

High climate velocity and population fragmentation may constrain climate-driven range shift of the key habitat former *Fucus vesiculosus*

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Abstract

Aim: The Baltic Sea forms a unique regional sea with its salinity gradient ranging from marine to nearly freshwater conditions. It is one of the most environmentally impacted brackish seas worldwide, and the low biodiversity makes it particularly sensitive to anthropogenic pressures including climate change. We applied a novel combination of models to predict the fate of one of the dominant foundation species in the Baltic Sea, the bladder wrack *Fucus vesiculosus*.

Location: The Baltic Sea.

Methods: We used a species distribution model to predict climate change-induced displacement of *F. vesiculosus* and combined these projections with a biophysical model of dispersal and connectivity to explore whether the dispersal rate of locally adapted genotypes may match estimated climate velocities to recolonize the receding salinity gradient. In addition, we used a population dynamic model to assess possible effects of habitat fragmentation.

Results: The species distribution model showed that the habitat of *F. vesiculosus* is expected to dramatically shrink, mainly caused by the predicted reduction of salinity. In addition, the dispersal rate of locally adapted genotypes may not keep pace with estimated climate velocities rendering the recolonization of the receding salinity gradient more difficult. A simplistic model of population dynamics also indicated that the risk of local extinction may increase due to future habitat fragmentation.

Main conclusions: Results point to a significant risk of locally adapted genotypes being unable to shift their ranges sufficiently fast considering the restricted dispersal and long generation time. The worst scenario is that *F. vesiculosus* may disappear from large parts of the Baltic Sea before the end of this century with large effects on the biodiversity and ecosystem functioning. We finally discuss how to reduce this risk through conservation actions, including assisted colonization and assisted evolution.

KEYWORDS

Baltic Sea, bladder wrack, climate change, connectivity, dispersal, fragmentation, local adaptation, range shift, salinity, species distribution model

1 | INTRODUCTION

Owing to the large and densely populated drainage area, the Baltic Sea is one of the most environmentally impacted seas in the world with habitat loss, eutrophication, pollution and overfishing (Diaz & Rosenberg, 2008; Halpern et al., 2008). In addition, recent invasions by non-native species form a strong pressure on the native biota (Ojaveer & Kotta, 2015). Moreover, the Baltic Sea is one of the fastest warming regions in the world, resulting in dramatic retreat of winter ice cover, rise of surface water temperature and reduction of salinity (IPCC 2013; Meier, Kjellström, & Graham, 2006; Meier et al., 2012a). Low functional diversity of the Baltic marine ecosystem exposes it to fast environmental deterioration and potential loss of essential ecosystem services due to low resilience capacity (Meier et al., 2012b; Österblom et al., 2007).

Climate-driven changes in temperature, winter ice cover, salinity and circulation pattern combined with changes in nutrient loading affect patterns of habitat availability. Species may track the displacement in habitat distribution, persist in the altered habitat due to plasticity or adaptation, or go locally extinct (Chevin, Lande, & Mace, 2010; Munday, Warner, Monro, Pandolfi, & Marshall, 2013). Successful range shifts may depend on dispersal capacity of essential genotypes, but changes in distribution pattern, for example increased fragmentation, may also affect the overall metapopulation persistence (Ovaskainen & Hanski, 2003). Clearly, to track environmental change, populations must shift their range at least as fast as does the environment.

Most successful colonizers of the Baltic Sea consist of marine and freshwater species with a generally broad salinity tolerance, but there is growing evidence for many examples of local adaptations to the Baltic environment (Berg et al., 2015; Johansson, Pereyra, Rafajlovic, & Johannesson, 2017; Momigliano et al., 2017; Pereyra, Bergström, Kautsky, & Johannesson, 2009; Serrão, Kautsky, & Brawley, 1996; Sjöqvist, Godhe, Jonsson, Sundqvist, & Kremp, 2015; Väinölä & Johannesson, 2017). Genetic variation is considered an essential component for persistence in a changing environment where new genetic combinations or the dispersal of locally adapted genotypes may retard the range shift of a species.

Bladder wrack (*Fucus vesiculosus*) is the only canopy-forming seaweed on hard bottoms in the Baltic Sea, and it constitutes a key habitat with many associated algae, invertebrate and fish species (Kersen, Kotta, Bučas, Kolesova, & Dekere, 2011; Schagerström, Forslund, Kautsky, Pärnoia, & Kotta, 2014; Wikström & Kautsky, 2007). At present, *F. vesiculosus* extends into the southern part of the Gulf of Bothnia, being less common or partly replaced by its sister species *F. radicans* further north. *Fucus vesiculosus* also extends into the inner parts of the Gulf of Finland. Locally, reduced light availability mostly driven by elevated nutrient loading and phytoplankton production may limit the depth range of *F. vesiculosus* (Törn, Krause-Jensen, & Martin, 2006). *Fucus vesiculosus* thus has rather well-defined range margins in the Baltic Sea, and predicted climate-driven changes together with ongoing eutrophication and habitat fragmentation may all modify the present

distribution of *F. vesiculosus* (Vuorinen et al., 2015). A loss of this habitat-forming species may have far-reaching consequences and lead to changes in biodiversity and functioning of major shallow ecosystems in the Baltic Sea.

In this study, we used a species distribution model to predict the current and future distribution of *F. vesiculosus* under the most plausible climate and nutrient loading scenarios. In addition, to explore whether locally adapted genotypes of *F. vesiculosus* (Ardehed et al., 2016) may track climate change, we applied a biophysical model to simulate dispersal, connectivity and ultimately habitat fragmentation at the receding margin where loss of connectivity may further endanger population persistence (Opdam & Wascher, 2004). The modelled rate of dispersal was compared with estimates of climate velocity, calculated as the migration of the isolines of temperature and salinity across the seascape in kilometre per decade (Burrows et al., 2011), to assess whether predicted spread of tolerant genotypes is sufficient to match the pace of climate change. Finally, we discuss potential ecosystem consequences related to shifting patterns in species distribution and connectivity and suggest some management actions to reduce possible ecosystem impacts.

2 | MATERIALS AND METHODS

2.1 | The study area—the Baltic Sea

The Baltic Sea was formed from a post-glacial freshwater lake and is only about 8,000 years old. More than 600 river and stream basins drain into the Baltic Sea that opens to the marine North Sea through the shallow Danish straits (Hannerz & Destouni, 2006). The non-tidal circulation creates a relatively stable salinity gradient through the Baltic Sea from its entrance to the inner parts (Figure S1). The latitudinal extent of the Baltic Sea also produces a strong temperature gradient with a significant development of sea ice in the winter–spring season in its northern parts, whereas its southern areas are typically ice-free. A short geological history, low salinity and low temperature compared to nearby coastal waters in the east Atlantic make the Baltic Sea a species-poor ecosystem with key ecosystem functions often provided by single species (Bonsdorff, 2006; Bonsdorff & Pearson, 1999).

2.2 | *Fucus vesiculosus* occurrence

The distribution data of *F. vesiculosus* were compiled from several sources (Table 1). The HELCOM dataset covered the whole Baltic Sea with a grid of 10 km × 10 km in which the presence or absence of *F. vesiculosus* was assessed. Only records from 1995 to the present (2015) were used. The resulting 10-km grid served as the input of current species distribution in the modelling tasks. Recently, a sister species to *F. vesiculosus* was described as *F. radicans* (Bergström, Tatarenkov, Johannesson, Jonsson, & Kautsky, 2005), which is endemic to the Baltic Sea. These two species may occur in the same habitat in the northern Baltic Sea (Schagerström et al., 2014) and they can be difficult to separate based on only morphological traits,

Source	References
1. HELCOM Red List dataset	HELCOM (2013)
2. Benthos database of the Estonian Marine Institute, University of Tartu	http://loch.ness.sea.ee/gisservices2/liikideinfoportaal/
3. <i>Fucus</i> mapping in Schleswig-Holstein, Germany	Landesamt für Natur und Umwelt des Landes Schleswig-Holstein (2008)
4. VELMU database, Finland	http://www.ymparisto.fi/en-US/VELMU
5. Database of the Swedish national monitoring programme	http://sharkdata.se/
6. Inventory data collected by AquaBiota, Sweden	http://www.aquabiota.se/en/research-services/inventories-using-underwater-video/

TABLE 1 List of sources for occurrence data of *Fucus vesiculosus*

and we acknowledge that occurrence data on *F. vesiculosus* may include also *F. radicans*.

2.3 | Environmental layers from regionalized general circulation model

The environmental layers used in the species distribution model (SDM, see below) were produced from simulations of a coupled physical-biogeochemical model of the Baltic Sea (Meier et al., 2012a) based on one climate change scenario (A1B) and two nutrient loading scenarios. The A1B climate scenario is a scenario proposed in the Special Report on Emissions Scenarios by the Intergovernmental Panel on Climate Change (Nakićenović et al., 2000). The A1 scenario group describes a future world of very rapid economic growth, a global population that peaks in mid-century and declines thereafter, and the rapid introduction of new and more efficient technologies. The two nutrient emission scenarios included “business-as-usual (BAU)” with increased river nutrient concentrations (HELCOM, 2007) and current levels of atmospheric deposition, and a “reference scenario (REF)” where nutrient concentrations in rivers and atmospheric deposition remain at current levels (Eilola, Meier, & Almroth, 2009).

The Baltic Sea coupled physical-biogeochemical model RCO-SCOB1 (the Swedish Coastal and Ocean Biogeochemical model coupled to the Rossby Centre Ocean circulation model; Eilola et al., 2009; Meier, Döschner, & Faxen, 2003) was forced by regionalized atmospheric data from the global climate model ECHAM5 (Roeckner et al., 2006) and the A1B emission scenarios for the atmospheric forcing of the three-dimensional circulation model. The regionalization of the atmospheric forcing was simulated with the coupled atmosphere-ice-ocean model RCAO (the Rossby Centre Atmosphere Ocean model developed at the Swedish Meteorological and Hydrological Institute; Döschner et al., 2002), using an atmospheric horizontal grid of 25 km (Meier et al., 2011).

The RCO-SCOB1 model is a Bryan-Cox-Semtner primitive equation circulation model with a free surface and open boundary conditions in the northern Kattegat (Webb, Coward, de Cuevas, & Gwilliam, 1997). For the present simulations, RCO-SCOB1 used a horizontal resolution of 3.7 km (2 NM) and with 83 vertical levels with a layer thickness of 3 m. Run-off changes were calculated with a hydrological model for the Baltic catchment area (Lind & Kjellström, 2009). The RCO-SCOB1 model produced the following physical and chemical data layers: Secchi depth, salinity, temperature, nitrate (NO_3) and phosphate (PO_4). Seasonal means for winter (December to February), and summer (June to August), were calculated for the periods 1978–2007 (current) and 2070–2099 (future climate).

2.4 | Calculations of climate velocities

Climate velocity (Burrows et al., 2011) was calculated from the climate scenario layers of projected temperature and salinity as a measure of the speed and direction of change in the Baltic seascape. Climate velocity has been suggested as a useful metric for comparing shifts in species distribution with the rate of climate change (Burrows et al., 2011; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). The grids (3.7 km) of temperature and salinity were first aggregated by calculating the average of 3×3 original grid cells. The gradient of scalars E ($^{\circ}\text{C}/\text{km}$ or psu/km) between neighbouring grid cells was then calculated using MATLAB (2016a, MathWorks Inc) for the whole domain as follows:

$$\nabla E = \frac{\partial E}{\partial x} + \frac{\partial E}{\partial y} \quad (1)$$

where x and y are orthogonal coordinates in space. The climate velocity (km/decade) was then calculated for each grid cell as follows:

$$\text{climate velocity} = \frac{1}{\nabla E} \cdot \text{change} \quad (2)$$

where *change* is the local change in temperature or salinity per decade as calculated from the control period (1978–2007) and future layers (2070–2099).

2.5 | Species distribution model

The RCO-SCOBI model provided environmental layers for the SDMs. The SDMs incorporated only summer and winter data from surface (0–3 m) and bottom layers (3–6 m) to optimize the number of candidate models. The climate projection together with nutrient emission scenarios resulted in a total of three *F. vesiculosus* modelling sets: (1) control period for years 1978–2007, that is present climate conditions (PRE); (2) future climate conditions (2070–2099) with nutrient scenario BAU (SCE_BAU); and (3) future climate conditions (2070–2099) with nutrient scenario REF (SCE_REF).

In addition to the RCO-SCOBI data layers, depth and wave exposure (simplified wave model) data were also used as modelling input variables. Depth data were acquired from the Baltic Sea Bathymetry Database (Baltic Sea Hydrographic Commission 2013). The model of surface wave exposure incorporates shoreline topography, fetch and wind data together with empirically derived algorithms to mimic diffraction (Isæus, 2004). The average values of all RCO-SCOBI variables (season × layer × scenario combinations) were added to each cell of the species distribution data of 10 km. This dataset served as the input for model calibration and prediction.

The general concept of species distribution modelling (Elith & Leathwick, 2009) was applied to predict the spatial distribution of *F. vesiculosus* under current and future climate conditions in the Baltic Sea. To investigate which season (summer and winter) and vertical layer (surface and bottom) of RCO-SCOBI data yields the best prediction accuracy, candidate models of all season × layer combinations were calibrated. When building up models, 85% of the input data (4,094 data points) were randomly selected and used as model calibration data, while 15% of the data (722 data points) were reserved for external validation. In the model calibration, the binary distribution data of *F. vesiculosus* (presence = 1, absence = 0) were used as the dependent variable and the RCO-SCOBI layers together with the depth and wave exposure served as independent predictors. The probability of occurrence of *F. vesiculosus* was predicted for each of the data points in the validation dataset, and the predictive performance of the candidate models was validated by calculating the area under the receiver operating curve (AUC) (Fielding & Bell, 1997). The candidate model that produced predictions with the highest AUC value was then used to build final models using 100% of the input data. All models were calibrated using the present state (PRE) values of ECHAM5/RCAO variables. The final model predictions that covered the whole Baltic Sea were produced for PRE, SCE_REF and SCE_BAU datasets. The predicted values of probability of occurrence were converted to presence–absence data using the sensitivity–specificity difference minimizer method (Jiménez-Valverde & Lobo, 2007) in the R package “PRESENCEABSENCE” (Freeman & Moisen, 2008).

Random forest (RF) was used as the modelling algorithm. RF is a machine learning method that generates a large number of regression trees, each calibrated on a bootstrap sample of the original data (Breiman, 2001). Each node is split using a subset of randomly selected predictors, and the tree is grown to the largest possible extent without pruning. For predicting the value of a new data point, the data are run through each of the trees in the forest and each tree provides a value. The model prediction is then calculated as the average value over the predictions of all the trees in the forest (Breiman, 2001). The package “RANDOMFOREST” (Breiman, Cutler, Liaw, & Wiener, 2015) was used to run RF models in the statistical software R 3.2.2 (The R Foundation for Statistical Computing 2015). The parameter *mtry* (number of variables randomly sampled as candidates at each split) was set to the square root of the number of variables in the model calibration dataset, which is the recommended default value of *mtry* in the RANDOMFOREST package (Liaw & Wiener, 2002), and the number of trees was set to 1,000 (Liaw & Wiener, 2002). The importance of predictor variables in the PRE model was assessed using the internal method of the package “RANDOMFOREST” (mean decrease in accuracy) using 10 permutations (Breiman et al., 2015). Partial dependence plots (*sensu* Friedman, 2001) were produced using *partialPlot* function in “RANDOMFOREST” to illustrate the dependence of model predictions on individual covariates. All geographical maps were produced in QGIS or ArcGIS (Esri).

2.6 | Biophysical model of dispersal and connectivity

Fucus vesiculosus may disperse in several ways including short-distance dispersal of gametes and zygotes to occasional long-distance dispersal of dislodged and rafting buoyant sexually mature plants (Rothäusler, Corell, & Jormalainen, 2015; Thiel & Gutow, 2005). Also, dispersal on intermediate scales may occur through bed load transport of negatively buoyant plants and in some cases vegetative, adventitious branches (Johansson et al., 2017; Pereyra et al., 2013). Genetic studies indicate population structure on scales ranging from, in the extreme case 10 m, but more usually 1 km, which suggest relatively short dispersal distances (Muhlin, Engel, Stessel, Weatherbee, & Brawley, 2008; Tatarenkov, Jonsson, Kautsky, & Johannesson, 2007). We estimated the dispersal and connectivity of *F. vesiculosus* with a biophysical model based on a Lagrangian particle-tracking model driven offline with flow fields from an ocean circulation model. The stored ocean transport data were produced with the NEMO-Nordic model (Hordoir, Axell, Löptien, Dietze, & Kuznetsov, 2015; Hordoir, Dieterich, Basu, Dietze, & Meier, 2013), a regional configuration of the NEMO ocean engine (Madec, 2010) covering the Baltic Sea and most of the North Sea. It has a horizontal spatial resolution of 3.7 km and 84 vertical levels with depth intervals of 3 m at the surface and 23 m for the deepest layers. Here, tidal harmonics defined the sea surface height (SSH) and velocities, and Levitus climatology defined temperature and salinity (Levitus & Boyer, 1994). The model had a free surface, and the atmospheric forcing was the re-analysis

dataset ERA40 (Uppala et al., 2005). Run-off was based on climatological data based on a number of different databases for the Baltic Sea and the North Sea. Validation of the NEMO-Nordic showed that the model is able to correctly represent the SSH, both tidally induced and wind-driven (Hordoir et al., 2015).

The Lagrangian trajectory model TRACMASS (De Vries & Döös, 2001) is a particle-tracking model that calculates transport of particles using stored flow field data. The velocity, temperature and salinity were updated with a regular interval for all grid boxes in the model domain, in this study every 3 hr, and the trajectory calculations were made with a 15-min time step. Particles simulating zygotes and drifting mature plants were released from all model grid cells ($3.7 \times 3.7 \text{ km}^2$) within the HELCOM area that had a mean depth above 10 m or were located adjacent to the land contour. From each grid cell, 49 particles were released (a 7×7 array) on four occasions between May and August in surface waters (0–2 m), which was repeated for 8 years (1995–2002), making a total of 20 million particles. To cover the uncertainty in realized dispersal of *F. vesiculosus*, particle positions were recorded after 5 and 30 days, representing the range between short- and long-distance dispersal. In the final analyses of dispersal and connectivity, only the grid cells containing *F. vesiculosus* according to the SDM predictions were considered. For each grid cell, the dispersal probability of all other grid cells was calculated from particle positions at the release and end of the

simulation. Probabilities were entered into a connectivity matrix where each element represents the probability to disperse from column i to row j (Jonsson, Nilsson Jacobi, & Moksnes, 2016). Elements along the diagonal represent local retention.

2.7 | Population model to assess expansion rate and fragmentation

A simplistic metapopulation model for *F. vesiculosus* was used to explore (1) the rate of spread of locally adapted genotypes and (2) the effect of future fragmentation caused by the predicted changes in habitat distribution and connectivity. The population model considered all sites (habitat grid cells) within the study domain as local populations connected by dispersal through a connectivity matrix produced by the biophysical model. Every grid cell was given the same growth rate, and the only mortality occurred for propagules dispersing outside the predicted habitat (from the SDM). The vector of local population sizes N_{t+1} at time $t + 1$ was simply projected in time using the connectivity matrix C as:

$$N_{t+1} = C * N_t \quad (3)$$

For the spread of locally adapted genotypes, an initial population was started at three locations in the Baltic Sea: the western (61.6°N,

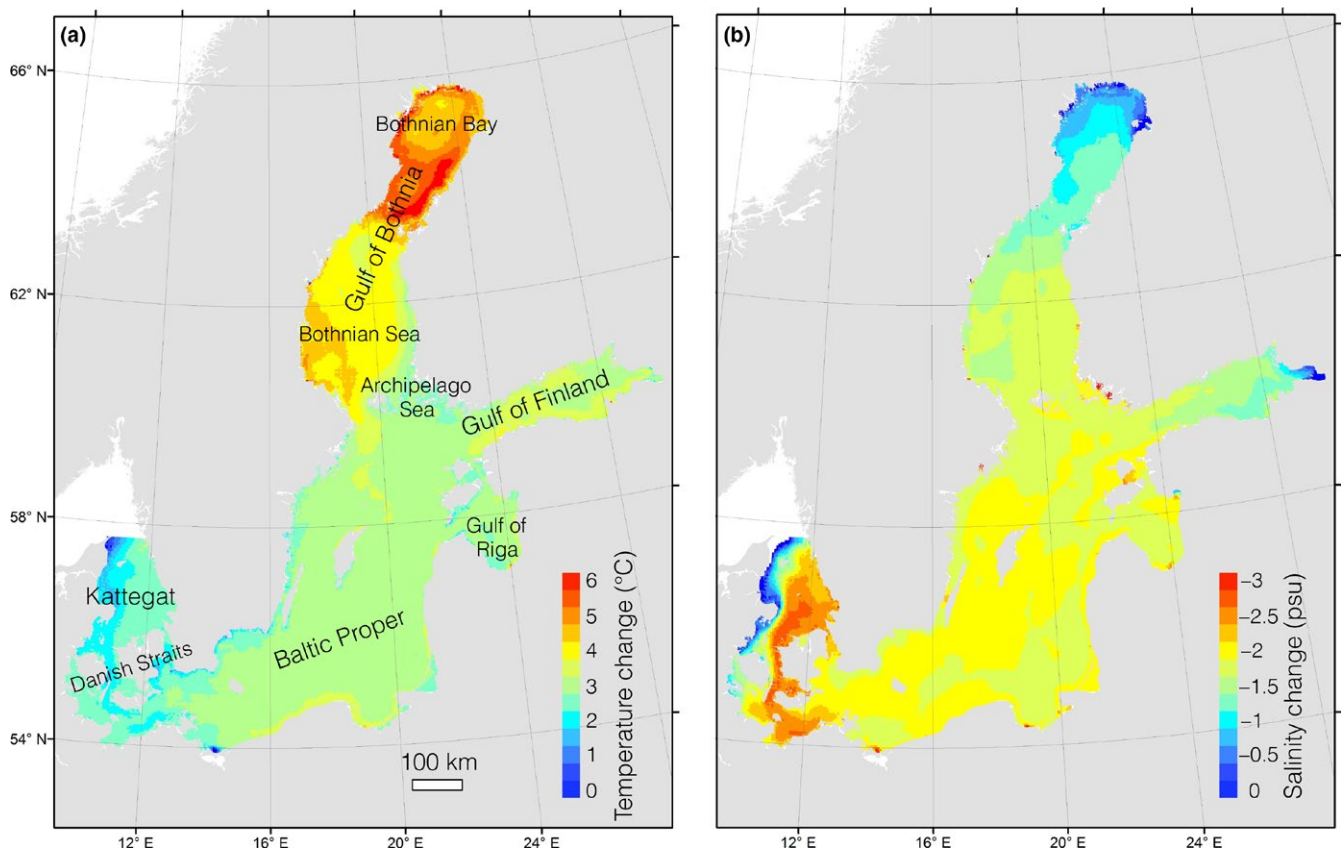


FIGURE 1 Projected change in sea surface temperature and salinity included in the species distribution model. The change is calculated as the difference between summer means (months June, July and August) for a control period (1978–2007) and a future climate period (2070–2099). (a) Surface temperature and (b) surface salinity

17.28°E) and eastern coasts (62.6°N, 21.1°E) of the Gulf of Bothnia and the northern coast (60.4°N, 27.2°E) of the Gulf of Finland. The displacements (to the nearest kilometre) of the population front between each of the five successive generations were measured, and the front velocity was compared to the calculated climate velocities.

For the analysis of fragmentation, the population was initiated with an equal number of individuals in each grid cell predicted as habitat from the SDM for the present distribution and the predicted future for the BAU nutrient scenario. The population was projected for 25 generations, spanning 100 years for *F. vesiculosus* with an assumed generation time of 4 years (Lüning, 1985). We arbitrarily considered a grid cell populated by *F. vesiculosus* over a range of population sizes covering six orders of magnitudes, for example from 1 individual per km² to 1 individual per 1 m², and as absent below this range. As the model of the spread of locally adapted genotypes did not include mortality or Allee effects, the predicted range expansion is likely an upper bound.

3 | RESULTS

3.1 | Predicted environment from the RCO-SCOBI scenario model

The coupled physical-biogeochemical model of the Baltic Sea forced with the climate change scenario A1B predicts an increase

of summer surface sea temperature of about 3–5°C at the end of this century (Figure 1a). Surface salinity is predicted to decrease with 1.5–2 psu in most of the Baltic Sea (Figure 1b). The change in nutrient loading of nitrogen and phosphorous was evaluated for two scenarios where the business-as-usual scenario produced higher nutrient concentrations in many areas although phosphorous is expected to decrease in the Gulf of Finland (Figure 2). With higher nutrient loading resulting in increased primary production and plankton biomass, the model predicted a general decrease in water transparency with a reduction in Secchi depth of 1–2 m (Figure 3). However, little change in water transparency is expected at the margins of the distribution of *F. vesiculosus*.

3.2 | Calculated climate velocities

From the modelled future change of temperature and salinity, we calculated fields of climate velocity showing the local rate of change (Figure 4). In particular, the latitudinal velocity of salinity change in the Bothnian Sea and the southern Baltic, and the longitudinal change in the Gulf of Finland, is expected to be rapid with maximum change exceeding 100 km per decade (Figure 4). The direction of the climate velocity field for salinity is shown in Figure S3.

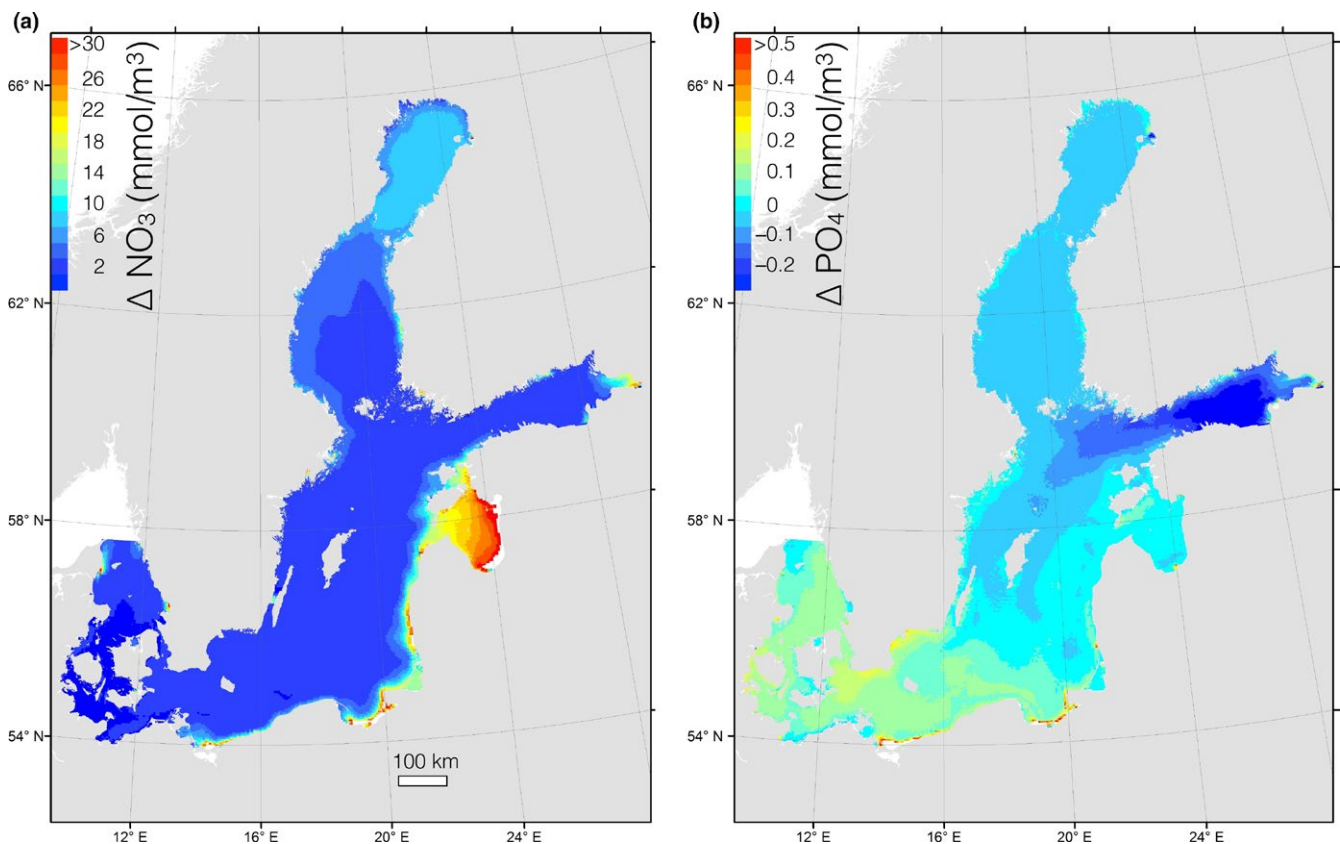


FIGURE 2 Projected future difference in nutrient concentrations between a future continuation of the present loads and the business-as-usual scenario. (a) Nitrate and (b) phosphate

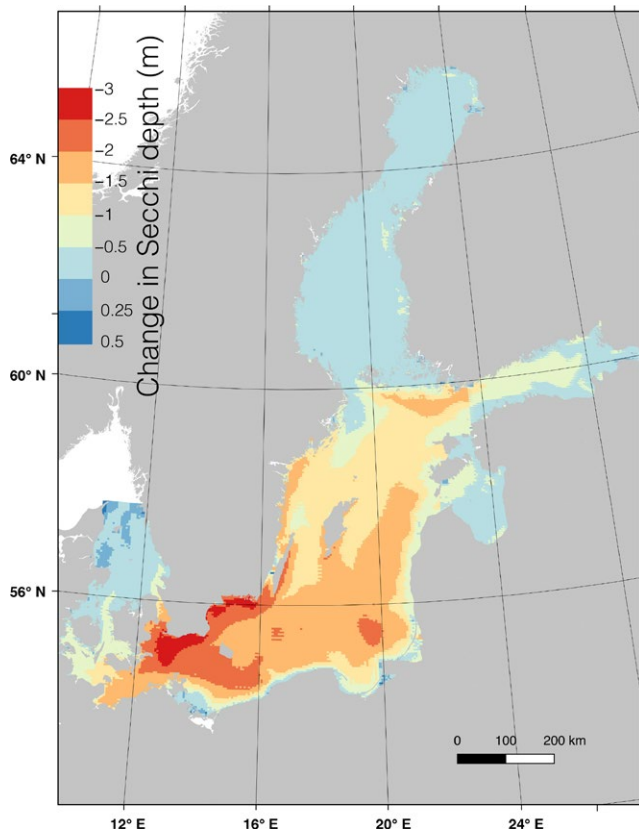


FIGURE 3 Projected future change in water transparency expressed as the Secchi depth, assuming a business-as-usual scenario for the nutrient loading

3.3 | Prediction of future distribution of *F. vesiculosus*

The candidate models including different combinations of water layer and seasonal data had very similar predictive performance (AUC values between 0.92 and 0.93). Final predictions of the distribution of *F. vesiculosus* were produced using bottom water layer (3–6 m) and summer values as this combination yielded marginally higher prediction accuracy (AUC = 0.93) compared to the other combinations.

The predictions of occurrence of *F. vesiculosus* under future climate and nutrient scenarios are shown in Figure 5. Compared to the current climate conditions, the nutrient scenarios BAU and REF under future climate predicted a reduction of 30% and 33% in the distribution area of *F. vesiculosus*, respectively. The decrease of distribution was most pronounced in the Gulf of Bothnia and the Gulf of Finland. As expected, depth was the most influential predictor variable in the RF model used (Figure 6). However, among variables that were expected to change in future scenarios, the reduced salinity was the main driver of the change in distribution, while nutrients, water transparency and other factors had smaller effects (Figure 6). Partial dependence plots of predictor variables are shown in the Supporting Information (Figure S2).

3.4 | Dispersal of *F. vesiculosus*

The biophysical model showed that a 5-day drift in surface waters is expected to result in dispersal distances typically between 5 and 15 km along the Baltic Sea coast (Figure 7a). The dispersal direction reflects the general circulation pattern with southward dispersal along the Swedish east coast and northward along the Finnish west coast (Figure 7b).

3.5 | Metapopulation model of fragmentation and genotype range shift

In a simplistic metapopulation model, we combined the distribution of *F. vesiculosus* predicted from SDM with the modelled dispersal in the seascape. The projection of the metapopulation over 25 generations showed that based on the current distribution of *F. vesiculosus*, the metapopulations are relatively persistent (Figure 8a), although some of the initially inhabited areas were lost, most notably along the eastern Bothnian Sea. The predicted future distribution of *F. vesiculosus* showed strong effects of fragmentation along the northern distribution boundary in the Bothnian Sea as well as in the Gulf of Finland where suitable habitats, as predicted by SDM, may be difficult to persistently populate (Figure 8b). Such fragmentation may further shift the predicted distribution limits to the south and the west.

The metapopulation model was further used to explore the along-shore spread of locally adapted genotypes to track their optimal environment under the changing climate conditions. The rate of population expansion from three sites in the Bothnian Sea and the Gulf of Finland was 35–55 km per decade when assuming dispersal duration of 5 days and around 200 km per decade for regularly occurring long-distance dispersal lasting for 30 days (Table 2).

4 | DISCUSSION

The species distribution model (SDM) based on a regional climate model predicts a dramatic 30% reduction of the inhabitable area for the habitat-forming seaweed *F. vesiculosus* in the Baltic Sea. The mechanism behind this range shrinkage is a dramatic southward and westward expansion of low-salinity water, most notably in the Gulf of Bothnia and the Gulf of Finland. Although the projected range of salinity decline is uncertain, most models in an ensemble simulation of 16 scenarios showed a decrease in salinity (Meier et al., 2006). In addition to the dilution effect, an increasing nutrient load may enhance plankton primary production leading to reduced water transparency as well as trigger blooms of epiphytic filamentous algae (Valiela et al., 1997). In either way, *F. vesiculosus* populations could be weakened dramatically. We further show that the loss of suitable habitat may result in reduced connectivity leading to lower metapopulation persistence and to further fragmentation, especially at the distribution margins where significant losses of local populations

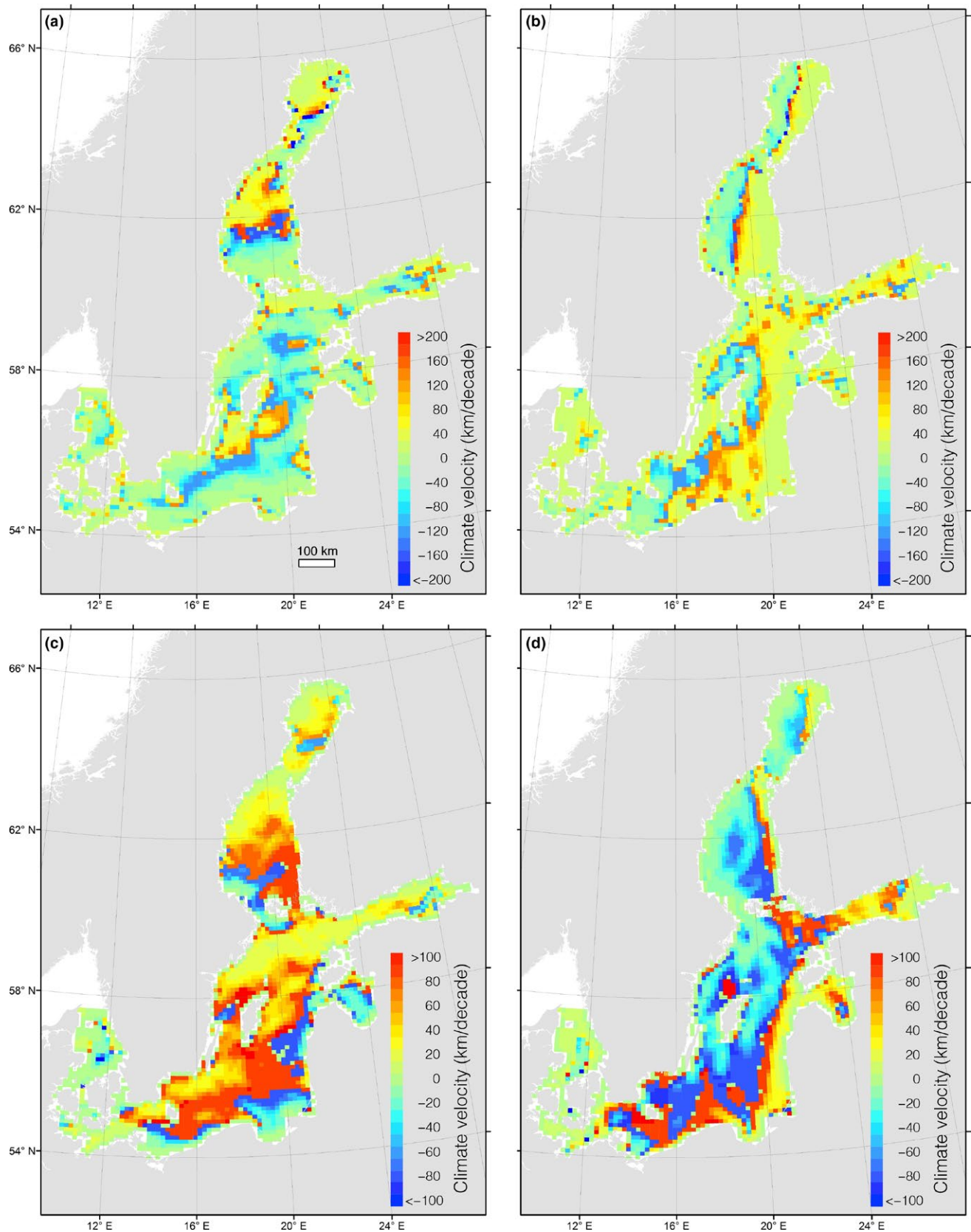


FIGURE 4 Climate velocity expressed in kilometre per decade. (a) Latitudinal velocity of surface temperature, (b) longitudinal velocity of surface temperature, (c) latitudinal velocity of surface salinity and (d) longitudinal velocity of surface salinity. Climate velocity was calculated for the change between a control period (1978–2007) and a future climate period (2070–2099) for the summer months June, July and August

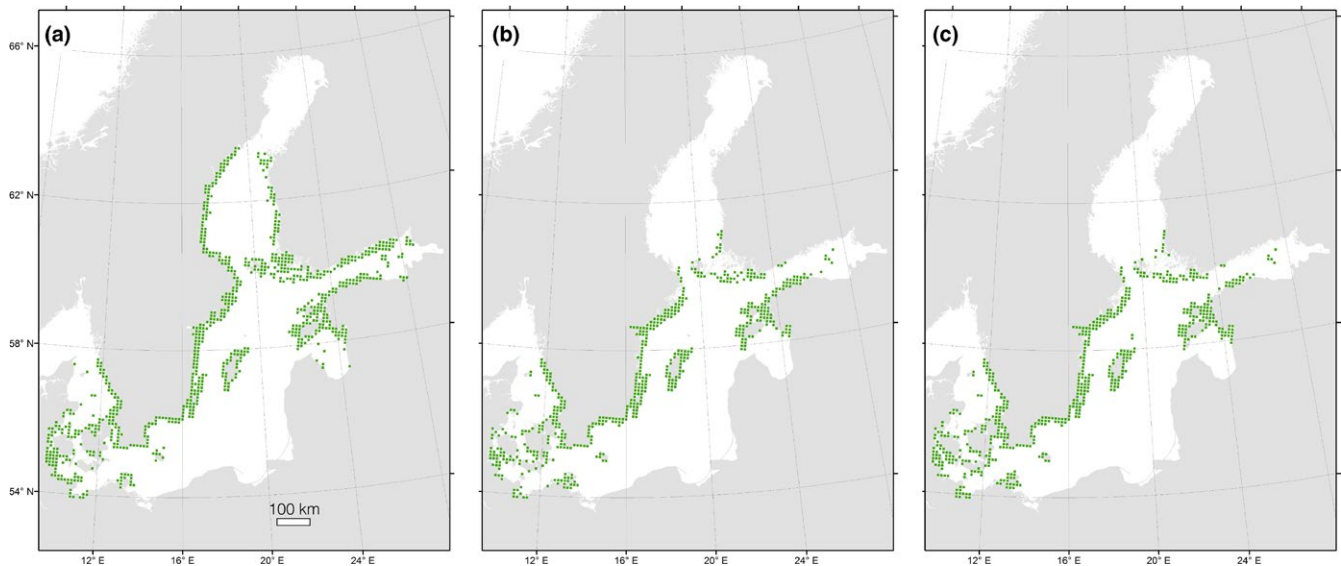


FIGURE 5 Species distribution model (SDM) of the change in the distribution of *Fucus vesiculosus* from a control period (1978–2007) to the projected future climate period (2070–2099). (a) Modelled present distribution, (b) modelled distribution assuming a future continuation of present nutrient loading and (c) modelled distribution assuming a business-as-usual scenario for the nutrient loading

within the metapopulation are expected. This fragmentation effect is likely strong along the Finnish and Estonian coasts.

Previous SDM studies have used global climate models in their projections. However, due to the coarse resolution of the global models, they are often not suitable for studies of regional conditions, while higher resolution models can give a more correct representation of air temperature, wind patterns and precipitation. Thus, it is not surprising that the projections of Assis, Serrão, Claro, Perrin, and Pearson (2014) and Leidenberger, De Giovanni, Kulawik, Williams, and Bourlat (2015) came to a different conclusion with a moderate increase in the future distribution of *F. vesiculosus* within the Baltic Sea. The simulated increase in these studies was mainly driven by an increase in temperature. In contrast, Vuorinen et al. (2015) quantified the range of low-salinity area within the Baltic Sea using the same climate scenario model as in the present study. The authors then compared the shifting salinity conditions with species tolerances under current environmental conditions and concluded similar range shrinkage under future climate as forecasted in our study.

Recent studies have pointed out that predictions of SDMs may both under- and overestimate future habitat loss if the population consists of locally adapted subpopulations (e.g., Hällfors et al., 2016; Oney, Reineking, O'Neill, & Kreyling, 2013). Predictions may be overly optimistic if locally adapted genotypes are dispersal-limited. This may apply to *F. vesiculosus* where poor dispersal ability with zygotes or clonal adventitious branches is generally expected (Johansson et al., 2017; Pereyra et al., 2013; Väinölä & Johannesson, 2017). Our biophysical model with drift duration of 5 days predicted relatively short dispersal distances, generally less than 10 km. Dislodged and drifting adult thalli may travel for longer distances and release gametes far from their native area (Rothäusler et al., 2015), which is also indicated for other fucoids (Buonomo et al., 2017). However, dislodged plants may only rarely lead to realized dispersal as spawning

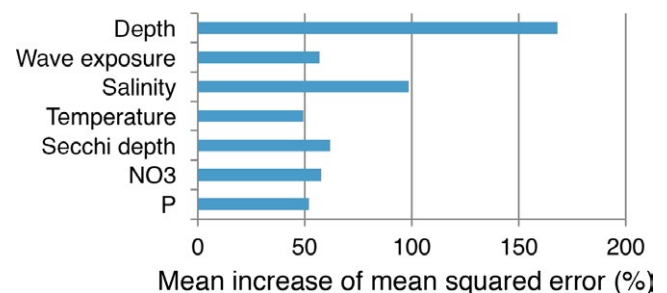


FIGURE 6 Importance of predictor variables in the final random forest model. The x-axis shows the decrease in accuracy as the increase of mean-squared error of the model when a variable is permuted

is often constrained by calm weather (Serrão et al., 1996), the moon phase (Andersson, Kautsky, & Kalvas, 1994) and the risk of beaching (Muhlin et al., 2008). At present, it is not possible to estimate the significance of drifting thalli to overall gene flow. Moreover, the oceanographical circulation models (RCO-SCOB1 and NEMO-Nordic) cannot accurately simulate currents close to the coast due to their relatively coarse spatial resolution. The values in the coastal grid cells used in this study are hence likely an overestimate of actual coastal current velocities. In the current paper's context, the modelled dispersal should then be viewed as an upper bound and *F. vesiculosus* may be even more dispersal-limited than the model predicted.

Studies of genetic differentiation and morphology suggest that the population structure of *F. vesiculosus* in the Baltic Sea may be very complex with a mix of sexual and asexual recruitment (Ardehed et al., 2016). In addition, a closely related species *F. radicans* has evolved as an endemic species from *F. vesiculosus* inside the Baltic Sea (Ardehed et al., 2016; Bergström et al., 2005; Pereyra et al., 2013). Although genomic information about geographical differences in adaptive loci

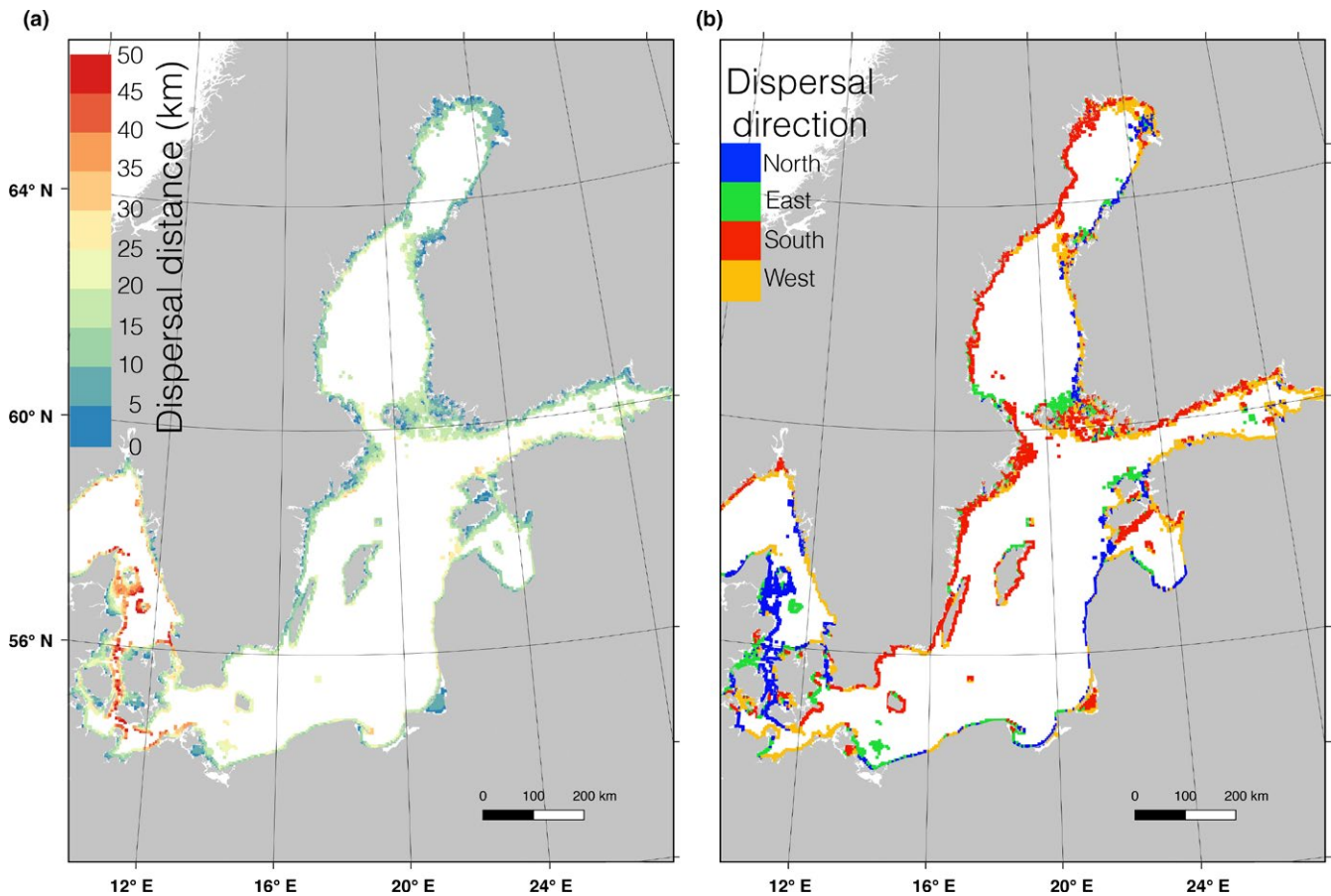


FIGURE 7 Dispersal within the Baltic Sea simulated with a biophysical model for propagules drifting in surface water (0–2 m) for a duration of 5 days. (a) Dispersal distance and (b) dispersal direction binned in the four cardinal directions (north: 315°–45°, east: 45°–135°, south: 135°–225°, west: 225°–315°). The data are an average of the years 1995–2002

is lacking, there are indications of trait differences that suggest the presence of locally adapted populations along the Baltic Sea gradient in both these species (Johansson et al., 2017; Pearson, Kautsky, & Serrão, 2000; Serrão et al., 1996).

If locally adapted genotypes will successfully track an advancing or receding optimal environment during a climate change scenario, the dispersal to and colonization of new areas must occur at a rate similar to the spatial change of critical environmental factors. Failing to track a receding critical environment boundary, for example salinity, may lead to local or even global extinction of unique genetic variants and adaptations. The calculated climate velocities for salinity in this study indicate that the dispersal rate is lower or of the same order as the rate of range shift for *F. vesiculosus* (Table 2; Figure 4). Only if long-distance dispersal of drifting thalli is an important contribution to gene flow, are locally adapted genotypes expected to outpace the receding boundary of critical salinity. This also assumes relatively rapid selective sweeps of locally beneficial alleles (Morjan & Rieseberg, 2004). In addition, García Molinos, Burrows, and Poloczanska (2017) recently showed that many ongoing range shifts are correlated not only with the climate velocity but also with the directional agreement between climate velocity and dispersal, especially for species with propagules strongly influenced by physical water transport. In a qualitative comparison between

the direction of decreasing salinity (Figure S3) and mean dispersal direction (Figure 7b), there is a match between directions of climate velocity of salinity and dispersal along the Swedish coast and within the Gulf of Finland, but generally a mismatch along the Finnish and Estonian coasts. A mismatch for the sessile *F. vesiculosus* should further obstruct a range shift of locally adapted genotypes. The increasing fragmentation of the marginal populations may also reduce successful dispersal and increase local extinction as predicted by the metapopulation model (Figure 8). Consequently, there is relatively high risk that locally adapted populations, evolved to tolerate low salinity in the Bothnian Sea and the Gulf of Finland, may go extinct under current IPCC climate scenarios. Such inability of adapted genotypes to track the spatial change in the environment may lead to an even more severe decline of *F. vesiculosus* in the future Baltic Sea than predicted by the SDM as there will be no locally tolerant genotypes when the critical salinity boundary sweeps south-west. This may lead to a reduced tolerance to low salinity at the population level with *F. vesiculosus* requiring higher salinity for persistence than today. This effect may be long-lasting unless evolution of new locally adapted populations is rapid. But the latter is not likely considering the long generation time and the potentially small size of fragmented populations of *F. vesiculosus*. There is also a need for more detailed information about the relative contribution of plasticity (Johansson

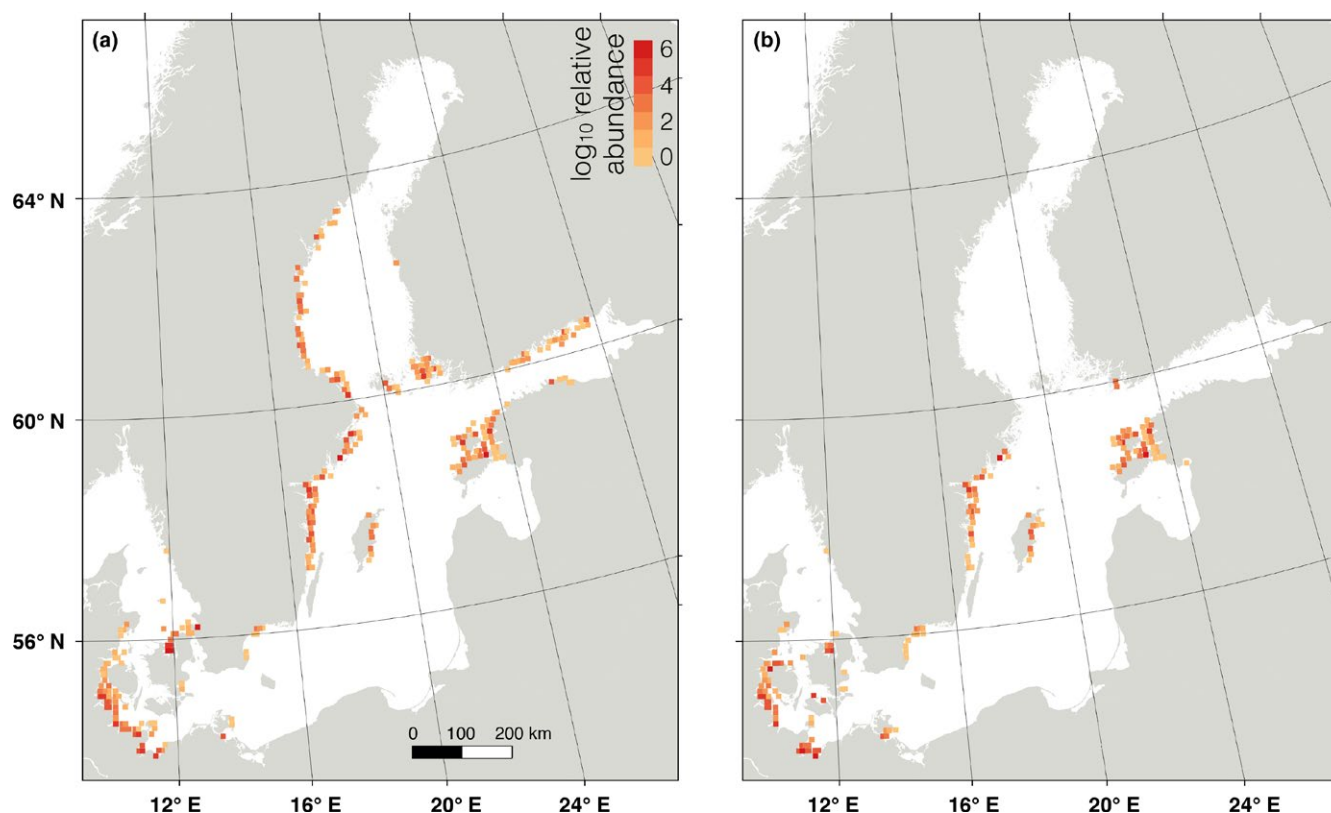


FIGURE 8 Distribution of *Fucus vesiculosus* produced by the metapopulation model (eq. 3) where habitat prediction from the species distribution model is combined with the connectivity estimated with a biophysical model. (a) Population density when metapopulation model is based on the present habitat prediction in Figure 6a and (b) population density when metapopulation model is based on the future habitat prediction in Figure 6c. Population density is given in relative units but was modelled as number of thalli per km²

et al., 2017) and local adaptations to salinity tolerance at multiple locations within the present salinity gradient.

A dramatic decline of *F. vesiculosus* due to reduced salinity will likely be accompanied by a severe structural and functional regime shift of the coastal ecosystem including a dramatic loss of biodiversity in the Baltic Sea (Kotta, Möller, Orav-Kotta, & Pärnoia, 2014; Vuorinen et al., 2015). Much of brackish and marine vegetation will be replaced by freshwater higher plants (Kotta et al., 2014). However, none of the freshwater habitat-building species can replace *F. vesiculosus* on rocky bottoms. Consequently, such habitats will likely lose much of their extant vegetation, become less complex and species-poor and be deprived of critical ecosystem services such as nutrient uptake, food source, refuge for juvenile fish and loss of aesthetic values for recreational activities. It is possible that if dispersal and colonization are sufficiently fast, the sister species *F. radicans* may replace *F. vesiculosus* in areas where salinity decreases over time, which could maintain canopies on rocky substrates. Further studies are here needed.

Conservation actions may mitigate the effect of low dispersal of locally adapted populations. Assisted dispersal and colonization through translocation of individuals of *Fucus* or zygotes is one option (Hiddink, Ben Rais Lasram, Cantrill, & Davies, 2012; Thomas, 2011). It may be even possible to produce zygotes or seedlings through assisted spawning and fertilization (Serrão, Brawley, Hedman, Kautsky,

& Samuelson, 1999). For some populations, as in the northern Baltic Sea with high rates of asexual reproduction (Ardehed et al., 2016), it may be possible to translocate clonal copies using adventitious branches of tolerant clones (Johannesson, Smolarz, Grahn, & André, 2011). Ultimately, even evolution could be assisted where genotypes are selected that are more tolerant to a rapidly changing environment (van Oppen, Oliver, Putnam, & Gates, 2015). Artificial selection may be a challenge for *F. vesiculosus* considering its long generation time of over 4 years.

TABLE 2 Rate of population expansion from three selected locations in the Gulf of Bothnia and the Gulf of Finland

Location	Drift duration (days)	Expansion rate (km/decade)
West Bothnian Bay	5	36
	30	226
East Bothnian Bay	5	41
	30	37
Gulf of Finland	5	57
	30	250

Rates are shown for two dispersal strategies with drift duration of either 5 or 30 days in surface waters (0–2 m) as a mean for the period May–August.

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DATA ACCESSIBILITY

If required, modelled data on present and future distributions of *F. vesiculosus* may be archived at Dryad Digital Repository with a 1-year embargo.

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BIOSKETCH

Per R. Jonsson is interested in how dispersal of marine organisms affects demography, evolution and strategies for management and conservation. Our research group covers multiple disciplines from several institutions with expertise in ocean circulation, climate change, population dynamics, ecophysiology, phylogeography and evolutionary biology to understand how biodiversity and ecosystem functions may adjust to global changes.

Author contributions: PRJ and JK conceived the ideas and designed the study; HCA provided modelled ocean circulation and climate projections; KJ contributed to the discussion of population genetics; KH, EV and ANS provided occurrence data; PRJ and JK led the writing of the manuscript. All authors contributed critically to the draft and gave the final approval for publication.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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