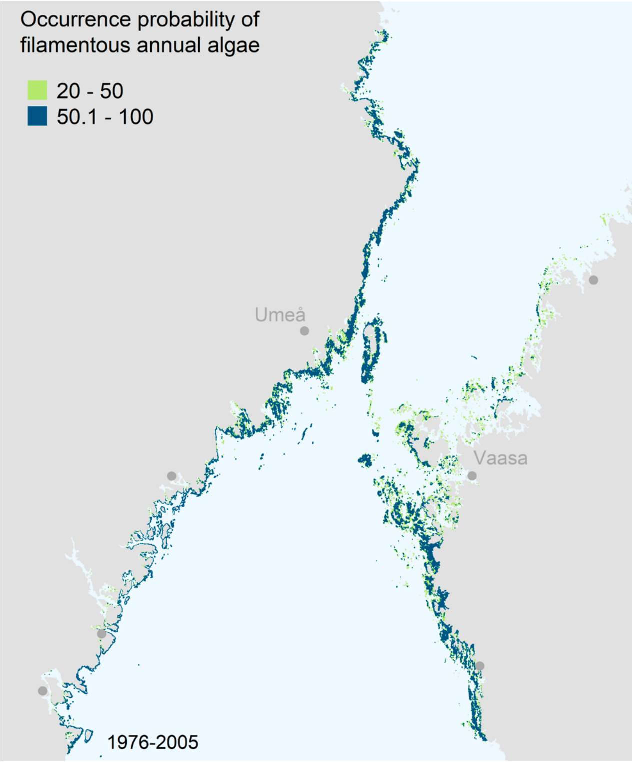


Figure 8. The occurrence probability of *Furcellaria lumbricalis* in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature, light availability and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is a hard substrate to which *F. lumbricalis* can attach.

highest at 10 degrees for *F. lumbricalis* after which it started to decline and fell almost to a minimum at 25 degrees. The predicted mean temperatures in the future exceed this optimum by far. Furthermore, the models used in this project concentrate on the mean temperature, but do not take into account that during the growing season in the future heatwaves could become more frequent and last longer, harming the originally deeper and cooler water-adapted *F. lumbricalis*. Thus, some of the modelled future high occurrence probabilities in relatively shallow water areas are most probably an overestimation.

5.2.3. Filamentous annual algae

Even though the successful implementation of the BSAP will decrease the amount of phosphorous available in the water for algal growth, the models suggest an increase in the areas potentially suitable for filamentous annual algae due to the large increase in temperature. The change is especially prominent in the Bothnian Bay (Fig. 9), where the increase in temperature means a relatively greater improvement in growing conditions than in the already warmer southern areas. However, the models most probably overestimate the future expansion of filamentous algae, as several plant and algae species are predicted to increase and their combined nutrient uptake, together with the implementation of the BSAP, may not leave enough nutrients for annual algae to expand the way the model predicts them to. As primary production in the Bothnian Bay is already phosphorous-limited (as opposed to nitrogen-limited in most other sea areas in the Baltic Sea) (Rolff & Elfwing 2015), the predicted reduction in phosphorous concentration in the sea water makes it unlikely that the area covered by annual filamentous algae would increase as much as suggested by the models. Filamentous algae dominate in nutrient rich waters, but as nutrient concentrations decline, other species such as *Fucus* spp. start to compete for space more. Another interesting factor affecting filamentous algae is the future ice-cover. Ice free winters make the overwintering of filamentous algae more successful, first leading to a diverse and more abundant algal community due to the lack



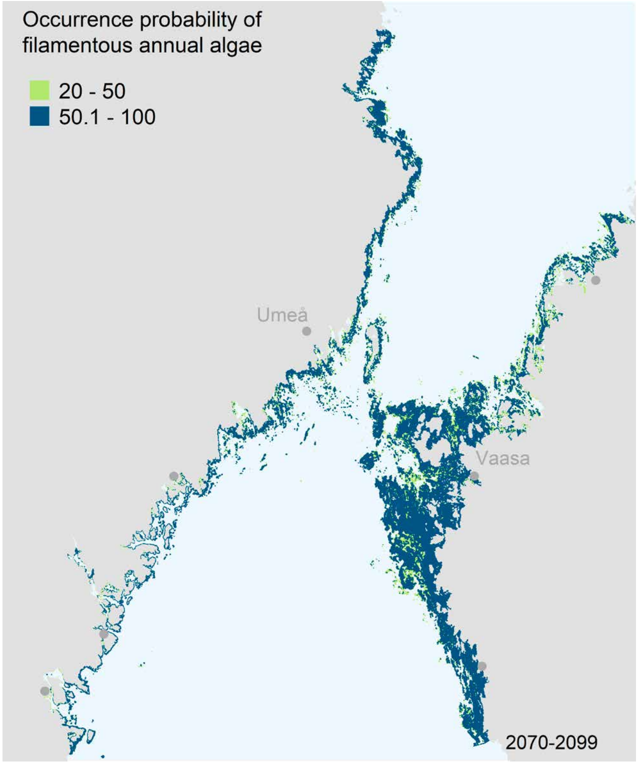


Figure 9. The occurrence probability of filamentous annual algae in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature, light availability and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is hard substrate to which the algae can attach themselves.

of ice-scour effect (Kiirikki & Lehvo 1997). However, in the case of several successive ice free winters, *Fucus* spp. begin to invade the shallow filamentous algal zone and start to compete over space with filamentous algae (Wallentinus 1979; Kiirikki 1996). As the species distribution models do not take competition or other biotic interactions into account, the future distribution of annual filamentous algae will probably be smaller than the future model predicts, but still greater than in the reference period.

5.2.4. Aquatic mosses

The models suggest that there will be substantially more suitable areas for aquatic mosses in the future (Fig.10), mostly due to warmer water and improved water conditions as a result of the reduced eutrophication as outlined in the BSAP. Longer growing seasons and higher water temperatures will benefit aquatic mosses in the northern Baltic Sea, and in clearer waters the mosses can grow in deeper areas. Low salinity would also benefit the originally freshwater bryophyte species, but because the models predict only a very small drop in salinity, the impact of a change in the salinity on the species' distribution will remain small in the future. Although, on a smaller scale and locally in coastal areas, the salinity levels may drop enough to benefit the species. In the future decreasing ice cover and thus the lessening ice-scour effect may also benefit the species in the shallowest coastal areas. A patchy existence is typical for aquatic mosses in the Baltic Sea and regardless of the increasing occurrence probability they are not expected to occur in high densities even in the future. Additionally, in the Bothnian Bay aquatic mosses have few competitors on the hard bottoms due to the low salinity, but the situation is different in Kvarken and south from there where *Fucus* sp., for example, will compete for space, and this will continue to limit the occurrence of aquatic mosses within the project area in the future.

5.2.5. Stoneworts

The predicted future changes in abiotic conditions will have only a small effect on the potential area

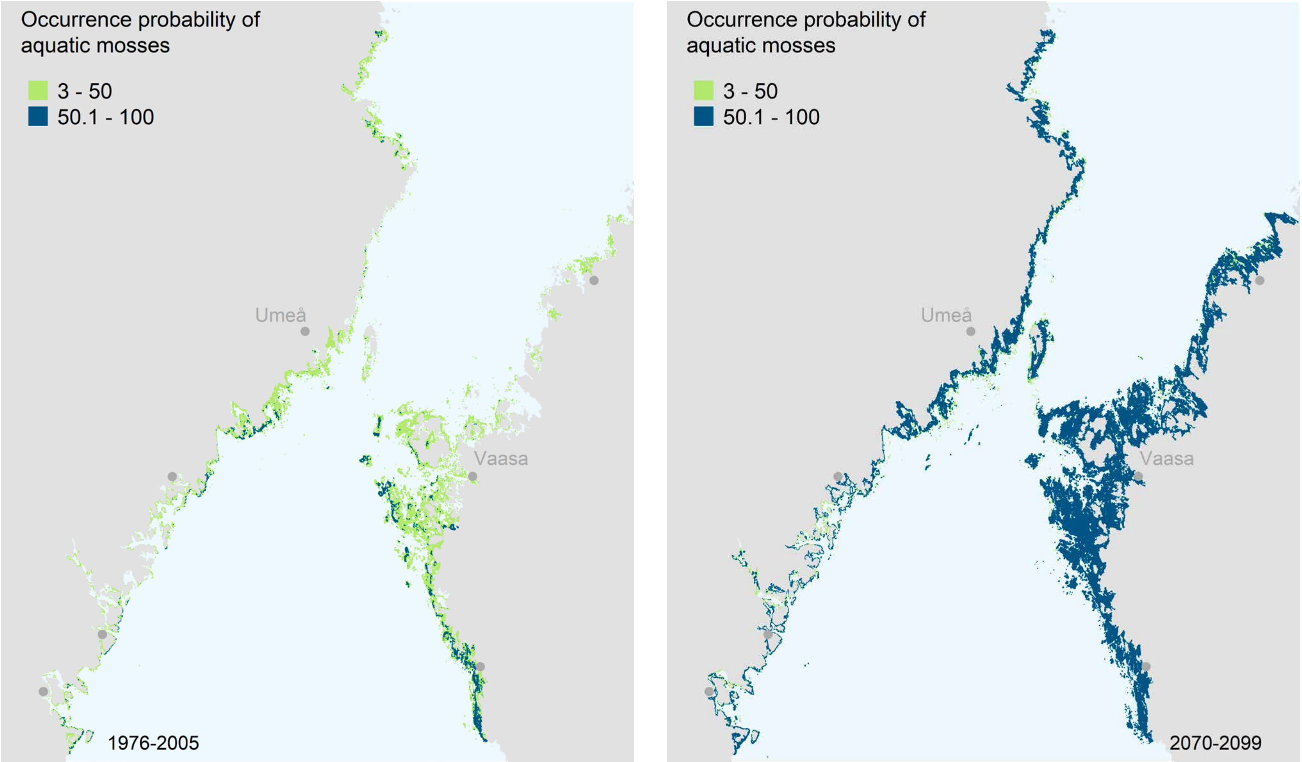


Figure 10. The occurrence probability of aquatic mosses in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature, light availability and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models are only suitable if there is hard substrate to which the mosses can attach themselves.

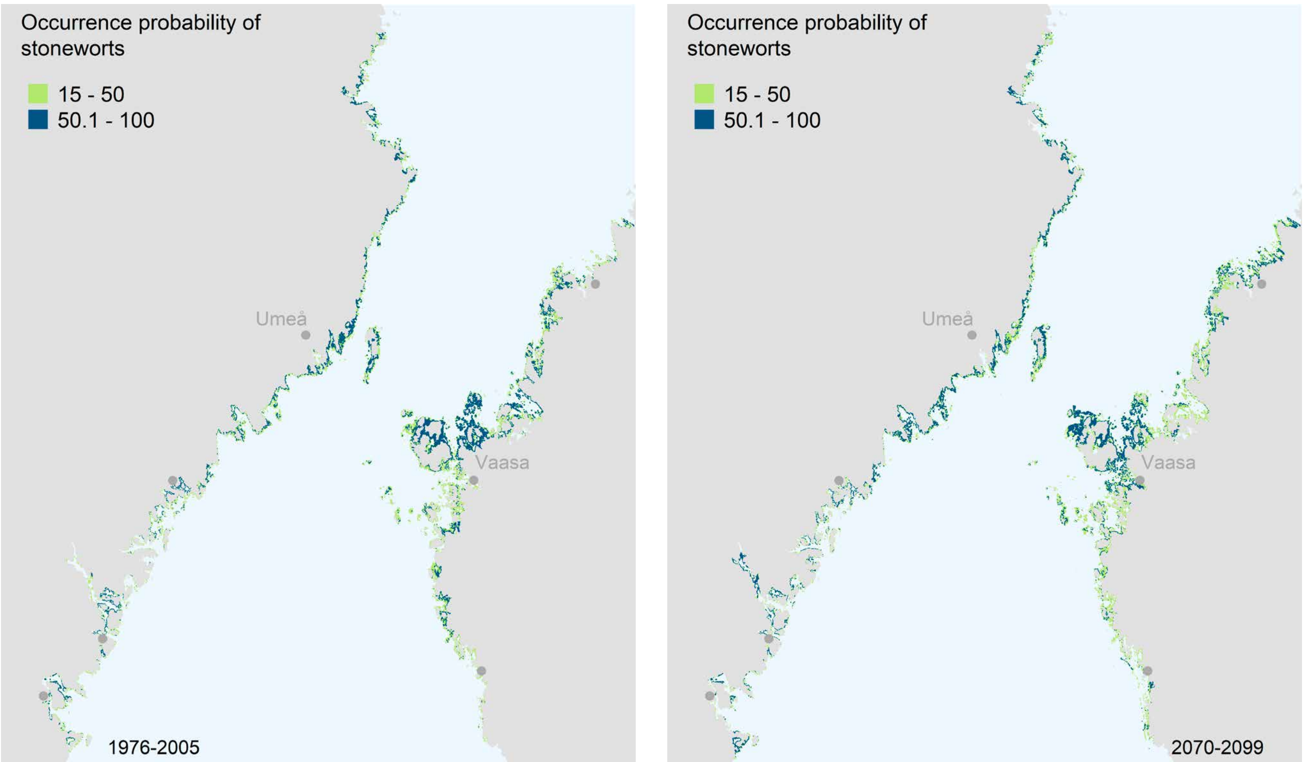


Figure 11. Suitable areas for stoneworts in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature, light availability and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models are only suitable if there is soft sediment upon which stoneworts can grow.

of distribution of stoneworts (Fig.11). In general, stoneworts in the project area may be more limited by the availability of suitable habitats, like flads and other sheltered and shallow areas with a soft bottom, than by the abiotic conditions included in the BRT models. Suitable areas for stoneworts are expected to slightly increase in some parts of the project area while decreasing in others, resulting in a small negative net change. The potential increase of stoneworts is mostly due to warmer and less eutrophicated sea water as well as increased light availability, which makes it possible for the species to inhabit new areas which previously might have been too turbid. Torn et al. (2020) also predicted the stonewort distribution to increase due to the increasing temperature and hence longer growing seasons. As freshwater species, stoneworts will not be harmed by the possible decline in salinity but might even slightly benefit from it.

In very shallow areas ice can have an effect in shaping charophyte and angiosperm communities (Herkül et al. 2017), and stoneworts may benefit from ice because it gives them a competitive advantage over pondweeds (Herkül et al. 2011). In the BRT models the effect of ice thickness on stonewort occurrence was modest but positive. The predicted decline in parts of the study area is therefore probably caused by the decline in ice thickness.

Some stonewort species are sensitive to wave activity and might prefer deeper areas in order to avoid waves (Torn et al. 2019). This occurrence in deeper areas has been limited by reduced light conditions in the past decades (Torn et al. 2019), but with the possible increase in the Secchi depth in the future there is a possibility for several species, including stoneworts, to move into deeper areas if other environmental conditions are favourable. Stoneworts suffer from the spreading of filamentous algae, which according to the models might increase in the future. However, as previously mentioned, the models do not consider species interactions and the future distribution of filamentous algae might not be as wide as suggested by the models. Stoneworts are sensitive to eutrophication due to turbidity, whereas filamentous algae benefit from eutrophication, but as the future scenario used here assumes that the

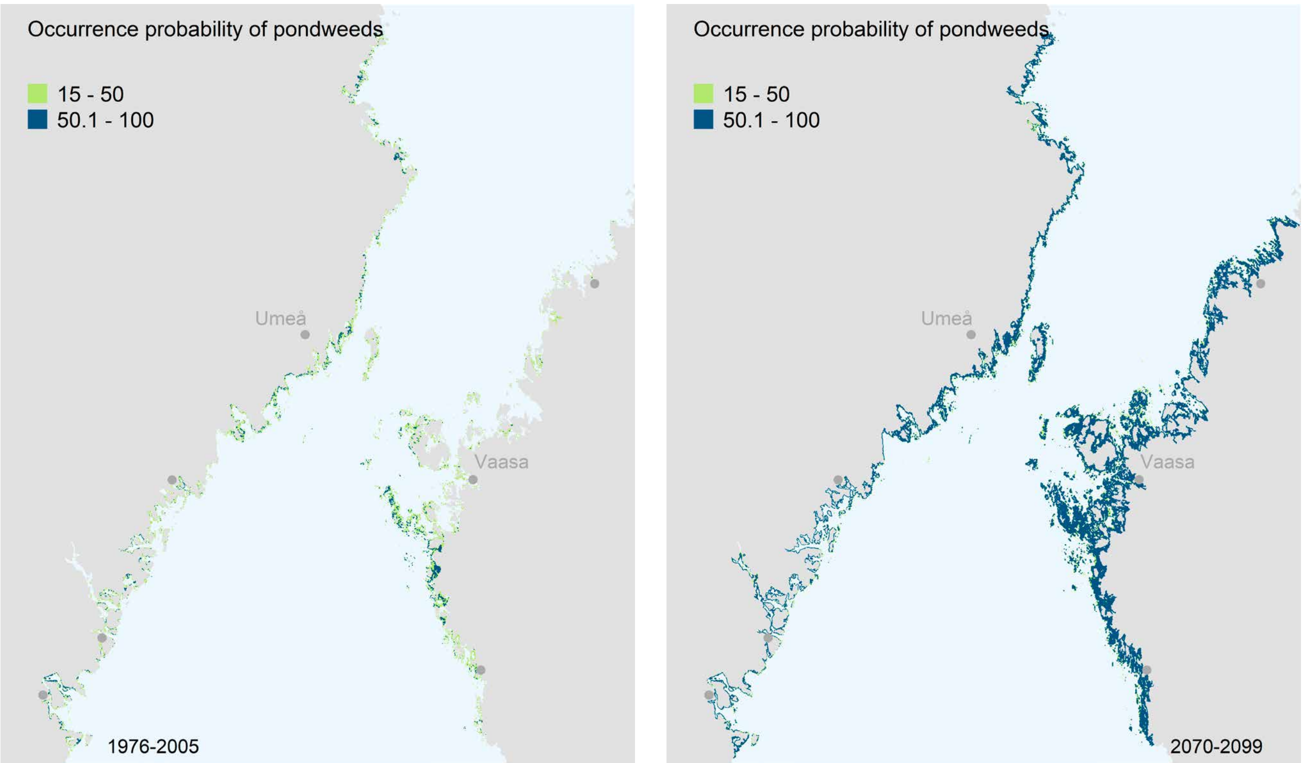


Figure 12. Suitable areas for pondweeds in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature, light availability and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is soft sediment upon which pondweeds can grow.

BSAP is applied, stoneworts should not be threatened in the future.

5.2.6. Pondweeds

The species distribution models suggest a significant increase in suitable areas for pondweeds in the whole project area in the future (Fig. 12). This is partially unexpected, because pondweeds are tolerant of eutrophication (Hansen & Snickars 2014), and the scenario used here assumes that eutrophication will decline due to the application of the BSAP. However, pondweeds will benefit from improved water clarity in the future, similarly to other macrophytes. In contrast to *Fucus* spp., for example, pondweeds will also benefit from warmer and less saline water as they are originally freshwater species. Herkül et al. (2017) also points out that the ice duration can influence pondweed communities because they are perennial. The models show that an average decrease in ice-thickness could benefit pondweeds in the shallowest coastal areas if the ice would not scrape them away every winter. However, the projected decrease in ice-thickness concerns average conditions and there will most probably still be winters with thick ice-cover occasionally.

All these favourable changes combined make pondweeds one of the most positively affected species group of all those that were modelled. Torn et al. (2019) also expects *Potamogeton perfoliatus* to be positively affected by climate change, but their studies did not find a notable effect for *Stuckenia pectinata*. Interspecific interactions were not taken into account in the modelling, and it is therefore not possible to say which soft bottom plants, or stoneworts, will occupy the areas where they are all modelled to expand.

5.2.7. The common reed

The species distribution models suggest that the area occupied by the common reed will not change much, as there will be only slightly more areas suitable for reeds in the future (Fig. 13). The common reed has vastly expanded in the past decades due to eutrophication and also due to the decline in shoreline grazing by cattle, and it can now be found

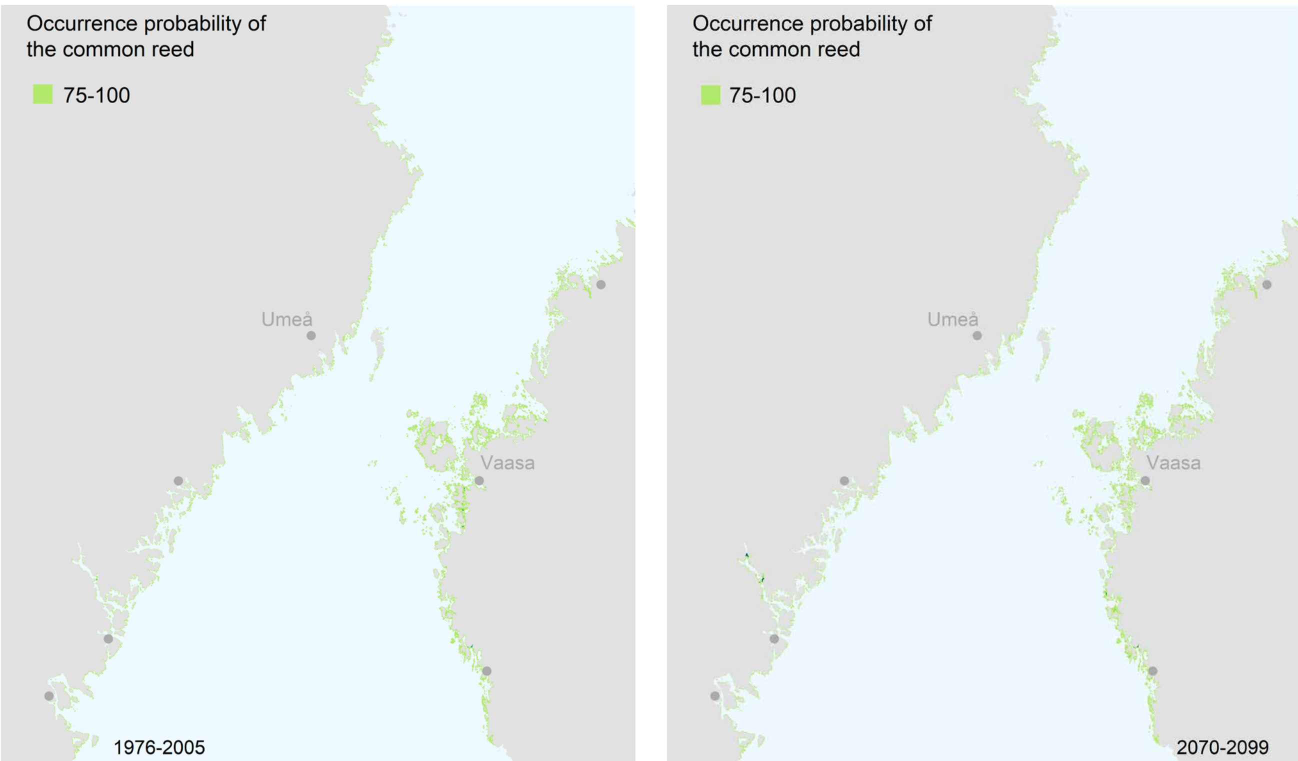


Figure 13. Suitable areas for the common reed in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature, light availability and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is suitable sediment for the reeds.

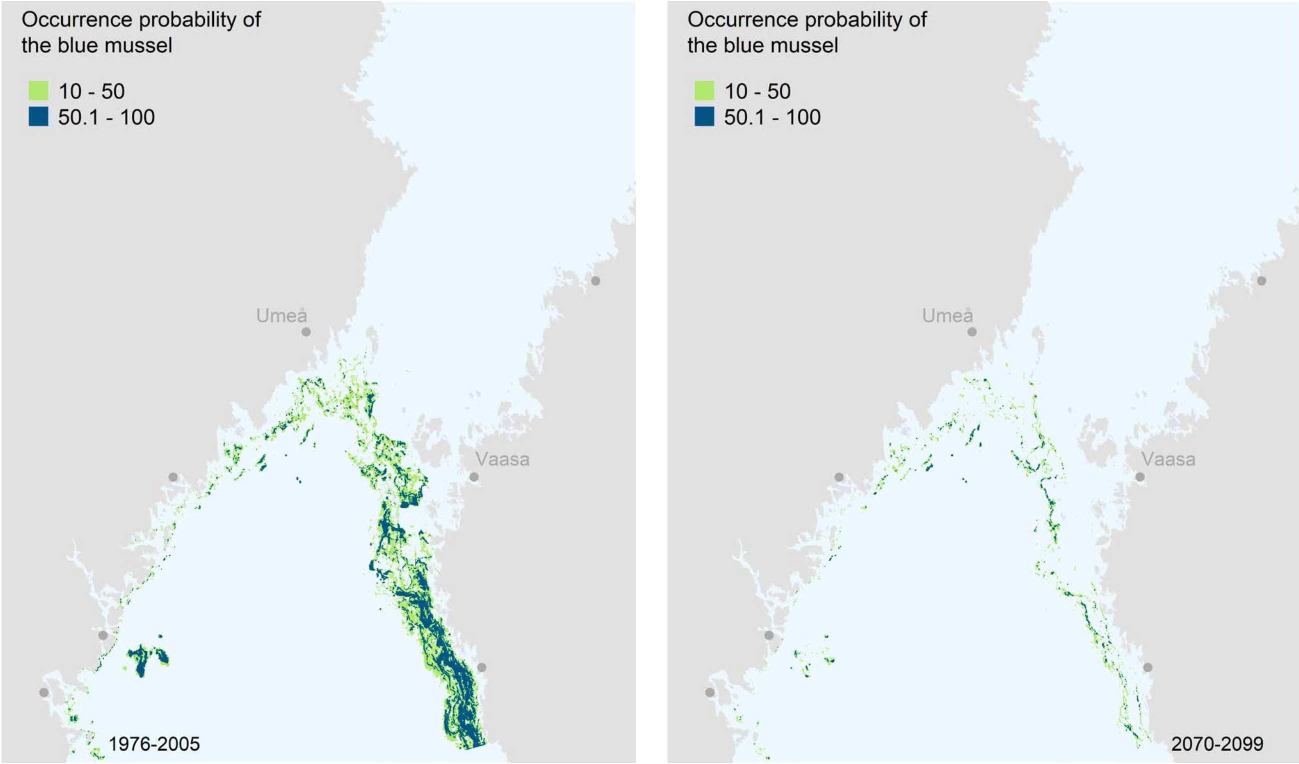


Figure 14. Modelled suitable areas for the blue mussel in the reference period (left) and in the future (right). The areas suitable for the blue mussel will probably shrink in the future due to warmer and less saline sea water. The models are based on environmental variables in the water such as the salinity, temperature and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is a hard substrate to which the mussels can attach themselves.

almost anywhere in shallow areas along the coast. Part of the reason for the small change is the fact that the (aptly named) common reed is already so common that it cannot expand much more. Warmer waters will be beneficial for the growth of the common reed, but reduced availability of phosphorous might limit its expansion.

5.2.8. The blue mussel

The species distribution models suggest that the blue mussel will be negatively affected by climate change (Fig. 14). Blue mussels already live at the limit of their tolerance for low salinity in the project area, and their northernmost occurrences are located in Kvarken. Any unfavourable changes may cause the populations to disappear because the environment is already highly stressful. The models suggest that the salinity will drop below 4.5 in the Gloppet sea area between the islands of Replot and Bergö on the Finnish coast where some marginal blue mussel populations occur today. The effect of the declining salinity will be greater on the blue mussel than the other key species, *Fucus* spp., because *Fucus* spp. was modelled on the genus level, and of the two species in the *Fucus* genus, *F. radicans* tolerates low salinity.

The increasing temperature will stress blue mussels and worsen the conditions in this shallow area even more, and the combined effects of lower salinity and much higher temperature may cause blue mussels to decline. Also other recent studies have reached the same conclusions (Jaatinen et al. 2020). Furthermore, a high mean temperature of the bottom water layer implies that the maximum temperatures will be even higher, and marine heat waves can be detrimental for blue mussels even in the present climate (Seuront et al. 2019). Blue mussels may vanish especially from shallow waters, because shallow areas are predicted to warm more than deeper ones. Indeed, the models predict that the areas that will remain suitable for the blue mussel in the future will be further away from the coast than today, in deeper areas. There is, however, a limit to how deep blue mussels can go in search for lower temperatures (and higher salinity), because there is not enough food (fresh phytoplankton) in areas deeper than about 40 m. Additionally, the bottom substrate is often soft sediment in deeper areas, and blue mussels need hard rock to attach to. Unfortunately, the models do not take into account the bottom substrate, so the predicted occurrence areas will only be suitable if there is hard substrate to which the mussels can attach themselves.

5.2.9. The Baltic clam

The originally marine species the Baltic clam tolerates lower salinity than the blue mussel, down to around 3 ‰, but also it could be slightly affected by the freshening of the water. The models suggest that the northern edge of its area of distribution could move a bit south, or at least the marginal populations, for example North from the city of Vaasa and Raippaluoto island on the Finnish coast, will be more fragmented in the future. Additionally, some coastal areas closest to the mainland both on the Finnish and Swedish coastline could become less suitable for the species (Fig. 15).

The species distribution models suggest that the phosphorous concentration of the sea water correlates positively with Baltic clam abundance. Baltic clam populations have increased in past decades, most probably due to eutrophication and increased food supply (Ehrnsten et al. 2019). In the future, as the phosphate concentration drops significantly according to the BSAP, the clams will again have less food, which may lead to a decline (Ehrnsten et al. 2020). The predicted decline in the future can therefore be a combination of at least two stress factors, less saline water at the population margin and lower food availability throughout the project area. However, the Baltic clam is a resilient and adaptive species, and when conditions change, it will probably adapt to the changes more easily than some other benthic animals, such as *Monoporeia affinis* (see below). The Baltic clam is likely to do well also in the future climate on the scale of the whole project area, but the actual distribution range and local population densities will be the result of many factors, such as environmental conditions, interspecific interactions, and perhaps most importantly, food availability.

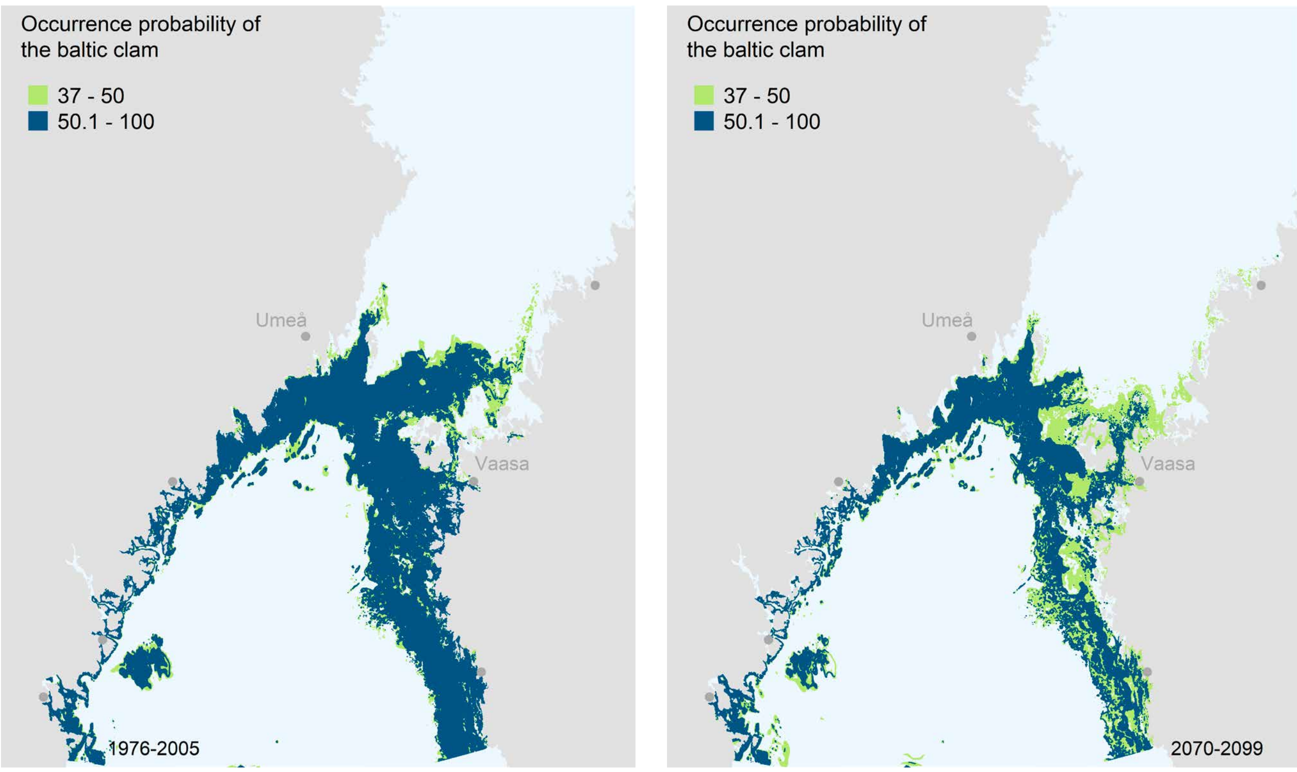


Figure 15. Suitable areas for the Baltic clam in the reference period (left) and in the future (right). The species will be abundant also in the future but may decline due to lower food availability and salinity. The models are based on environmental variables in the water such as the salinity, temperature, and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is soft sediment.

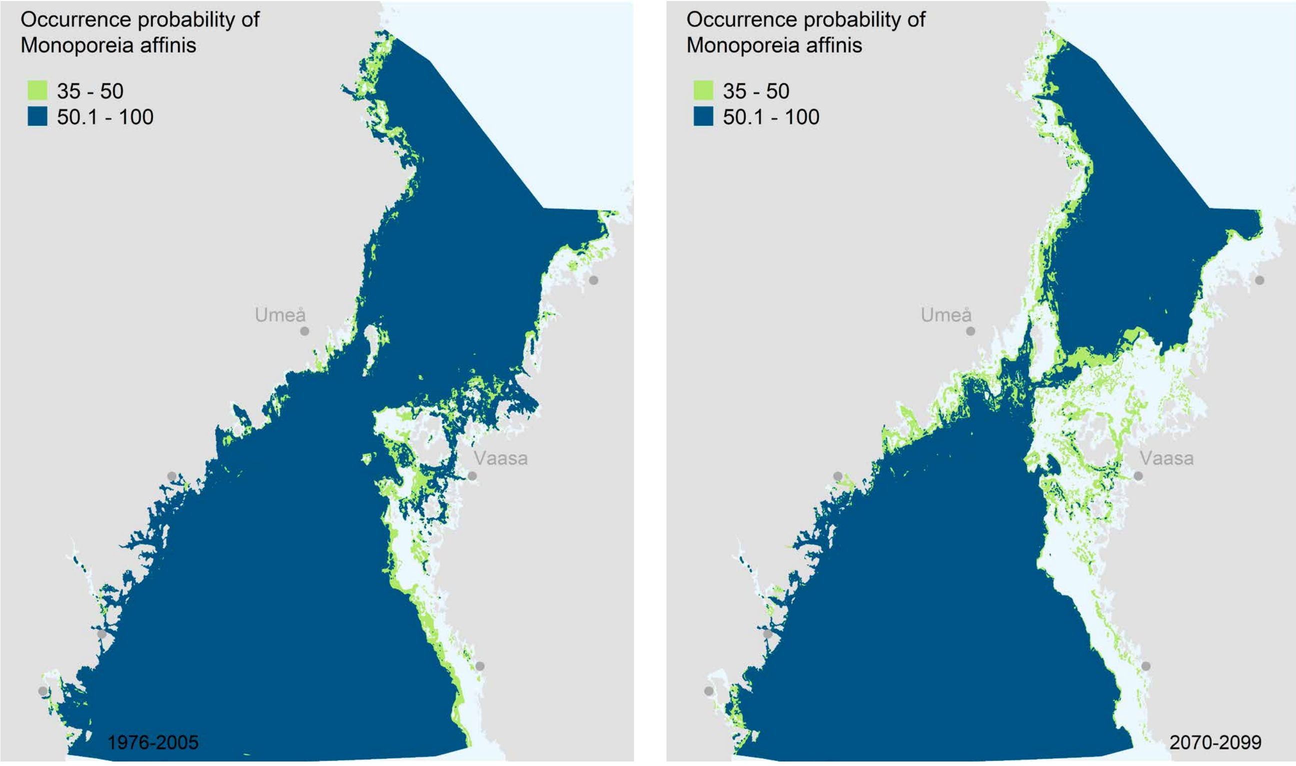


Figure 16. Modelled suitable areas for *M. affinis* in the reference period (left) and in the future (right). Rising water temperatures are expected to make the shallow middle parts of Kvarken less suitable for the species. The models are based on environmental variables in the water such as the salinity, temperature, oxygen and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is soft sediment.

5.2.10. *Monoporeia affinis*

As *Monoporeia affinis* thrives in deep, cold waters, it will suffer from the increasing temperature. However, as it is a species of freshwater origin, it will not be affected by the declining salinity, so in contrast to marine species such as the blue mussel, it will not have to tolerate the combined stress of the environment becoming too fresh and too warm. *M. affinis* is also sensitive to eutrophication and oxygen levels in the water. The future models do not show a considerable change in oxygen levels nor an increase in eutrophication due to the implementation of the BSAP. Hence, these two factors are not expected to affect the distribution of *M. affinis* in the future.

However, based on the future model, it is the most negatively affected soft-bottom species of those that were modelled (Fig. 16). The models suggest that most of the coastal areas in the project area, especially in the middle of Kvarken, might become unfavourable for the species due to rising water temperatures. In an extreme case, the population may even split into a northern Bothnian Bay population and a southern Bothnian Sea population. However, the species distribution models were run for a certain minimum density, and the absence of a predicted occurrence does not mean that the species would not occur there at all, only that the area is not likely to be suitable for such high densities the model was made for. In other words, the *M. affinis* population in the middle parts of Kvarken is more likely to decline in the warm, shallow areas than to disappear entirely.

The models do not take into account the diverse interspecific interactions within the zoobenthos community. In the Gulf of Bothnia there has been a shift in the benthic fauna as *M. affinis* has decreased and *Marenzelleria* spp. has invaded the area. The two species share the same phytoplankton food source (Kotta & Ólaffson 2003; Eriksson Wiklund & Andersson 2014), and with the declining primary production in the future as a result of the BSAP, the availability of phytoplankton will be lower than today. This could further negatively impact the state of *M. affinis* in the area (Eriksson Wiklund & Andersson

2014). There was a shift in the benthic community in the late 1990s and early 2000s that may have occurred as a consequence of the lower-than-normal primary production in the Gulf of Bothnia during which *M. affinis* drastically reduced, making room for *Marenzelleria* spp. to occupy the area (Eriksson Wiklund & Andersson 2014). However, Karlson et al. (2015) showed that *Marenzelleria arctica* does not compete with native species, but appears to occupy a different, previously vacant niche. The Baltic clam has also been seen to take advantage of the decline in *M. affinis* and inhabit areas previously inhabited by *M. affinis* (Kauppi et al. 2015), but the mechanism seems to be that *M. affinis* inhibits the settlement of young Baltic clams (Ejdung et al. 2000).

5.2.11. Chironomid larvae

Chironomids are considered a group of species that can survive in a broad range of environmental conditions and are therefore abundant in many habitats. Some of the chironomid species (such as *Chironomus plumosus*) are able to tolerate lower oxygen levels than most other bottom animals. However, many of the chironomid species are also considered to indicate the good ecological state of water bodies. Because chironomid larvae are a vast group that consists of many genera and species, some of them may respond to changes in environmental conditions differently to others. Therefore, their responses as a group are not as straightforward to model or to interpret as those of a single species.

Chironomid larvae are abundant and widely distributed at present, and nothing in the future seems to threaten them. It is possible that water temperatures at the seafloor limit their depth range at present, and if this is the case, there may be some potential for an increase in the future. Additionally, the BRT models show a clear positive response by chironomids to the water temperature. If the increase in water temperature is beneficial for chironomid larvae, it may lead to an expansion of the area of distribution to deeper waters. Other changes are not expected to have much impact on chironomid larvae as a group, but it is possible that the relative abundances of genera and species may change. Species that benefit most from future conditions will have a competitive advan-

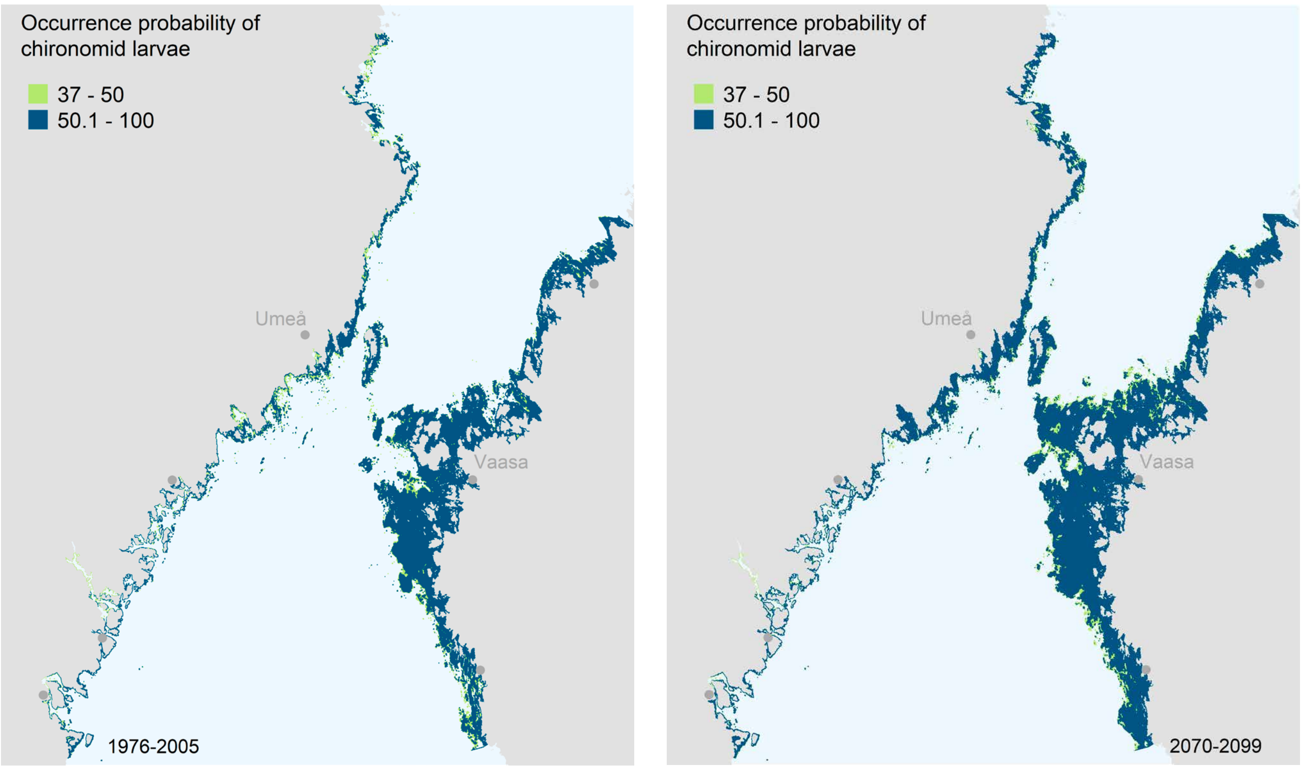


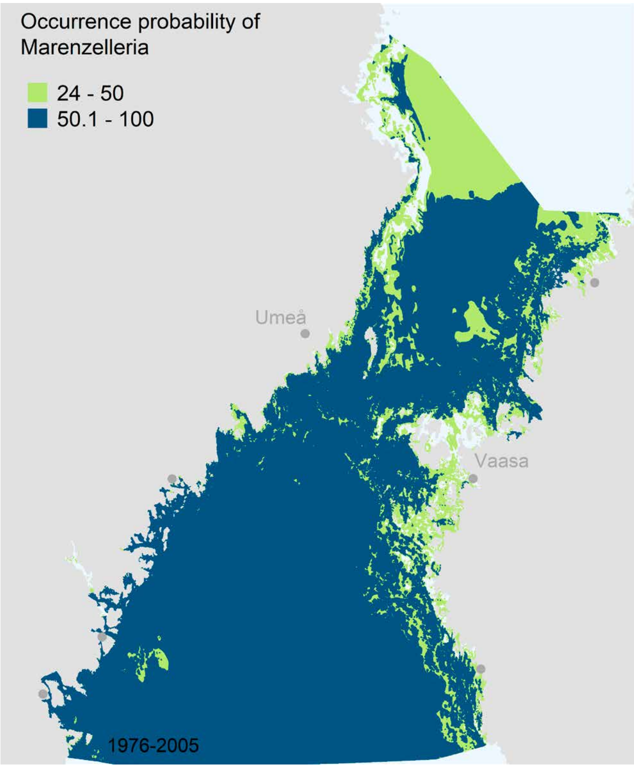
Figure 17. Chironomid larvae, which are abundant and widely distributed at present (left), will also do well in the future (right). Increasing water temperatures may make deeper areas more favourable for them as a habitat, increasing the depth range where they occur. The models are based on environmental variables in the water such as the salinity, temperature and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only be suitable if there is soft sediment.

tage over those species for which past conditions were better. Additionally, changes taking place in terrestrial ecosystems and in abiotic conditions on land can have an effect on chironomids, because only the larvae are aquatic. Such effects, however, are beyond the scope of this project.

5.2.12. *Marenzelleria* spp.

Non-native *Marenzelleria* species are of marine or brackish water origin, but they are tolerant to a wide range of salinities (e.g. Zettler et al. 2002). They also occur at a wide range of depths and therefore also different water temperatures. Because of this broad niche, they are widely spread in the Baltic Sea and will not be affected much by the projected climate change. The deeper bottoms of the most northern parts of ECOnnect project area may become slightly less favourable for the species due to lower salinity. Although, it is important to note that *Marenzelleria* spp. occur further north in the Bothnian Bay in very low salinity (VELMU 2020), so even if the occurrence probability of the species were to slightly drop at the deep bottoms of the northern areas, the environmental conditions would still be good enough for the species to remain viable in the area. In contrast, many regions in the project area, especially shallow coastal areas, will become more favourable for the species due to the expected temperature rise. *Marenzelleria* spp. are known to benefit from higher temperatures (Zettler et al. 2002; Andersson et al. 2015), but they often do not reach high abundances in shallow bottom areas if vascular plants or stoneworts are abundant (Janas & Kendzierska 2014). Thus, the highest numbers of individuals will most probably be found in deeper areas that are free from vegetation also in the future.

In the southern and eastern Baltic Sea *Marenzelleria* spp. have occupied bottom areas from which *M. affinis* has disappeared mostly due to low oxygen. In the Gulf of Bothnia the same has happened possibly due to a decline in primary production (Eriksson Wiklund & Andersson 2014). Should the occurrence of *M. affinis* continue to decline in the future, it is possible that *Marenzelleria* spp. will colonize the empty bottom areas. However, an increase of the *Marenzelleria* population is not necessary a consequence of *M. affinis* decline, but a result of continuing spreading after introduction, just taking place at the same time. Additionally, it is important to note that the interspecific relations of *Marenzelleria* spp. and other benthic invertebrates occupying similar niche are still not entirely clear and some uncertainties remain of their competitive position in relation to each other.



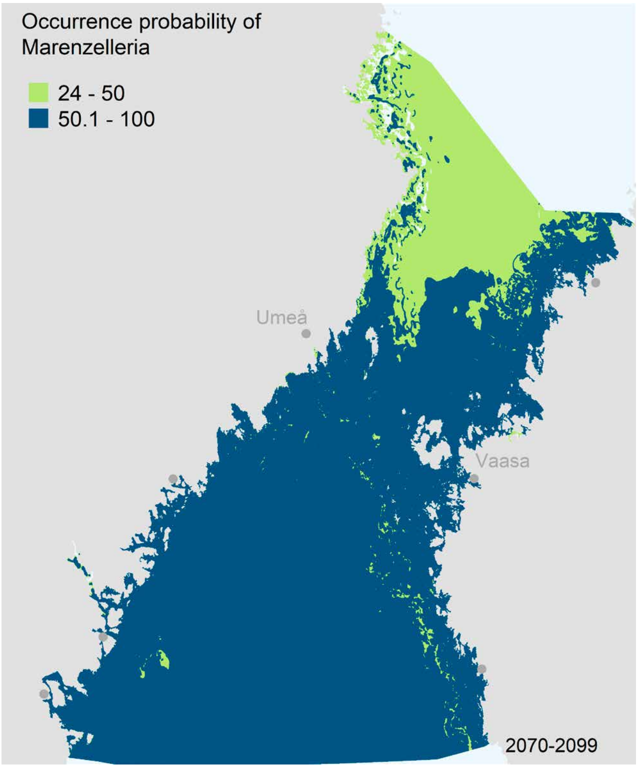


Fig. 18. Suitable areas for *Marenzelleria* spp. in the reference period (left) and in the future (right). The models are based on environmental variables in the water such as the salinity, temperature and nutrients. The bottom substrate is not taken into account, so the areas predicted to be suitable by the models will only suitable if there is soft sediment.

6. Discussion

The underwater nature in the project area in the future will most probably resemble the one that is familiar to us today. The same species will occur in the area, but locally they may have disappeared or appeared in new areas, or their relative abundances and hence dominance hierarchies may have changed. For those species that were modelled here as species groups, there may also be changes in the species composition and the relative abundances of species. The main factors causing these changes are the increase in water temperature, the thinning of the ice, and the decline in salinity. The improving ecological state of the sea and resulting increase in light penetration will benefit most species. Several plants and algae will thrive in a wider depth zone or have a broader distribution extending from the open sea to inner waters in the future. This widening of the occurrence areas will be due to thinner ice, warmer water, greater light availability, or a combination of these, depending on the species. In many cases, the broadening of suitable areas in the middle and southern parts of the project area will more than compensate for the possible loss of the northernmost populations in terms of total area.

Although the changes in salinity are highly uncertain, the recent models suggest a slight decline in salinity. The predicted decline is small, especially compared to several earlier projections (e.g. Meier et al. 2006), and the shifts in species distributions resulting from it are on the magnitude of some tens of kilometres. Still, even that small decline may lead to changes in the occurrences of the blue mussel and the Baltic clam. The key species *Fucus* spp., in contrast, are not expected to decline, because *F. radicans* tolerates low salinity and may benefit from other environmental changes, mainly the increase in light availability and lower mean ice thickness. On a larger scale, the species will therefore not disappear, but only shift, or not respond at all to the small change in salinity.

In several previous studies, *Fucus* spp. have been predicted to decline rather than increase in the future (Vuorinen et al. 2015; Jonsson 2018; Kotta et al. 2019; Saari 2021; Viitasalo & Bonsdorff 2021). The key differences between this study and most of the previous ones lie in the notably different salinity projections and in the effect of ice. Ice is destructive for perennial vegetation because it scrapes shallow shores clean every winter. It is possible that the effect of the ice, even though genuinely positive, is exaggerated in the models used in this project due to the underlying data structure. Both the ice thickness and *Fucus* spp. occurrence have a strong latitudinal gradient, which could affect the results. Additionally, the resolution of the data is not optimal for detecting the effect of ice reliably. To test the effect of ice in the *Fucus* spp. model, also a model without ice was run. Without ice, the BRT model predicted that areas suitable for *Fucus* spp. would decline because of decreasing salinity and increasing temperatures, similarly as for example Saari (2021) showed. However, the decline in the ice thickness is one of the future changes with the least uncertainty. In other words, it seems more likely that the ice will become thinner than that the salinity will decline. Therefore, the full model with ice was used, but it is noteworthy that without ice the results do look different. The thinning of ice is not the only positive change in the future for *Fucus* spp., as also the increase in light availability will be favourable for them. The (small) decline in salinity might not even be so detrimental to *Fucus* spp. as generally thought, because under experimental conditions some *F. radicans* individuals have grown even better under future conditions, down to 2.5‰ salinity (Rugiu et al. 2018). To conclude, it seems possible that areas suitable for *Fucus* spp. will increase, even though it has to be kept in mind that also another kind of future is possible.

The warming of the water and the thinning of the ice, which are the strongest predicted environmental changes and also the ones with least uncertainty, will also cause the most remarkable and extensive changes in species distributions. Especially the blue mussel and *Monoporeia affinis* will decline in large areas, while pondweeds, filamentous algae, aquatic mosses, and *Furcellaria lumbricalis* will expand in most areas, and especially in the shore areas of the Bothnian Sea. Additionally, chironomid larvae could be expected to benefit from increasing temperatures.

Marine heat waves are an emerging phenomenon that has been discussed a lot lately (Smale et al. 2019; Paalme et al. 2020). These events can cause mass deaths of not only fish, but also invertebrates, such as the blue mussel, and even macroalgae (Graiff et al. 2020; Takolander et al. 2017a). However, mean growing season conditions of a period of 30 years were used in the species distribution modelling in this project, so the occurrence or impact of extreme conditions such as marine heat waves were not studied. In reality, extreme conditions might have a profound impact especially on *Fucus* spp. and the blue mussel that have already now been observed to die during extreme or repeated heat events (Takolander et al. 2017b; Seuront et al. 2019). Mean environmental conditions were used in this work because they can be modelled with less uncertainty and by definition, will prevail most of the time, in contrast to minimum or maximum values, but it is good to keep in mind that climate change is predicted to increase the probability of extreme weather events also in the sea (Meier et al. 2019).

There are also several species for which the models do not predict any major changes. Species expected to thrive about as well in future conditions as in the reference period include the common reed, stoneworts, chironomids, and species of *Marenzelleria*. On a large scale, their areas of distribution will remain similar to how they have been in the reference period.

Some of the predicted changes are at least partially a return to the previous state rather than an actual new situation for the species. This is the case for *Fucus* spp. and *F. lumbricalis*, which may return to deeper areas if light conditions improve close to historical levels, and also for the Baltic clam, which may slightly decline due to lower food availability. The Baltic clam has increased due to eutrophication, so a small decline is to be expected when nutrient concentrations in the sea water return closer to their natural level.

Several of the predicted future species distributions are conditional on the application of the BSAP. Many species will benefit from the lower phosphate concentrations in the water, leading to decreased phytoplankton production, and hence clearer waters with increased light availability. If the countries surrounding the Baltic Sea fail to execute the nutrient load reductions required by the BSAP, the future may look very different. Indeed, several studies have concluded that at least in the short term, nutrient inputs have a greater effect on the sea than climate change (Saraiva et al. 2019a; Pihlainen et al 2020; reviewed in Viitasalo & Bonsdorff 2021). Studies suggest that climate change will amplify the effects of eutrophication (Saraiva et al. 2019a), which may exceed the stress tolerance of several marine key species, including *Fucus* spp. and the blue mussel. Marine species can hardly tolerate both changes simultaneously, so it is essential to reduce nutrient loads so that marine life can use its resilience for adapting to climate change.

Finally, it must be kept in mind that the climate scenario used here was RCP8.5, which is considered as the worst-case scenario. If GHG emissions are reduced sufficiently and global warming is reduced accordingly, the changes in the sea would resemble the trends presented here, but be much smaller, which would be a safer path for both the ecosystem and the people ultimately dependent on it.

6.1. Sources of error and uncertainty

There is inevitable uncertainty related to all kinds of future projections and modelling. The scenarios and results presented here have several underlying sources of uncertainty and possible error, which need to be considered when evaluating the results. Uncertainty here refers to the fact that it is not possible to know exactly how the climate, society, and ultimately, GHG concentrations and other abiotic variables affected by it will function and develop in the future. Error, on the other hand, refers to shortcomings of the models, methods and data. For example, the effect of increasing GHG concentrations on salinity is *uncertain*, because it is not very well known how much precipitation and river run-off, for example, will increase, but if precipitation is wrongly accounted for in climate models, there will also be *errors* in the salinity estimate. Here, we discuss possible sources of uncertainty and errors in the order of the workflow from climate models to changes in species distributions in 100 years.

All values and estimates for future species distributions, ecosystem services (ES), and connectivity in project ECOnnect are ultimately based on the chosen future scenarios, RCP8.5 and the BSAP. Achieving the goals of the BSAP is possible and seems reasonably likely, as discussed in Section 3.1. The RCP8.5 scenario, in turn, is often used and referred to as a worst-case climate scenario, and it is possible that the future will not be as extreme when it comes to climate change as RCP8.5 suggests. Regardless of what scenario was used, the choice of scenario always brings inherent uncertainty, because it is not possible to know what the future will be like.

Another source of uncertainty is related to the circulation model (RCO-SCOBI) and the Earth System models (A, B and D) on which the environmental variables are based. Uncertainty is handled here by using the average of the predictions of the three different models (A, B and D). Still, there is great uncertainty left, as for example salinity is affected by several processes, none of which can be modelled perfectly. Here exist also possible sources of error, as the conversion of circulation model outputs into raster layers used in BRT modelling includes several steps where it is possible but unlikely that information gets distorted.

BRT modelling is a robust modelling procedure, which can handle missing values and correlated variables, among other common problems. However, like with all other modelling techniques, its output is only as good as the input data, at best. In practice this means that the species distribution models for both the reference period and the future are impacted by the quality of the species observation data and environmental layers that were used to create them. While the observation data especially for plants and algae has an exceptionally large sample size for a biological data set, comprising of tens of thousands of observation points, for example the ratio of presences to absences, or so-called prevalence, affects the result. Prevalence, in turn, is partially the result of treating values smaller than some threshold as absences. The threshold values are somewhat arbitrary, but they were used so that the modelling would focus on thriving populations that could form nature types and provide ecosystem services, and not to mix these dense populations with observations of just one or a few individuals.

The quality of the species data is high, and the only potential issue is related to the detection probability. For example, some very small individuals might not be seen in drop videos if they are covered with filamentous algae. As observations of very low densities would anyway be treated as absences, this has no effect on the results.

The most obvious and severe source of uncertainty and error in the modelling process is the lack of sufficiently good maps of the sea floor (bottom) substrate from both Finland and Sweden. The right kind of substrate is required for any sessile species to occupy an area. As the species distribution models lack a layer for the substrate, the areas predicted to be suitable are inevitably an overestimate.

The raster layers for environmental variables have a relatively coarse resolution. The species distribution models have the same resolution because they are essentially made from the environmental variables. As a result, small scale gradients in archipelago areas or along the coast may not be well reflected in the maps. The species distribution maps may both underestimate or overestimate the occurrence of species. Most of the environmental variables originally had an even lower resolution, but they were resampled to match the depth and exposure that had the smallest cell size.

The BRT models were run separately for each species and any information on the presences of other species was not used. In practical terms this means that the models do not take into account interactions between species. In reality, competition is an important factor in shaping species communities and distributions. This shortcoming means that the areas predicted to be suitable by the species distribution models are probably in many cases too large, as parts of the area will be occupied by some competing species. Therefore, considering the lack of bottom substrate and interspecific interactions in the models, the predicted areas should be viewed as maps of potentially suitable areas, if the bottom substrate happens to be favourable for the species and if no other species prevents the modelled species from colonizing that place.

A key feature in the BRT modelling process is that the response of species to environmental variables is inferred from the species observation data and the values of environmental variables at species observation sites. These responses are then used to predict the suitability of those areas where biological data has not been gathered. In the case of future species distribution modelling, the responses inferred from reference period data are applied to future environmental conditions to find where suitable areas might be located in the future. This approach has an underlying assumption that the species' responses to and tolerances for environmental variables will not change in the future. In more biological terms, species are assumed not to adapt to changing conditions, but to only shift their distribution and try to remain in a similar kind of environment that was suitable for them in the past. It is unlikely that species responses and tolerances would change in a short time, and that is the very problem with fast environmental changes.

The modelling process includes several choices of parameters, such as the fraction of data used to fit the model (versus testing it), which can affect the result to some extent. In some cases, these can lead to slightly different outcomes and can thus be seen as sources of uncertainty, but on a larger scale these play only a minor role. The modelling process in general is a complex one where the possibility of human error is always present. This was minimized by evaluating the reference period species distribution models with local experts, who confirmed their accuracy was sufficient.

An important feature and step in BRT models are the so-called response curves, that the modelling process infers from the data. For some species and abiotic variables, there is a priori knowledge of what a species' response to the variable is, like for example, that *Fucus* spp. favour more saline water. However, it is not possible to directly modify the response curves, and only by modifying the input data can the shapes of the curves be affected. In a few cases, where the "right" response was known and where the inferred response curve appeared biased at some end, the input data was filtered so that the response was improved. For most responses, however, this was either not needed (the responses seemed correct) or was not possible, as the tolerances of the species are not known.

7. Conclusions

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.

Climate models used in this project indicate that the most drastic environmental changes will happen in water temperature and winter ice-cover and thus they will have the greatest effect on species and ecosystems. The salinity, which strongly affects the distribution of species, is not expected to change dramatically within 100 years, although future predictions of the salinity are highly uncertain. If the salinity were to decrease more than the models predict, then the changes in species occurrences could be more pronounced and in turn affect the ecosystem services they produce. In general, the models show a similar flora and fauna in the future compared to the reference period in the project area. The most notable future changes in species distribution are expected due to warmer and clearer waters, decreasing ice-cover and slightly lower salinity. The marine species that are already living at the limit of their tolerance for low salinity (e.g. the blue mussel) might decline in the future as well as the species which prefer cool waters (e.g. *Monoporeia affinis*). Then again, the declining ice-cover will especially benefit perennial algae and vegetation as the ice will not scrape them off each year. The nutrient reductions according to the BSAP will result in clearer waters which will benefit most species that are originally adapted to lower nutrient levels.

Changes in the connectivity and the provisioning of ecosystem services in many parts in the future are expected and follow the changes in species distribution and abundance. Regarding the ecosystem services produced by the modelled species, the quantity of the services is not expected to change much, but since the species distribution areas are expected to change, also the areas where certain services are produced will shift to different areas. A lot more on the expected future changes in ecosystem services can be found in the ECOnnect report *Ecosystem services in the central Gulf of Bothnia*.

Results from connectivity analyses suggest that Kvarken is an important route for species to move between Sweden and Finland. The Finnish side of the Gulf of Bothnia promotes the movement of species because the coastline is shallow and thus fosters lush ecosystems for many species to occur. On the Swedish coast, the movement of species is restricted in many places due to the deep coastline, which limits the occurrence of many species to a rather narrow zone and weakens the possibilities for dispersal between habitat patches. The Swedish coastline in the central Gulf of Bothnia can thus be considered naturally fragmented and sensitive. Further results from the connectivity analyses can be read in the ECOnnect report *Ecological connectivity and resilience of marine protected areas in the central Gulf of Bothnia*. Species and ecosystems adapt to changes in their environment if the changes are gradual and happen over a long period of time (Jansen et al. 2007; Viitasalo et al. 2015). However, human induced climate change is not gradual but rapid in nature (Jansen et al. 2007; Viitasalo et al. 2015) and poses major challenges to the ability of species to adapt (Viitasalo et al. 2015; Urban 2015).

The changes in environmental variables according to the project's models are in line with current predictions from other sources concerning the future in the Baltic Sea and Gulf of Bothnia, most notably HELCOM & Baltic Earth 2021 and Meier et al. 2021. It should be kept in mind that the project's results are specific to certain scenarios, species, ecosystem services, and connectivity analyses in the project area. The results provide an insight into how the studied species may react to climate change and how different ecosystem services and the connectivity linked to those species could be affected. However, if the future follows another climate scenario or if the BSAP is not successfully implemented, the future can look different from how it is presented here. Moreover, as previously discussed there is great uncertainty regarding future projections of the effects of climate change in the sea.

The ECOnnect project has focused on the effects of climate change on the central Gulf of Bothnia. However, as mentioned throughout the report, there are additional pressures with a profound impact on the sea area. One of these pressures is biodiversity loss which is closely connected to climate change. A balanced and functional ecosystem is the foundation for human well-being and failing to address the joint challenges can jeopardize a good quality of life for people (IPBES-IPCC 2021). It is crucial not to separate actions to fight biodiversity loss and climate change, but to take actions that simultaneously tackle both problems (Pörtner et al. 2021). The same can be said for other environmental problems such as eutrophication, pollution, marine litter, and other increased human activities affecting the Baltic Sea and the Gulf of Bothnia. The functions in our sea are interlinked and tackling eutrophication, for example, helps to simultaneously reduce the effects of climate change. This realization will get us closer to achieving a healthy sea than focusing on each problem separately.

Appendix

Table A1. Latin names of the study species and the taxa included in larger species groups.

Species / species group	Species or genera included
Fucus **spp. (brown algae)**	*Fucus vesiculosus, F. radicans*
Pondweeds	*Potamogeton perfoliatus, Stuckenia pectinata* (syn. *Potamogeton pectinatus*)
Aquatic mosses	*Drepanocladus* spp., *Fissidens* spp., *Fontinalis* spp., *Marchanthiophyta*, *Warnstorfia* spp., *Calliergon* spp., *Platyhypnidium* spp.
Furcellaria lumbricalis	*Furcellaria lumbricalis*
Common reed	*Phragmites australis*
Stoneworts	*Chara* spp., *Nitella* spp., *Nitellopsis* sp., *Tolypella* sp.
Filamentous annual algae	*Acrosiphonia* sp., *Aglaothamnion* sp., *Bangia* sp., *Batrachospermum* spp., *Ceramium* spp., *Chaetomorpha* sp., *Cladophora fracta*, *Cladophora glomerata*, *Dictyosiphon* spp., *Ectocarpus* sp., *Elachista* sp., *Enteromorpha* spp., *Mougeotia* sp., *Pylaiella* sp., *Rhizoclonium* sp., *Spirogyra* sp., *Spongomorpha aeruginosa*, *Stictyosiphon* sp., *Ulothrix* spp., *Ulva* spp., *Urospora* sp., *Zygnema* sp.
Blue mussel	*Mytilus trossulus x edulis*
Baltic clam	*Limecola balthica* (syn. *Macoma balthica*)
Chironomid larvae	*Ablabesmyia* sp., *Ablabesmyia monilis*, *Ablabesmyia phatta*, *Chironominae*, *Chironomini*, *Chironomus* sp., *Chironomus anthracinus*, *Chironomus plumosus -t.*, *Chironomus semireductus -t.*, *Chironomus thummi -t.*, *Cladopelma viridulum*, *Cladotanytarsus* sp., *Cryptochironomus* sp., *Demicryptochironomus vulneratus*, *Dicrotendipes* sp., *Dicrotendipes nervosus*, *Dicrotendipes pulsus*, *Endochironomus albipennis*, *Endochironomus tendens*, *Harnischia curtilamellata*, *Microchironomus tener*, *Micropsectra* sp., *Orthocladiinae*, *Pagastiella orophila*, *Parakiefferiella* sp., *Parakiefferiella smolandica*, *Paralauterborniella nigrohalteralis*, *Polypedilum* sp., *Polypedilum nubeculosum*, *Polypedilum pullum*, *Procladius* sp., *Psectrocladius* sp., *Psectrocladius psilopterus -agg.*, *Psectrocladius sordidellus -agg.*, *Pseudochironomus* sp., *Pseudochironomus prasinatus*, *Sergentia* sp., *Stempellinella edwardsi*, *Stictochironomus* sp., *Tanypodinae*, *Tanypus punctipennis*, *Tanypus vilipennis*, *Tanytarsini*, *Tanytarsus* sp.
Monoporeia affinis **(amphipod)**	*Monoporeia affinis*
Marenzelleria **spp. (polychaete)**	*Marenzelleria* sp., *Marenzelleria viridis*, *M. neglecta*

Table A2. Model statistics and the relative influences of the environmental variables in the species distribution models.

	Fucus spp.	Blue mussel	Baltic clam	Chironomid larvae	Monoporeia affinis	Pondweeds	Aquatic mosses	Furcellaria lumbricalis	Common reed	Stoneworts	Filamentous annual algae	Marenzelleria
Depth	32.4	10.9	18.6	46.7	37.6	21	14.80	14.5	78.2	25.4	15.1	33.4
Nitrate NO_3, surface/ bottom*	14.7	16.4	26.4	5.1	9.6	8.7	11.80	8.8	2.2	9.1	7.3	6.3
Ice thickness	12.9	8.3	7.1	3.6	8.2	6.9	6.60	8.3	1	7.8	6.3	7.5
Exposure	9.6	4.2	8.5	3.7	4.5	13.1	11.40	7.2	1.4	10.7	18.7	5.8
Salinity, bottom	7.5	10.6	4.5	8.2	6.3	10.4	7.00	17.7	1.2	8.9	7.2	19.2
Temperature, bottom	5.8	13.8	4	13.7	18.3	6.7	11.60	10	12.1	6.6	12.2	7.8
Vertical light attenuation	6.6					14.4	9.10	14.2	1	8.4	10.9	
Phosphate PO_4, surface/bottom	5.6	7.7	19.5	12.1	3.3	9.1	15.40	6.2	2.3	8.8	6.2	8.8
Oxygen concentration		13.3	7.8	3	7.3		6.50	7		7.9	7	4.5
Distance to coast	4.7	14.8	3.6	4	4.9	9.7	5.80	6.1	0.6	6.4	9.1	6.7
Model statistics												
AUC	0.97	0.96	0.88	0.92	0.79	0.92	0.94	0.94	0.98	0.92	0.83	0.84
D^2	0.62	0.52	0.35	0.47	0.22	0.36	0.45	0.46	0.69	0.39	-0.27	0.27

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