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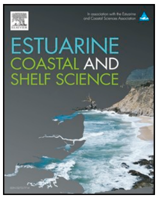

Substrate limitation of a habitat-forming genus *Fucus* under different water clarity scenarios in the northern Baltic Sea

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ABSTRACT

Canopy-forming macroalgae living on rocky bottoms provide valuable ecosystem services but long-term eutrophication has narrowed their distribution and depth zonation in the Baltic Sea. The spatial distribution of macroalgae is shaped by many factors, such as light, salinity, nutrients and wave exposure. In addition, the lack of suitable hard substrates limits the distribution of algae in many areas. Analysing how the spatial distribution of macroalgae is modified by changes in environmental conditions is relevant for focusing management actions. To quantify the resultant distribution under various environmental and management scenarios, both current environmental conditions and substrate limitation need to be considered. We estimated the potential distribution area of bladderwrack *Fucus* spp. under 11 water transparency scenarios in 9 Finnish sea areas differing in morphology and eutrophication status. The prevailing averaged long-term water transparency conditions were interpreted from satellite images. Ten scenarios were calculated based on hypothetical changes in euphotic depth from −50% to +50% of the present. Species distribution modelling was used to assess the potential distribution areas of *Fucus*. In addition, to quantify the influence of substrate limitation, we estimated the average substrate limitation with two correction methods: (i) by using field data from underwater videos within the predicted distribution areas and (ii) by using a habitat model representing the distribution of reefs (i.e. rocky bottoms) in the study area. The decrease of euphotic depth by 50% from the present level narrowed the distribution area of *Fucus* by 24–53% in the Southwestern archipelago, 55–70% in the Gulf of Finland, 37–66% in the Bothnian Sea and 59–100% in Kvarken. An increase in euphotic depth significantly broadened the spatial distribution of *Fucus*. Decreasing share of suitable hard substrate along depth gradient however hinders broadening of the distribution area. If all areas were suitable for growth, a 50% increase in euphotic depth would expand the distribution area by 124–803%, depending on area. When only suitable substrates were taken into account, this percentage remained at 9–270%. We conclude that substrate limitation needs to be taken into account when estimating macroalgal species distribution in the marine environment. We show how this can be done also when comprehensive bottom substrate maps are not available. Our results are valuable when setting the targets for environmental management plans, and for balancing the local management measures in a cost effective manner.

1. Introduction

Canopy forming macroalgae inhabiting rocky shores are key species and ecosystem architects in coastal marine ecosystems (Beaumont et al., 2005), providing breeding and feeding areas for many invertebrate species (Parker et al., 2001) as well as economically important fish (Smale et al., 2013; Tupper, 2007). In addition, fast-growing macroalgae are important primary producers (Gao and McKinley, 1994) and they can also be used as indicators of eutrophication (Ferreira et al., 2011, and references therein).

Light is one of the most important abiotic environmental factor affecting marine flora and the optical properties of the water affect the quantity and quality of light on the seabed. Therefore eutrophication – inducing a decline in water clarity – limits distribution, depth zonation and abundance of macroalgae especially in areas burdened by human-induced nutrient loads (Kautsky and Van der Maarel, 1990; Kiirikki, 1996; Bäck and Ruuskanen, 2000; Domin et al., 2004; Eriksson and Bergström, 2005; Krause-Jensen et al., 2009).

The condition of many coastal areas has been deteriorating due to human activities (Millennium Ecosystem Assessment, 2005). Macroalgal communities are especially threatened by eutrophication in the Baltic Sea (Pyhälä et al., 2014) as well as in other eutrophied coastal

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areas (Cloern, 2001; Smith, 2003). Improving the state of the marine environment by reducing eutrophication is a common interest as it would increase the benefits gained from marine ecosystem services (Ahtiainen and Vanhatalo, 2012).

Future physical conditions of the marine environment can be predicted by scenario models. For example, Meier et al. (2014) modelled salinities and temperatures across the Baltic Sea until the end of the century. Analysis of historical changes in optical properties of the sea has been conducted for coastal zone (Tolvanen et al., 2013) and open sea (Fleming-Lehtinen and Laamanen, 2012). Furthermore, the past depth and future distributions of important key taxa, such as bladderwrack *Fucus* spp., have been estimated (Torn et al., 2006; Jonsson et al., 2018).

The EU Marine Strategy Framework Directive (Directive, 2008/56/EC, MSFD) aims for Good Environmental Status and the Water Framework Directive (Directive, 2000/60/EC, WFD) for Good Ecological Status of surface waters (ES), which requires mitigation of eutrophication. When the water clarity increases and light penetrates deeper the vertical distribution of macrophytes expands. Therefore the lower depth distribution limit of *Fucus* has been used as an indicator of water quality in implementing the WFD (Bäck et al., 2006). The change in water clarity also results in a shift in horizontal distribution area of light dependent species. The knowledge of spatial horizontal change is crucial when estimating, for example, the coverage or biomass of the new habitats and associated fauna in altered water quality. This information can be used in marine protection, coastal management and marine spatial planning.

Euphotic depth, Z_{eu}, is used to describe the optical properties of the water column by noting the depth of the photic zone based on a compensation point where photosynthesis equals respiration (Kirk, 2011). Another way of describing the euphotic depth is to use the depth were 1% of the radiation right below the surface remains.

The spatial extent of euphotic seafloor has decreased by 50% from 1930 to 2007 and the annual cycle and historical trend has been demonstrated geographically (Tolvanen et al., 2013). Species distribution models (SDM) have been applied to predict potential distribution of *Fucus* in eutrophication scenarios in the northern Baltic Sea (Bergström et al., 2013), estimating that the distribution area of *Fucus* will change −10–+50% if Secchi depth changes −10–+48%. However, the distribution and zonation of macroalgae are quite often limited by the availability of hard substrate because loose sediment prevents the recruitment of epilithic species also in well illuminated environment (Rinne et al., 2011). If the sufficiently illuminated bottom does not contain hard substrates or their share is low, the increase in spatial ranges of macroalgae following mitigation of eutrophication might remain low. None of the previous studies have taken into account the availability of suitable rocky substrates within the potential distribution areas of key species.

Coastal areas of the northern Baltic Sea have unique geological features and high geodiversity which make its archipelago areas exceptionally complex (Kaskela and Kotilainen, 2017; Kaskela et al., 2017). Thousands of islands, islets and reefs, numerous substrate types and varying depth contours add variability to the physical environment. In addition, there are large-scale differences in the habitats between sheltered inner archipelago, lightly exposed middle archipelago and very exposed outer archipelago. Unfortunately, even though substrate maps would be needed in the modelling, substrate maps are often not available (Snickars et al., 2014), or they must be generated with a limited amount of data (Rinne et al., 2014). Typically accurate topographical or geological maps are only available for limited areas, such as fairways, and their use might be limited by national legislation. As many perennial macroalgae are vulnerable to sedimentation (Eriksson and Johansson, 2003, 2005), the substrate maps used in the species distribution modelling of these species should describe the top substrate layer on the seafloor, not the geologically relevant substrate type.

Our study focuses on spatial distribution modelling of *Fucus* spp. in different light scenarios in the northern Baltic Sea. The basic hypothesis is that the clarification of water column results in deeper zonation of *Fucus*, but that the spatial expansion is limited by the availability of hard substrates when advancing further from the shore. We aimed to quantify this phenomenon in an area from where excellent species data exists, i.e., the Finnish coastal waters. We studied the potential changes of *Fucus* distribution under different water clarity scenarios, analysed the effect of bottom substrate limitation to *Fucus* distribution areas and studied its regional differences. We built a species distribution model for *Fucus* and predicted its spatial distribution in the 'present' (2003–2011) situation and under 10 scenarios where euphotic depth varied from −50% to +50%. As comprehensive substrate maps were not available, we applied two correction methods to original SDMs to estimate the substrate limitation of *Fucus*: (i) utilising substrate data from field data (randomized drop-videos) and (ii) using a habitat model for reefs. Our results can be used for estimating how much new *Fucus* spp. habitats could realistically be formed with the improvement, or be lost due to deterioration, of the environmental status of coastal marine areas.

2. Materials and methods

2.1. Study area and species

The Baltic Sea is one of the most studied seas that can be considered as a 'time machine' to study consequences of future coastal perturbations (Reusch et al., 2018). The study focuses on Finnish sea areas differing in geomorphology and eutrophication status: the Gulf of Finland, the Archipelago Sea, the Bothnian Sea and Kvarken located in the atidal northern Baltic Sea (Fig. 1). The division was also made to inner, middle and outer archipelago following WFD coastal types: Gulf of Finland inner (GFi) and outer (GFo) archipelago; the coastal waters of inner (SAi), middle (SAm) and outer (SAo) Southwestern Archipelago; Bothnian Sea inner (BSi) and outer (BSo) archipelago and Kvarken inner (Ki) and outer (Ko) archipelago. As *Fucus* does not occur in the Bothnian Bay (the northernmost and least saline sea area of the Baltic Sea), this area was excluded from the analyses.

The WFD coastal types are national management units that were recognised and defined based on geographical and other scientific characteristics of the coastal waters. Having unique morphological and hydrological features, the coastal types can be used when assessing the environmental state of the sea areas to fulfil the requirements of national legislation and the WFD. The Finnish coastal types were divided to sea areas based on differences in salinity, depth, currents and duration of ice cover: Gulf of Finland, Southwestern Archipelago, Bothnian Sea, Kvarken and Bothnian Bay (Pilke, 2012). Inner, middle and outer archipelago each represent different levels of wave exposure and other environmental factors.

Steep environmental gradients exist along the Finnish coast. Salinity in the study area ranges from 7 (Practical Salinity Scale) in the outer Southwestern Archipelago to basically fresh water within the river estuaries. Water transparency varies spatio-temporally and the most transparent water can usually be found in the outer archipelago while the transparency decreases towards the inner archipelago. The study area is relatively shallow with mean depth of 15 m and maximum depth of 132 m. Exposure to wave action is low in the bays and increases towards outer archipelago and the open sea.

Bladderwrack *Fucus* spp. is the most important canopy-forming alga on shallow rocky bottoms in the northern Baltic Sea. Two species of bladderwrack (*Fucus vesiculosus* and *F. radicans*) occur on the Finnish coast. *F. vesiculosus* is the overwhelmingly dominant species, while *F. radicans* mainly occurs in Kvarken and the Bothnian Sea (Viitasalo et al., 2017). We conducted our study on a genus level as the two species are difficult to distinguish in the field and because they together form the ecologically important *Fucus* belt.

There are numerous biotic and abiotic factors shaping the

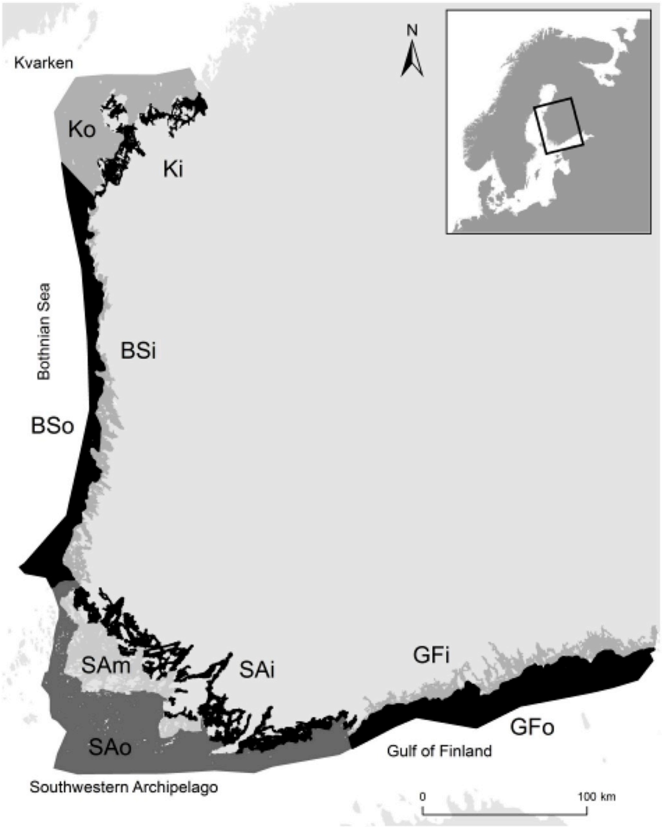

Fig. 1. Study area divided into national coastal water types, defined according to Water Framework Directive: Gulf of Finland inner archipelago (GFi), Gulf of Finland outer archipelago (GFo), Southwestern inner archipelago (SAi), Southwestern middle archipelago (SAm), Southwestern outer archipelago (SAo), Bothnian Sea inner coastal waters (BSi), Bothnian Sea outer coastal waters (BSo), Kvarken inner archipelago (Ki) and Kvarken outer archipelago (Ko).

distribution of *Fucus* (Eriksson and Bergström, 2005; Alexandridis et al., 2012; Wahl et al., 2011). Salinity and eutrophication gradients determine the geographical distribution of *Fucus* in the Baltic Sea (Wahl et al., 2011), while light environment and wave exposure, both affected by depth, shape the local distribution patterns (Bäck and Ruuskanen, 2000; Eriksson and Bergström, 2005). In addition, the availability of suitable bottom substrate sets limits for the occurrence of *Fucus* (Eriksson and Johansson, 2005; Rinne et al., 2011).

2.2. Species data

Inventory data for *Fucus* were available for 2004–2015 collected by the Finnish Inventory Programme for the Underwater Marine Environment (VELMU) along the Finnish coast. Scientific diving was used for dive transects where the coverages (%) of all visible macrophytes and different bottom substrates were estimated every horizontal 10 m or vertical 1 m. Drop-videos were recorded on randomized locations and approx. 20 m^2 of bottom were surveyed to estimate coverages of species and seabed substrates. The sampling scheme followed stratified sampling based on environmental gradients. Stratified-random sampling was conducted by randomising a set of video points to different combinations of environmental variables, such as depth, exposure, salinity and turbidity. The dataset also included grid-videos that are clustered drop-videos with sampling points placed in a grid at 100 m intervals. The grid-video clusters, each containing hundreds of video points, were located on sites of particular interest, e.g. sandbanks or reefs.

For modelling purposes, the species data were converted to presence-absence data and randomized to fitting (70% of observations) and validation datasets (30% of observations). Both dive and video data were used as *Fucus* can be reliably recognised by both methods. Only randomly chosen 25% of the grid-videos were used in the modelling in order to reduce spatial autocorrelation caused by clustered observation data.

The dive transects cover a depth range from the surface to the depths of the deepest macrophytes or slightly deeper. Thus, most of the dive data were collected from areas shallower than 20 m. Video data were also mostly recorded within this depth range. To calibrate the species distribution models to increase prediction also on deeper areas, benthic invertebrate samples (Ekman, Ponar, Van Veen and other grab samples for soft sediment sampling) from a depth range 17–286 m were added to the fitting dataset as known *Fucus* absences. These data originated from the Finnish environmental database HERTTA.

The scenario models might underestimate the potential distribution areas in positive scenarios when the observations in the fit data do not cover the whole range of variation tolerated by the species. The depth zonation of *Fucus* was remarkably wider a hundred years ago (Torn et al., 2006) when the euphotic depth was 40–55% higher than at present in the open sea areas of the Bothnian Sea, the Nordic Baltic Proper and the Gulf of Finland (Secchi depths from 1905 to 1909 and 2005–2009 (Fleming-Lehtinen and Laamanen, 2012) transformed to Z_{eu} following Luhtala and Tolvanen (2013)). Therefore, to obtain the accurate presence of *Fucus* in all depth zones of our increased water clarity scenario models, a subset of the presence observations were duplicated and the duplicate part was used as pseudo-presences where Z_{eu} was multiplied by 1.25 and 1.5 to represent same sites as already observed in the inventories but with a greater water transparency that is still realistic according to historical data. All other environmental variables were kept constant.

The dataset for model fitting consisted of 54504 observations including 3387 presences, 3429 absences from benthic invertebrate samples and 2898 pseudo-presences. Validation dataset was 24300 observations with 2220 observed presences.

2.3. Environmental data

Five environmental layers (resolution 20 m) were used in the modelling: depth, depth-attenuated wave exposure, surface salinity, unstable bottom and mean euphotic depth. Depth-attenuated wave exposure, representing wave exposure on the seabed, was estimated by utilising the grid exposure index from the Simplified Wave Model (SWM) (Isæus, 2004) following calculation procedure by Bekkby et al. (2008). Surface salinity was modelled with random forests (Breiman, 2001) and predicted as a spatial layer. The layer represents average salinity conditions throughout the growing season. Salinity measurements for the summer period June–August 2004–2015 were extracted from the national marine monitoring databases. The salinity near river mouths was corrected by estimating the level of dilution with fresh water by multiplying the distance of riverine input with the average river flow. A correction was calculated for the 57 largest rivers along the Finnish coast. Unstable bottom represents a share of soft bottom substrates (0–100%), thought to be unstable as growing foundations (gravel, sand, silt, mud, clay; < 60 mm). It was modelled with random forests using substrate data from VELMU inventories and physical environmental variables. Euphotic depth was derived from an optical model using satellite images.

Euphotic depth was calculated from Envisat-MERIS (Medium Resolution Imaging Spectrometer) satellite images for the summer periods (May–September) 2003–2011 with the spatial resolution of 300 m. The calculation of Z_{eu} layer was based on an optical model with concentrations of total suspended matter, chlorophyll-*a* and humic substances as well as sun altitude angle and specific inherent absorption and scattering coefficients as input. Concentrations of total suspended matter and chlorophyll-*a* were derived from the full resolution images

(300 m, 3^{rd} reprocessing) of the MERIS satellite sensor using the C2R (Doerffer and Schiller, 2007) and FNU-processors (Schroeder et al., 2007), respectively. The measure of humic substance concentration was absorption coefficient (m^{-1}) of a filtered sample at 400 nm. Humic substance concentration was not estimated from satellite images but rather a map of average humic substance concentrations was used as an input to the optical models. The map was based on routine *in situ* measurements at coastal monitoring stations in 2003–2011 (data obtained from PIVET database of the Finnish environmental administration) and on measurements (Pasi Ylöstalo, Finnish Environment Institute SYKE, unpublished data).

The mean $K_d(\lambda)$ in the euphotic zone was estimated with Kirk's (1984) equation (Equation (1)):

$$K_d(\lambda) = \frac{1}{u_0}(a_{Tot}(\lambda)^2 + (g_1 u_0 - g_2)\, b_{Tot}(\lambda) a_{Tot}(\lambda))^{\frac{1}{2}} \tag{1}$$

where u_0 is the cosine of the solar zenith angle in the water, a_{Tot} is total absorption coefficient, b_{Tot} is total scattering coefficient, $g_1 = 0.425$ and $g_2 = 0.190$. a_{Tot} and b_{Tot} were calculated from concentrations and specific inherent optical properties (Kallio, 2006). Euphotic depth (1% radiation level) was calculated from K_d by $Z_{eu} = 4.6 * K_d(400 - 700nm)^{-1}$. Monthly medians of Z_{eu} were calculated from the processed images. The final layer, mean Z_{eu}, was calculated from the monthly images and resampled to 20 m resolution to meet the resolution of depth model and other environmental variable layers.

2.4. Species distribution modelling

Species distributions were modelled using *dismo* and *gbm* packages and raster data were edited with *raster* package in R 3.1.2 (R Development Core Team, 2015). Species observations and the environmental variables related to point coordinates were used for Boosted Regression Tree (BRT) modelling (e.g. Elith et al., 2008). BRT models were created using 3750 trees, tree complexity set to 5, learning rate of 0.05 and bag fraction of 0.5. In order to calculate coast specific distribution areas, probability models were transformed to presence-absence models with the *Presence-Absence* package using the most optimal threshold, Sensitivity = Specificity (Sens = Spec).

The model performance was evaluated using the cross-validated area-under-the-ROC-curve value (cvAUC) generated during the model run (Elith et al., 2008). The validation dataset consisted of individual observations that were not included in the fitting data. The final classified model representing the current state of the distribution was validated using true-skill-statistics (TSS) according to Allouche et al. (2006) and AUC.

2.5. Scenarios

The water transparency scenarios were chosen to represent states where the euphotic depth has changed −50% to +50% from the mean 2003–2011 level. The upper limit was chosen according to historical values of euphotic depth in the open sea areas: Z_{eu} 40–55% higher in 1905–1909 compared to 2005–2009 (see above). Lower limit was chosen to be more pessimistic than the business-as-usual scenario (Secchi depth −10%) in the study by Bergström et al. (2013).

The BRT model was fitted with the present field and environmental data and the predictions were made for the present state and the 10 scenarios where Z_{eu} increased or decreased in 10% steps. The value of Z_{eu} in each pixel was changed according to the scenario, e.g. all Z_{eu} layer values were increased by +20%. Other environmental variables were kept constant.

2.6. Substrate data

As the bottom types vary along the coast and depth gradients and not all substrates are suitable to support growth of *Fucus*, the effect of substrate on the predicted distribution of *Fucus* was tested. The spatial distribution of *Fucus* was estimated using original SMDs and two correction methods: (i) substrate correction and (ii) reef layer method. Then results from the correction methods were compared to the results derived from original SDMs.

In the substrate correction method, the potential substrate-corrected *Fucus* distribution area was calculated for every scenario in all study areas. The mean shares of each bottom substrate class (0–100%) were assessed from the same VELMU random drop-video data (only random videos, no dive or grid video data), that were used for the species observations. The advantage of these data is that video analysis observes the ecologically relevant substrates on the top layer of the seafloor, in contrast to acoustic surveys that typically omit thin sediment or sand layers on rocky surfaces. The substrate correction was performed by extracting the video points inside predicted *Fucus* areas (in total 7319 video points), calculating the mean share of suitable substrates (classes solid rock and stone; > 60 mm) from these video points and multiplying the resulting share with the total distribution area predicted by the original classified SDM.

In the reef layer method, the corrected distribution area was estimated using a model describing potential underwater reefs (Kaskela and Rinne, 2018; VELMU, 2015), representing hard rocky surfaces along the coast, an approach modified from Rinne et al. (2014). The model predicts the spatial distribution of reefs (1170) described in Annex 1 of the EU Habitats Directive (Council Directive 92/43/EEC). In this method, the corrected potential distribution area was the intersection of the reef layer and the original predicted distribution areas of *Fucus*.

The total coverages of the potential *Fucus* areas and the changes from the present state were calculated using original SDM and two correction methods for 11 water clarity scenarios (from −50% decrease to +50% increase in euphotic depth) within all nine study areas and within inner and outer archipelagoes. In addition, the shares of substrate classes from the potential *Fucus* distribution areas were calculated for all scenarios and all study areas.

3. Results

3.1. Model performance

Mean euphotic depth had the highest relative influence (28%) in the model fitting, followed by depth (27%), surface salinity (18%), unstable bottom (17%) and depth attenuated wave exposure (10%). The model cvAUC ± standard error was 0.977 ± 0.001 and AUC calculated with validation data 0.924 ± 0.003 (AUC ± standard deviation) that are considered excellent. The threshold for classifications was 0.10 that represents the point where sensitivity equals specificity. Having a TSS of 0.69, the model appeared as ‘good’ (TSS > 0.6) (Landis and Koch, 1977).

3.2. Distribution areas of Fucus in relation to euphotic depth and suitable substrates

The horizontal distribution of *Fucus* changes with altered water transparency (Fig. 2). The differences between the three area calculation methods, the original SDM and two correction methods, followed similar pattern in every WFD coastal type. The original SDM had the largest distribution areas in every scenario and the substrate correction and reef layer methods showed remarkably smaller areas, especially in positive scenarios (Fig. 3). The reef layer based estimate is smaller in every coastal type and in every scenario, even though the relative change is smaller in substrate correction method in some coastal types (Fig. 4).

The original SDM areas extend broader as water transparency increases but the substrate correction and reef layer methods limit the horizontal broadening in almost every coastal type. This is because the

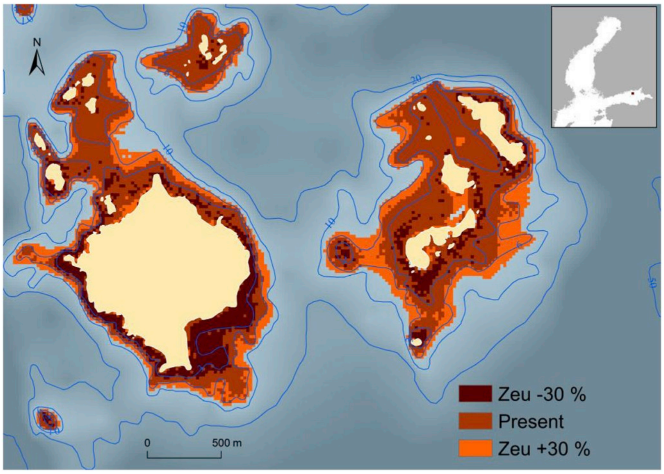

Fig. 2. An example of predicted distribution of *Fucus* in scenarios Z_{eu} -30%, present water transparency (2003–2011) and Z_{eu} +30% in the outer archipelago of the eastern Gulf of Finland. Depth contours 3 m, 6 m, 10 m & 20 m (Finnish Transport Agency).

average proportion of suitable substrates (rock & stone) decreases and the amount of soft sediment increases within the predicted distribution area (Appendix, Fig. 2). The outer Southwestern Archipelago (SAo) and the outer archipelago of the Gulf of Finland (GFo) were predicted to have the greatest potential for new *Fucus* areas as the suitable substrates are not limiting the horizontal expansion as fast as in other areas.

The substrate correction method gave larger estimates than the reef layer method but the phenomenon of suitable substrate limiting the changes in distribution areas in changing water transparency was present in both cases. The total areas of distribution were different when applying different methods (Fig. 3), but for most of the coastal types the relative change from the present state was rather similar for all methods in negative and in some positive scenarios (Fig. 4). The differences became more pronounced as the euphotic depth increased. The relative distribution area in a scenario compared to the current state differs between the coastal types and methods. Predicted by the most extreme scenario, the decrease of Z_{eu} by 50% from the present level narrows the distribution area of *Fucus* by 24–53% in the Southwestern archipelago, by 55–70% in the Gulf of Finland, by 37–66% in the Bothnian Sea and by 59–100% in Kvarken.

The increase of Z_{eu} by 10–50% results in areal growth of *Fucus* distribution area. If all areas were suitable for growth, a 50% increase in Z_{eu} would expand the distribution area by 124–803%. As only suitable substrates are taken into account, this percentage remains at 9–270%. The original SDM method predicts higher proportional areal growth than more conservative substrate correction and reef layer methods. The proportional changes in the broadened distributions are higher in the outer than in the inner archipelagos except in the stony Kvarken.

The potential changes in the *Fucus* distribution area differ between inner (GFi, SAi, BSi and Ki) and outer (GFo, SAo, BSo and Ko) archipelago (Fig. 5). The distribution area increases with increasing water clarity both in inner and outer archipelago, but the substrate correction limits the growth of potential areas especially in inner archipelago. The absolute change from the present area as well as the total distribution area are larger in the outer archipelago.

3.3. Regional substrate quality within Fucus distribution areas

The shares of substrate classes within the *Fucus* distribution area differ between regions in present (2003–2011) scenario. The main outcome is that the share of rock and stone is larger in the outer archipelago and softer bottom types are more pronounced in the inner archipelago except in Kvarken where stone is the main bottom type both in the inner and outer archipelago (Appendix, Fig. 1).

The shares of bottom substrates within *Fucus* distribution area

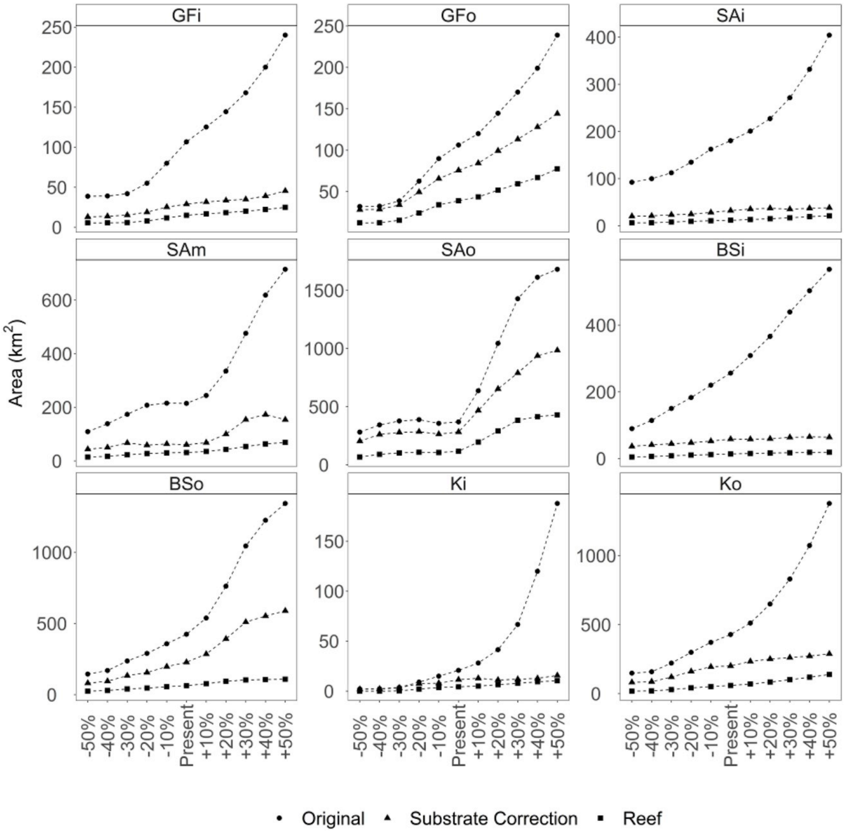

Fig. 3. Potential distribution area of *Fucus* for the WFD coastal water types (Fig. 1) using three different methods: original area predicted by SDM, substrate correction method and reef layer method. Original SDM predicts area as is, substrate correction applies correction using substrate data from random videos and reef method extracts only *Fucus* areas that are located on reefs. The scenarios on x-axis present the change of Z_{eu} from the present state in percentages. Note the changing scale on y-axis.

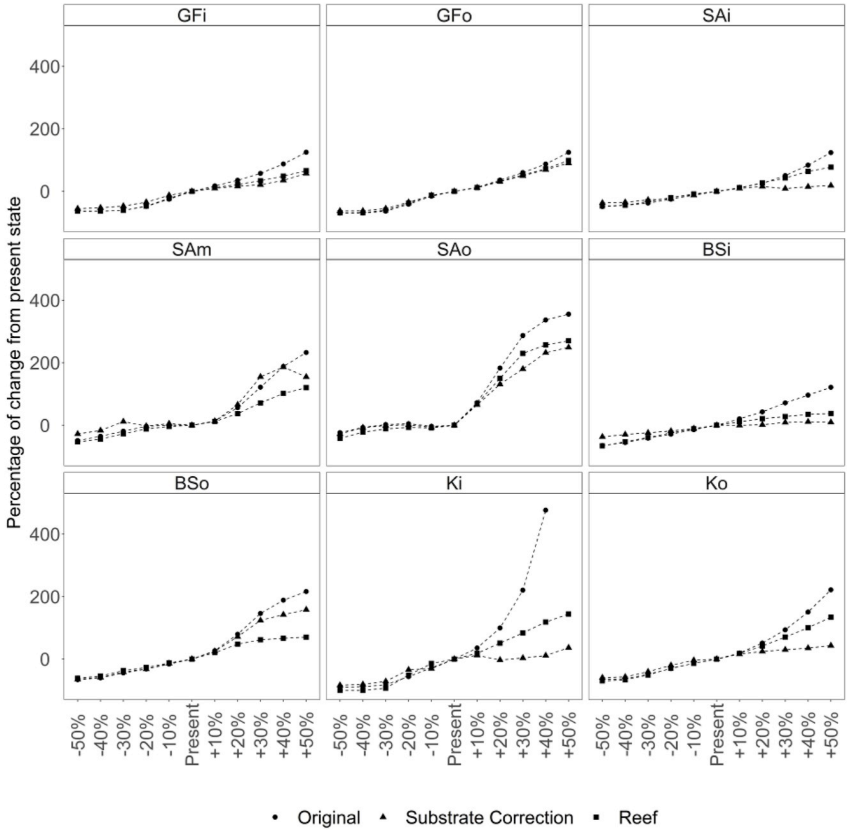

Fig. 4. Relative potential distribution area of *Fucus* compared to predicted present 2003–2011 distribution for the WFD coastal water types (Fig. 1) using three different methods: original area predicted by SDM, substrate correction method and reef layer method. Original SDM predicts area as is, substrate correction applies correction using substrate data from random videos and reef method extracts only *Fucus* areas that are located on reefs. The scenarios on x-axis present the change of Z_{eu} from the present state in percentages.

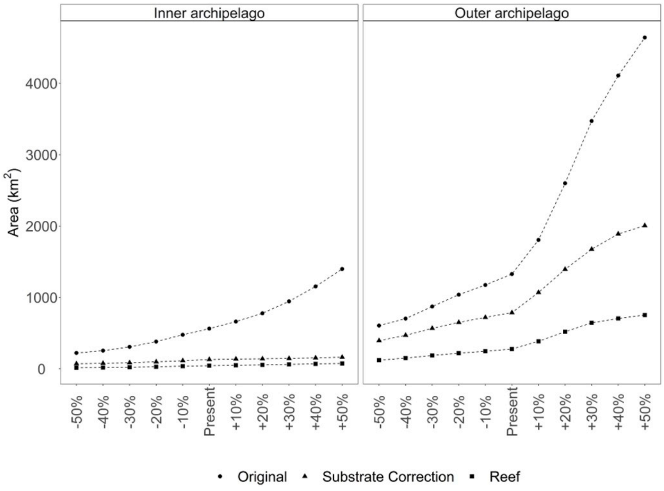

Fig. 5. Potential distribution area of *Fucus* in inner and outer archipelago using three different methods: original area predicted by SDM, substrate correction method and reef layer method. Original SDM predicts area as is, substrate correction applies correction using substrate data from random videos and reef method extracts only *Fucus* areas that are located on reefs. The scenarios on x-axis present the change of Z_{eu} from the present state in percentages.

change when the changing euphotic depth results in growing or narrowing potential distribution areas. In general, there was a clear gradient from rocky substrates to soft bottoms as the potential distribution of *Fucus* changes with increasing water clarity (Appendix, Fig. 2).

4. Discussion

4.1. Potential distribution area of Fucus

Light availability is one of the most important factors affecting spatial distribution of macroalgae, especially in relatively turbid waters, such as the Baltic Sea. The potential expansion of macroalgae due to improved water clarity can be readily estimated using SDMs. Our study is however, to our knowledge, the first to take into account the effect of substrate suitability in the estimates.

The long-term deterioration of *Fucus* populations has been a dominant issue in the northern Baltic Sea (Torn et al., 2006; Vahteri and Vuorinen, 2016), and management measures are intended to improve both water clarity and the state of the *Fucus* populations. According to our results, and previous studies (Torn et al., 2006; Bergström et al., 2013), the increase in water clarity will result in vertically deeper and thus horizontally broader distribution areas. However, seabed substrate type can be an important factor for many macroalgal species, especially brown and red algae, limiting their spatial distribution and depth zonation in the northern Baltic Sea (Rinne et al., 2011). Our analysis supports this hypothesis: as there is a gradient from rocky and stony substrates towards more sandy and soft bottoms within the predicted *Fucus* distribution area, progressively smaller proportions of new bottom will be suitable for the species with improving light conditions. The availability of suitable bottom substrate becomes a limiting factor for the areal growth especially in the inner archipelago areas. Most probably this is also the case with other macroalgal species that attach to hard substrates.

The negative scenarios, in contrast, lead to a decrease in the predicted distribution area in all study areas. The relative decrease in the area from present to a −50% Z_{eu} state is the lowest in the Southwestern archipelago and highest in Kvarken, where the most negative scenarios and the reef layer method predict a complete absence of *Fucus*. When comparing the present state to the most negative scenario Z_{eu} -50%, the reef layer method shows higher decrease in the potential distribution area than substrate correction method (except BSo).

4.2. Model accuracy and relevance

Species distribution modelling of benthic marine species in the northern Baltic Sea is a useful tool for estimating the regional distributions along environmental gradients, and under different environmental scenarios. The model accuracy can be improved by using geomorphological and geological data layers in the modelling, but the uncertainties need to be taken into account (Rinne et al., 2014). Many sea areas lack the crucial high-resolution information of the bottom substrates, or its public use is restricted by law, which are both the case in Finland. Thus, the correction to take substrate limitation into account when estimating distribution areas of species needs to be made using other approaches.

In our SDM we used the ‘unstable bottom’ variable to predict the probable share of soft sediment bottoms. The layer was an important variable in the model (17%) but it did not effectively limit the distribution of *Fucus*, as could be seen from the large differences in area estimates between original SDMs and the substrate correction or reef methods. Substrate correction from field observations can be used to estimate the potential distribution area when there are no substrate maps available for the study area. Using reef layer or other substrate layers in the post processing provides another way to estimate the availability of hard substrates, but the method is likely to be crude as it does not take into account micro-habitats and small scale variation in characteristics of the seafloor.

In our study, the estimated area of species distribution varied depending on the method used to estimate the amount of suitable substrate. The substrate correction method usually predicted greater increase in the distribution areas in positive scenarios than the reef layer method. The increase in the share of stony bottoms in positive scenarios may explain this as the reef model may not recognise stony areas as reefs. In addition, the reef layer might not include large shallow rocky areas as a reef if the area is larger than the radius used in the reef model calculation (Kaskela and Rinne, 2018).

We used euphotic depth scenarios as a proxy for regional eutrophication, instead of nutrient scenarios that can be unreliable (Meier et al., 2014). Many macroalgae are vulnerable, not only to reduced amount of light, but also to sedimentation (Eriksson and Johansson, 2005) and overgrowth by epibionts (Rohde et al., 2008), which are both increased by eutrophication. Thus, our estimates for the negative scenarios may be too optimistic, especially in sheltered inner archipelago, where sedimentation increases along with the decreasing water clarity.

5. Conclusions & recommendations

The horizontal distribution of *Fucus* is dependent on euphotic depth and a decrease in water clarity will narrow the *Fucus* zone. Increasing water clarity, in turn, will enable the species to occur deeper and thus to occupy horizontally broader bottom areas. This change is, however, limited by the lower share of hard substrates in deeper water, as the average bottom substrate shifts towards soft bottoms that are unsuitable for macroalgal growth.

The decrease of Z_{eu} to half from the current level causes the distribution area of *Fucus* to narrow by 24–53% in the Southwestern archipelago, by 55–70% in the Gulf of Finland, by 37–66% in the Bothnian Sea and by 59–100% in Kvarken. The increase of Z_{eu} by 50% results in an increase of the distribution area. If all areas were suitable for growth, a 50% increase in Z_{eu} would result in 124–803% broader distribution areas. Given the substrate limitation, the increase is only 9–270%. Substrate limitation therefore plays a major role in restricting the expansion of distribution areas. Our results suggest that *Fucus* benefits from the increased water clarity, but that the change in is generally smaller in the inner archipelago, except in Kvarken, where a large share of stony bottoms prevail. The largest increase in the distribution area occurs in the outer Southwestern Archipelago and in the outer Bothnian Sea.

Table 1
Change in euphotic depth needed to achieve good ecological status of surface waters (ES), as defined by EU Water Framework Directive. Good ES for Z_{eu} was calculated from national Good ES target levels for Secchi depth described for national EU Water Framework Directive coastal types (Aroviita et al., 2012) following Luhtala and Tolvanen (2013). *Fucus* distribution area in good ES is estimated linearly from the scenarios.

	Average Z_{eu} (2003–2011)	Good ES Z_{eu}	Change needed for good ES	*Fucus* distribution in good ES
GFi	6.0	9.6	+59%	> +57–125%
GFo	7.9	11.4	+45%	+80–106%
SAi	6.6	9.8	+50%	+18–124%
SAm	8.9	11.8	+33%	+80–164%
SAo	10.6	14.0	+33%	+196–302%
BSi	7.1	9.2	+29%	+8–69%
BSo	9.9	10.8	+9%	+19–24%
Ki	6.5	7.0	+7%	+9–25%
Ko	9.0	10.0	+12%	+18–26%

Achieving Good Ecological Status, as defined by the EU Water Framework Directive, would mean a significant increase in water clarity and thus an increase in the vertical and horizontal distribution of *Fucus*. However, the stronger substrate limitation in the inner archipelagoes implies that relatively more effort is needed to mitigate the effects of eutrophication on *Fucus* in the inner than in the outer archipelago areas.

The Baltic Sea countries have agreed to improve the state of the marine ecosystem and have set up an ambitious Action Plan (HELCOM, 2007) to achieve this by year 2021. Also, according to the Water Framework Directive, member countries need to achieve Good Ecological Status of surface waters (ES). The Good ES target for water transparency has been calculated from measurements of Secchi depth, and the national Good ES levels for coastal areas have been set for each of the coastal types (Aroviita et al., 2012). We estimated that, to achieve good ES, the euphotic depth should increase by 7–59%, depending on the coastal type (Table 1). The largest change is required in the Gulf of Finland (45–59%) and in the Southwestern Archipelago (33–50%), whereas in the outer parts of the Bothnian Sea and in Kvarken, the change needed is only 7–12%.

The increase in euphotic depth to the good ES level would in all areas result in a wider distribution of *Fucus*, but the increase in most areas would be limited by the availability of suitable substrates (Table 1). According to our results, the sheltered inner archipelago is the area where substrate limitation will slow down expansion of *Fucus* with improving water clarity. This suggests that, to reach the Good ES target also for macroalgae, the management effort should be strongest in the inner archipelago areas.

To conclude, scenario modelling can produce useful information for management purposes. Our study shows that substrate limitation of key habitat forming species can be estimated by using relevant data, even in the absence of accurate substrate maps. However, it is important to note that regional differences in seabed structures affect the level of substrate limitation. This needs to be taken into account when planning and implementing local mitigation measures.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2018.11.010.

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