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Forecast climate change conditions sustain growth and physiology but hamper reproduction in range-margin populations of a foundation rockweed species

Eva Rothäusler*, Luca Rugiu, Veijo Jormalainen

Department of Biology, University of Turku, Turun yliopisto, Turku, Finland

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ABSTRACT

Intensifying environmental changes due to climate change affect marine species worldwide. Herein, we experimentally tested if the combination of forecasted warming and hyposalinity adversely affected growth, receptacle formation, and photosynthesis of three marginal populations of the brown alga *Fucus* from the northern Baltic Sea. Growth was not impaired by the projected consequences of climate change but genotypes varied in their responses, suggesting existence of genetic variation in phenotypic plasticity. Climate change further prevented receptacle formation, implying that *Fucus* fail to reproduce sexually. Photosynthesis was not affected by climate change but varied among populations. Our results show that *Fucus* populations photosynthesized, grew, and survived well under the projected climate change but their sexual reproduction ceased. This suggests that the marginal populations tested herein are resilient to future conditions but only if asexual reproduction enables them to proliferate.

1. Introduction

Ongoing climate change is recognized to challenge the persistence of aquatic and terrestrial species worldwide (Parmesan, 2006; Bellard et al., 2012; Knouft and Ficklin, 2017). Especially for populations that exist at the range margins of species' distributions, climate related environmental changes may be exceptionally severe (Pearson et al., 2009; Ferreira et al., 2014). The bladder wrack *Fucus vesiculosus* (Fucales, Phaeophyceae, hereafter *Fucus*) represents one of these marine species at their range margin within the littoral and sublittoral zones of the northern Baltic Sea (60–65°N) where low saline waters, ranging from 2 to 6 PSU prevail (Wahl et al., 2011). Thus its distribution has been attributed to the salinity tolerance of its gametes (Serrão et al., 1996). As a foundation species, it facilitates the existence and survival of other species, therefore influencing the structure and functioning of the coastal ecosystem. However, during the coming 70–100 years a drop in seawater salinity down to ~2.5 PSU is foreseen, and is expected to occur in concert with a rise in seawater temperature (Meier and Eilola, 2011). In light of this harsh changes, there is an urgent need to learn whether these marginal populations can persist in their new physical environment.

Low salinity is considered to be a strong selective agent on Baltic marine organisms, especially on those living at the northern boundary areas of their distribution such as the Gulf of Bothnia and the Gulf of Finland. Probably, in these sea areas the low salinities (2–6 PSU) selected for the resistant phenotypes during the exposure to a progressive decrease in salinity since the Post-Littorina Sea times (Russell, 1985), so that *Fucus* populations are locally adapted to tolerate the low salinity. Tolerance to low salinity is evidenced by several studies on fertilization, growth and/or physiology of the species (Bäck et al., 1992; Serrão et al., 1996; Pearson et al., 2000; Nygård and Dring, 2008; Rothäusler et al., 2016; Johansson et al., 2017). Empirical studies suggest that small-sized populations near range margins tend to have lower genetic diversity and are thus expected to be more affected by stressful environmental conditions because this may impair their potential for adaptation to new selective regimes (Johannesson and André, 2006; Kawecki, 2008). If so, the predicted and already ongoing climate change (Meier and Eilola, 2011) sets challenges for *Fucus* inhabiting marginal areas.

Fluctuations in salinity have a deleterious effect on marine macroalgae by affecting reproductive patterns (Serrão et al., 1996; Steen, 2004; Mantri et al., 2011). For instance, the salinity tolerance of *Sargassum muticum* was lowest during fertilization (Steen, 2004) and too hyposaline waters profoundly increased the risk of polyspermy and sperm malfunctioning in *Fucus*, thus impeding sexual reproduction (Serrão et al., 1996). As marginal habitats in the northern Baltic Sea

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* Corresponding author.
E-mail address: evanro@utu.fi (E. Rothäusler).

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become less suitable due to salinity dependent physiological constraints, some *Fucus* populations tend to reproduce asexually at ∼4 to 6 PSU via the formation and settling of adventitious branches (Tatarenkov et al., 2005; Johansson et al., 2017). Asexual reproduction has been suggested to be the strategy allowing the persistence of *Fucus* in these habitats, where they live at the edge of their environmental tolerance (Rafajlović et al., 2017). Consequently, species living near their tolerance range margins are particularly susceptible to the environmental alterations due to climate change. Changes in physiology, growth, and reproduction of species in marginal areas can thus act as early warning indicators before the more ultimate survival effects.

Indeed, previous studies revealed significant hyposalinity but also warming effects on growth, physiology, and reproduction of *Fucus* from the Baltic Sea (Russell, 1988; Bäck et al., 1992; Bergström et al., 2005; Nygård and Dring, 2008; Kraufvelin et al., 2012; Graiff et al., 2015, 2017). For instance Nygård and Dring (2008) showed that *Fucus* from northern Sweden (5 PSU) reached highest maximal photosynthesis at low salinities (5–10 PSU) as compared to their Irish counterparts (35 PSU) where photosynthesis declined sharply at salinities below 20 PSU. Similarly, growth of *Fucus* from the Gulf of Finland was more vigorous at 4 PSU than at 6 PSU (Takolander et al., 2017). Moreover, rising sea surface temperatures triggered by climate change negatively affected *Fucus* performance (Nygård and Dring, 2008; Maczassek, 2014; Graiff et al., 2015; Gutow et al., 2016) and pose overall serious challenges for macroalgae survival in coastal areas (Harley et al., 2012). For instance, simulated short-term heat waves with temperatures exceeding 27 °C are lethal for adult thallus but also for juveniles of *Fucus* (Graiff et al., 2015; Al-Janabi et al., 2016). In adults, a high temperature stress reduced both the growth rate and photosynthetic performance (Graiff et al., 2015). On the contrary, moderate warming accelerated receptacle formation in *Fucus* from the Gulf of Finland (Kraufvelin et al., 2012).

Within the Sea of Bothnia and the Gulf of Finland, the low salinity is caused by freshwater runoff from rivers but also by a weak exchange of the Baltic Sea saltwater with the Atlantic Ocean (Omstedt and Axell, 2003). The surface summer salinity is predicted to decrease further by ∼2.5 PSU (The BACC Author Team, 2008) because of increased precipitation in and consequent freshwater runoff from the northern Baltic Sea catchment. Within this marginal sea area, sea surface temperature can drop below zero in winter due to ice cover, while in summer it usually reaches 20 °C (Swedish Environmental Protection Agency, 2001) with occasionally occurring heat waves (HELCOM, 2013). During summer months, the sea surface temperature is predicted to rise in these areas on average ∼2.5 °C by 2070–2099 (The BACC Author Team, 2008). Thus, the predicted climate change (Meier and Eilola, 2011) makes the living conditions in the northern Baltic Sea for *Fucus* more stressful and may force populations to shift to lower latitudes.

In fact, a recent study by Rugiu et al. (2018) showed that a long-term exposure to a combination of predicted hyposalinity and warming negatively affected growth and survival of *Fucus* populations near their range-margin, whereas among them one population of *Fucus radicans* tolerated well future conditions (Rugiu et al., under revision). Similarly, *Fucus* from the Gulf of Finland showed extensive tissue necrosis when exposed for 3 weeks to a combination of extreme temperature (26 °C) and low salinities (4 PSU), which also damaged the photosynthetic apparatus (Takolander et al., 2017). Furthermore, hyposalinity and warming induced changes in the food quality of *Fucus* for associated mesograzers, so that their grazing pressure increased (Rothäusler et al., 2017). Altogether, these results highlight the among population differences in tolerance to the forecasted changes in environmental conditions.

To date, there have been numerous studies detailing the single effects of temperature or salinity on the responses of *Fucus* (Serrão et al., 1999; Nygård and Dring, 2008; Maczassek, 2014; Wilson et al., 2015; Graiff et al., 2015; Gutow et al., 2016) but little has been done to examine the combined effect of the predicted rise in temperature and drop in salinity. These abiotic factors will change in concert (IPCC Climate Change, 2007) and they can have synergistic or antagonistic interactive effects (Wahl et al., 2011). Therefore, we combined warming with a drop in salinity predicted for the end of this century (Meier and Eilola, 2011), to detect their simultaneous effect on *Fucus* performance. We reared three marginal populations of *Fucus* in future and current conditions to test the following hypotheses: (i) future combination of warming and hyposalinity negatively affect growth and photosynthesis, and (ii) compromise receptacle formation. We further hypothesize that (iii) performance and tolerance to future conditions may vary geographically among the range-margin populations and among genotypes within the populations.

2. Materials and methods

2.1. Sampling of algae at their edge of range

The experiment was carried out in autumn 2015 at the University of Turku (UTU) situated in SW Finland. On the 15th and 16th of September, we sampled one population in the shallow subtidal (0.5–1 m depth) from the Gulf of Finland, Porvoo (60°15′N, 25° 39′ E), and two populations from the Bothnian Bay, Rauma (61° 08′N, 21° 27′ E) and Kaskinen (62° 22′N, 21° 13′ E) (Fig. 1).

Within Porvoo and Rauma, we collected from N = 16 and N = 15 holdfasts, respectively, one single stipe (hereafter individual). Since in Kaskinen, *Fucus radicans* and *Fucus vesiculosus* can be present, we collected a total of 27 individuals, of which we assigned 7 individuals to the radicans-like morphotype based on the morphological characteristics described in Bergström et al. (2005). All individuals were tagged for later identification and transported in coolers to UTU, where they were stored for 24 h in seawater at ambient temperature and salinity before being processed further.

From all 58 individuals we took tissue samples to genotype them at nine microsatellite loci (L20, L38, L58, L85, L94: Engel et al., 2003; and Fsp1, Fsp2, Fsp3, Fsp 4: Perrin et al., 2007). This was done to ensure that each individual presented a unique multilocus genotype. We found that the 7 radicans-like individuals from Kaskinen did not separate genetically from all the rest of the individuals. Thus, we denominate our samples as *Fucus* without species distinction (for a more detailed description of genetic structure, see Rothäusler et al., 2017). In Kaskinen, we found three out of 27 individuals representing the same clone and

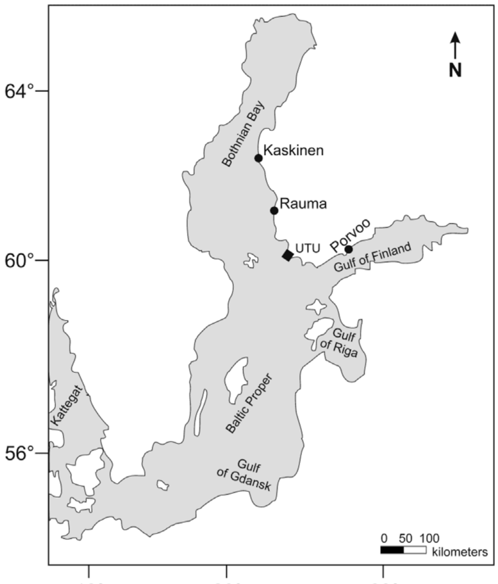

Fig. 1. Map of the Baltic Sea with the three sampling sites, and the different sea regions. The experiment was conducted at the University of Turku (UTU).

these were coded in the further analysis as replicates of the same genotype, leading to N = 24 individuals. In the two other populations, all the sampled individuals represented distinct molecular genotypes. Thus we hereafter refer to our individuals as genotypes.

2.2. Culture conditions and simulation of climate change

Treatments simulating current and future climatic conditions were applied in two units in an indoor recirculating aquarium system at UTU. Each unit consisted of a bottom reservoir (~300-L) and 12 aquaria of 24-L that were distributed over three shelves. The bottom reservoirs were equipped with a chiller/heater unit (TECO TR 15) to regulate water temperature.

Temperature and salinity data extracted from VELMU (http://www.ymparisto.fi/en-US/Sea) showed that all three sites had similar salinity and seawater temperature conditions during summer: Kaskinen, 4.7 PSU, 14 °C; Rauma, 4.7 PSU, 14 °C; Porvoo, 4.7 PSU, 14 ± 3 °C. However, temperature can vary between 0 °C in winter and 25 °C in summer. During our sampling, the temperature was 15 °C and the salinity was 5.2 PSU. Hence, the aquarium unit for the current conditions was set to these abiotic conditions. The future conditions simulated the stress levels projected by the model of Meier and Eilola (2011) for the summer season (average of June to August) in the Northern Baltic Sea when growth of *Fucus* is highest (for more details see Rothäusler et al., 2017 and Rugiu et al., 2018). Accordingly, the aquarium unit for the future conditions was set to a temperature of 17.5 °C and a salinity of 2.5 PSU. Each aquarium unit was equipped with 6 LED lamps (Radion ™ XR30w Pro lamps) composed of two groups of LEDs, so that every aquarium received light from one group of LEDs. A 10 h light to 14 h dark rhythm was applied, which corresponds to late summer light conditions. To mimic the course of the sun, the light smoothly increased in the morning during few hours reaching a peak of 300–540 μmol photons m^{-2} s^{-1}at 1200 h (depending on the position of the algae in the aquarium) that lasted for 1 h and then again smoothly decreased towards the evening. To avoid variation due to algae facing microclimates, we relocated the position of the algae inside each aquarium every other day.

The two aquaria systems were filled with natural seawater (a total of ~600-L each) and with an equal amount of distilled water. We did this to lower the salinity for the future treatment but also to equalize the initial nutrient conditions. We adjusted for the current salinity by adding extra sea salt. The water in both bottom reservoirs was biologically filtered and UV-sterilized (SCHURAN Jetskim 120) before it was pumped up and delivered independently into each aquarium.

Every second week, an enriched seawater medium (Guillard and Ryther, 1962; Guillard, 1975), composed of micro (trace metals and vitamins) and macro (phosphate and nitrogen) nutrients was added to the bottom reservoirs, according to the in situ surface concentrations present in the Archipelago Sea region during September to November (SYKE, Finnish Environment Institute). During the experimental period, from the 30th of September to 16th of November 2015 (6 weeks), the water temperature (pedant onset HOBO data logger) and salinity (pH/mV 110 set, VWR portable instruments) were measured daily from the aquaria. Average aquaria seawater temperature and salinity was for the current treatment 15.1 ± 0.2 °C and 5.3 ± 0.1 PSU and for the future treatment 17.5 ± 0.4 °C and 2.7 ± 0.2 PSU. We also measured pH regularly, with average values of 8.23 ± 0.01. To keep the water level and salinity in the aquaria constant, we regularly added ion-exchanged water into the bottom tanks.

2.3. Preparation of experimental algae

The 55 genotypes (Kaskinen N = 24, Rauma N = 15, Porvoo N = 16) were rinsed under flowing freshwater, and associated epiphytes and grazers were carefully removed. Thereafter, each genotype was split into six similar-sized ramets (totaling to N = 330 ramets) (Fig. 2), weighed (mean ± SD: weight 7.6 ± 0.6 g), counted the numbers of apical meristems (mean ± SD: 87 ± 17) and marked with a plastic tag to distinguish them from each other. Three of the six ramets were then distributed randomly among the 12 current aquaria, and the other three among the 12 future aquaria with the result that every aquarium unit received a total of N = 165 ramets. The random distribution was done so that each aquarium contained a mix of at least 14 ramets. We installed filter pumps in every aquarium to maintain ramets in constant movement. Before the actual experiment started (30th of September 2015), ramets were acclimated to the future treatment by increasing the temperature and lowering the salinity slowly within 2 weeks.

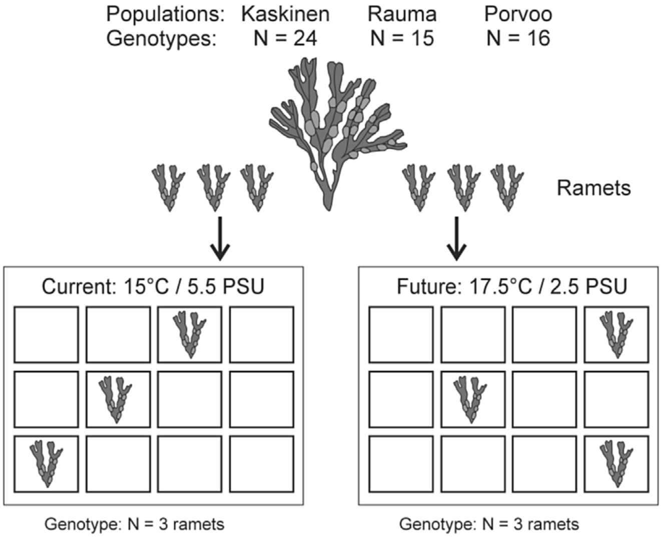

Fig. 2. Schematic illustration of the two aquaria units (current and future) and the distribution of the genotypes from the three populations (Kaskinen, Rauma, and Porvoo) over current and future aquaria. Each genotype was cut into six ramets, three of which were distributed randomly among the 12 current aquaria and the other three ramets randomly among the 12 future aquaria.

2.4. Measures of performance

After 6 weeks in their respective climate change treatments we measured growth, receptacle formation, and photosynthetic responses of *Fucus* genotypes. Growth (G) was expressed as rate and measured in terms of gain in the number of apical meristems (= meristem formation) and in terms of elongation in length (mm). For the meristem formation, we counted the number of meristems of each ramet at the beginning (day 0, G0) and at the end (6 weeks, G6) of experimentation (G = (G6 − G0)/G0).

For the length gain (LG), we measured the ramets at day 0 (L0) and again after 6 weeks (L6) (LG = L6 – L0).

During ontogeny, part of the vegetative meristems transform into receptacles. At day 0, we inspected the ramets for the presence of receptacles and observed that none of the ramets had receptacles. However, after 6 weeks many branches of the ramets had formed early stage receptacles, and thus we recorded presence or absence of these in each ramet. We did not count the receptacles but just observed their occurrence. Receptacle formation are thus present (1)/absent data (0) at the level of ramet. The final number of vegetative meristems as well as the probability of receptacle formation during the experiment of each genotype were based on the mean of the three replicate ramets in the current and future conditions. So, at the level of the genotype the probability of receptacle formation can have values of 0, 1/3, 2/3, and 1, depending on how many of the ramets had at least one receptacle.

We measured photosynthetic performance as the maximum quantum yield of fluorescence (Fv/Fm) as well as photosynthesis versus light curve (P-E) parameters at the end of the experiment. This was done *in vivo* by using a computer-aided portable pulse-amplitude-modulated fluorometer (PAM, 2000; Walz, Effeltrich, Germany). For all photosynthetic responses we used the newly grown apical thallus. First, we determined Fv/Fm by taking from every ramet ($N = 330$) one sample disk (10 mm diameter). The sample disk was incubated for 20 min in the dark and then measured two times for Fv/Fm, so that one genotype is represented by the mean of the two measurements from each three ramets kept in future and current treatment.

We estimated the photosynthetic rate as an electron transport rate (ETR) from the P-E curves. Since we herein used the absolute ETR, which is more time consuming, we measured five genotypes from Porvoo and Rauma, and ten genotypes from Kaskinen, each represented by one ramet. From each ramet, we cut off three samples from the newly grown apices and put separately in test tubes wrapped with aluminum foil and irradiated individually with increasing intensities of photosynthetic active radiation (PAR: 0–500 μmol photons $m^{-2} s^{-1}$) as described in Rothäusler et al. (2016). Thus, for the ETR measurements, each genotype is represented by the mean of the three algal disks from one ramet.

We used the absolute ETR, meaning we included the absorptance of every algal disk in our calculations to account for variation in tissue thickness and pigment content of the disks. Absorptance was measured on a cosine corrected PAR sensor (LI-190SA, Lincoln, USA) (for details see Rothäusler et al., 2016). The light transmission was calculated as follows:

$$A = 1 - E_t E_o^{-1}$$

Where E_t is the irradiance below the sample disk (transmitted light) and E_o the incident irradiance.

Then, the ETR was estimated by relating the effective quantum yield (Φ PSII) and the intensity of the radiation as follows:

$$\mathrm{ETR} = \Phi\ \mathrm{PSII} * E_{\mathrm{PAR}} * \mathrm{A} * 0.8$$

Where E is the incident irradiance of PAR and A the absorptance of the sample disk. For brown algae a factor close to 0.8 has been estimated (Grzymski et al., 1997), and represents the fraction of absorbed quanta directed to PSII, which is needed to assimilate one CO_2 molecule. The hyperbolic tangent model of Jassby and Platt (1976) was fitted as follows:

$$\mathrm{ETR} = \mathrm{ETR}_{\max} * \tan h * (\alpha_{\mathrm{ETR}} * \mathrm{E} / \mathrm{ETR}_{\max})$$

Where $\mathrm{ETR}_{\max}$ (μmol $e^{-} \cdot m^{-2} \cdot s^{-1}$) is the maximal electron transport rate, tan h is the hyperbolic tangent function, α_{ETR} (μmol $e^{-} \cdot m^{-2} \cdot s^{-1}$ [μmol·photons·$m^{-2} \cdot s^{-1}$]) is the initial slope of the P-E curve and an indicator of the efficiency of the electron transport, and E is the photon fluence rate of PAR. The saturation irradiance for the electron transport, E_k (μmol·$m^{-2} \cdot s^{-1}$), was calculated as $\mathrm{ETR}_{\max}/\alpha_{\mathrm{ETR}}$.

From the same algal disks as used for the ETR, we also determined the non-photochemical quenching (NPQ, photoprotective dissipation of excess energy) capacity of *Fucus* genotypes by using the maximum chlorophyll fluorescence recorded during the P-E curves when all the PSII reaction centers were closed (Fm or Fm', without or with non-photochemical quenching, respectively). NPQ was calculated as follows:

$$\mathrm{NPQ} = (\mathrm{Fm} - \mathrm{Fm}') / \mathrm{Fm}'$$

2.5. Statistics

We used generalized linear mixed models implemented by the GLIMMIX (SAS Institute Inc. 2013) procedure in SAS 9.4 to analyse meristem formation, length, receptacle formation, and photosynthetic responses (Fv/Fm, α, $\mathrm{ETR}_{\max}$, E_k and NPQ). For all analyses we used climate change treatment (two levels: current and future conditions), which was treated as a fixed factor, while population, genotype, and aquarium were treated as random factors. All possible interactions between random factors and climate change were tested. The presence or absence of receptacles was treated as a binary response variable. Models were simplified by removing non-significant effects based on the Akaike Information Criterion (AIC). F-statistics was used to test for the significant effect of climate change with the denominator degrees of freedom estimated by the use of the Kenward-Roger approximation (Kenward and Roger, 1997). We tested the significance of random factors and their interactions as well as their interactions with the fixed factor with the likelihood ratio test (Roy, 2007).

We checked the homogeneity of variance for meristem formation, photosynthetic responses and receptacle formation by visual inspection of the residuals. Since the variance of meristem and receptacle formation were heteroscedastic among populations, we used the Satterthwaite's approximation to estimate the denominator degrees of freedom and estimated the variance separately for each population.

In order to explore the cost of reproduction in terms of growth rate, we analysed the relationship between meristem formation and the probability of receptacle formation within populations using a logistic regression based on Wald chi-square statistics implemented by the logistic procedure in SAS 9.4. The logistic regression was only conducted for the current treatment since no receptacles were formed in the future treatment.

3. Results

3.1. Growth and receptacle formation under climate change

Growth in terms of meristem formation was not affected by climate change and did not vary among populations (Fig. 3, Table 1). However, different genotypes within populations expressed varying tolerance to the climate change treatment (Table 1: significant climate change × genotype -interaction). Similarly, growth in terms of length gain was not affected by climate change but varied among populations (Table 1) with Kaskinen having highest length gain (mean ± SE; 22.0 ± 2.0 mm) followed by Rauma (16.0 ± 3.0 mm) and Porvoo (13.3 ± 3.0 mm). Also the different genotypes varied in their length gain. Notably, climate change strongly affected receptacle formation (Fig. 4, Table 1). Only 1% of the ramets kept in the future treatment formed receptacles, while 28% formed receptacles in the current treatment. The receptacle formation was different among genotypes (Table 1). According to the logistic regression, in the current treatment, there was an overall trend though not significant that *Fucus* with more receptacles produced less vegetative meristems ($\chi^2 = 3.04$, $p = 0.08$). When conducting the analysis separately for the three populations, genotypes from Porvoo that formed receptacles grew significantly fewer meristems ($\chi^2 = 4.7$, $p = 0.03$) but no significant trend was observed for Rauma ($\chi^2 = 0.09$, $p = 0.76$) or Kaskinen ($\chi^2 = 1.4$, $p = 0.23$).

3.2. Photosynthesis under climate change

Climate change had no effect on any aspects of photosynthetic performance. Neither the maximal electron transport rate ($\mathrm{ETR}_{\max}$), the saturation irradiance (E_k), the initial slope alpha (α_{ETR}), nor the non-photochemical quenching (NPQ) and the maximal quantum yield (Fv/Fm) (mean ± SE, 0.62 ± 0.01), $F(1, 24.7) = 0.82$, $p = 0.37$) were affected by climate change (Table 2). All of these responses, however, varied among populations. Fv/Fm was slightly higher in Kaskinen (0.62 ± 0.01) and Porvoo (0.62 ± 0.01) as compared to Rauma (0.60 ± 0.01) ($\chi^2 = 5.34$, $p = 0.01$). Highest $\mathrm{ETR}_{\max}$ was shown for *Fucus* from Porvoo (mean ± SE, 19.8 ± 2.09) followed by *Fucus* from Rauma (16.74 ± 1.88) and Kaskinen (15.2 ± 1.68) (Fig. 5a). This is also reflected in the E_k, showing that *Fucus* from Porvoo (75.33 ± 4.33) had higher light requirements to reach its $\mathrm{ETR}_{\max}$ while *Fucus* from Rauma (41.39 ± 4.32) and Kaskinen (35.91 ± 3.59)

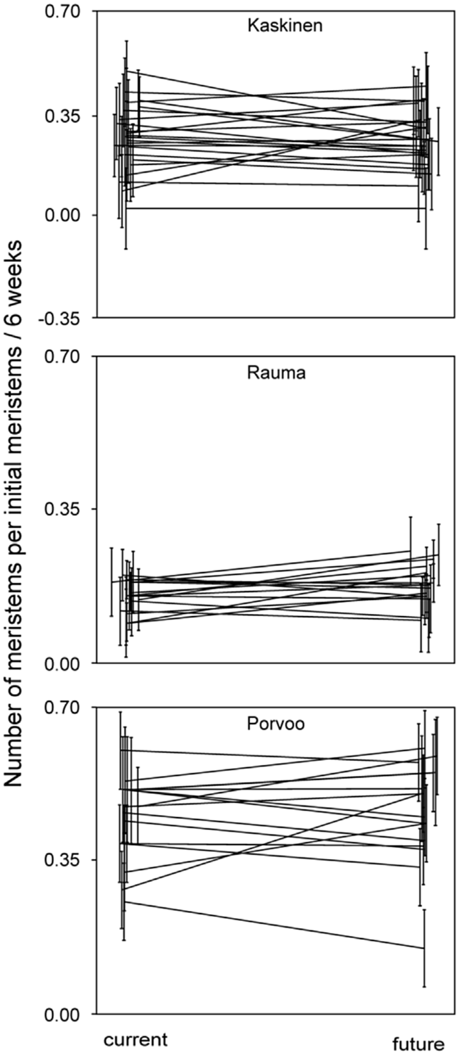

Fig. 3. Genotypic estimates for meristem formation (as the increase in the total number of meristems per initial number of meristems) in current and future treatments for the three populations (Kaskinen N = 24, Rauma N = 15, and Porvoo N = 16). Lines are connecting the estimates of each genotype in the two treatments (current and future). Data are showing genotypic means, N = 3 ramets for each treatment ± SE.

became saturated at lower irradiances (Fig. 5b). However, the α_{ETR} was lowest in Porvoo (0.31 ± 0.03) as compared to Rauma (0.40 ± 0.03) and Kaskinen (0.43 ± 0.03) (Fig. 5c). In accordance with the patterns for ETR_{max} and E_k, lowest NPQ values were evident for *Fucus* from Porvoo (3.05 ± 0.3) and highest for *Fucus* from Rauma (4.6 ± 0.3) and Kaskinen (4.5 ± 0.3) (Fig. 5d). This implies that *Fucus* from Porvoo used more of the absorbed light energy for photosynthesis while *Fucus* from Rauma (4.6 ± 0.3) and Kaskinen (4.5 ± 0.3) emitted more of the absorbed light energy via heat (Figure 4d). Furthermore, genotypes used herein only varied in their Fv/Fm ($\chi^2 = 20.9$, $p < 0.001$) and ETR_{max} responses (Table 2).

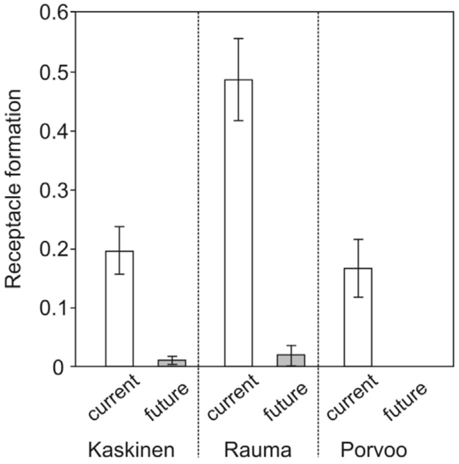

Fig. 4. Probability of *Fucus* receptacle formation for the three different populations (Kaskinen N = 24, Rauma N = 15, and Porvoo N = 16) grown for 6 weeks under current and future treatments. Data are mean ± SE.

4. Discussion

4.1. Sexual reproduction and growth under climate change

Interestingly, future conditions ceased receptacle formation almost completely. Even after seven months of the climate treatment (as reported in Rothäusler et al., 2017) under future conditions no receptacles were present. Some studies have indicated that small increases in temperature alone or in combination with higher light and CO_2 availability often induce earlier receptacle formation and maturation (Kraufvelin et al., 2012; Graiff et al., 2017), while hyposaline waters have been shown to hamper the development, discharge, and fertilization ability of gametes (Serrão et al., 1996; Malm et al., 2001; Steen, 2004; Maczassek, 2014). As an initial response to hyposalinity, algae start to metabolise energy rich compounds, such as e.g. mannitol (Reed et al., 1985; Bisson and Kirst, 1995; Benjamin et al., 1999) to reduce intracellular osmotic pressure and thus lowering cell turgor (Kirst, 1990). Indeed, low mannitol levels have been detected in range-

Table 1
Results from Generalized Linear Mixed Models (GLMM) that tested the fixed effect of climate change and the random effects of population (pop) and genotype (geno) on meristem formation, length, and receptacle formation. If an interaction did not improve the models on the basis of AIC, these were excluded from the analysis (indicated by*).

Source of variation	Meristem formation			Length			Receptacle formation		
	ndf, ddf	F	P	ndf,ddf	F	P	ndf, ddf	F	P
Fixed factors									
climate change	1, 136.2	0.15	0.7	1, 20.66	0.91	0.3	1, 345	26.58	< **0.001**
		X^2	P		X^2	P		X^2	P
Random factors									
population		0	1		8.1	**0.005**		2.35	0.1255
genotype (pop)		5.05	**0.02**		23.21	< **0.001**		13.14	**0.0003**
climate change × pop		*			*			*	
climate change × genotype (pop)		15.98	< **0.001**		*			*	
aquarium		0	1		1.58	0.21		0	1

Table 2

Results from Generalized Linear Mixed Models (GLMM) that tested the fixed effects of climate change and the random effects of population (pop), genotype (geno), and aquarium on photosynthetic responses (ETR_{max}, E_k, alpha and NPQ). If an interaction did not improve the models on the basis of AIC, these were excluded from the analysis (indicated by*).

Source of variation	ETR_{max}			E_k			alpha			NPQ		
	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P
Fixed factors												
climate change	1, 6.16	1.95	0.211	1, 9.44	0.21	0.656	1, 12.85	0.62	0.447	1, 31.25	0.74	0.398
		X^2	P		X^2	P		X^2	P		X^2	P
Random factors												
population		4.14	**0.021**		20.65	< **0.001**		6.98	**0.004**		12.18	**0.0005**
genotype (pop)		11.52	< **0.001**		0	1		1.88	0.085		0.3	0.586
climate change × pop		*			*			*			*	
climate change × geno		*			*			*			*	
aquarium		0.54	0.232		0	1		0	1		0	1

margin populations of *F. vesiculosus* when facing low salinity and extreme temperatures (Graiff et al., 2015; Takolander et al., 2017). Based on these considerations, it is reasonable to assume that *Fucus* in our future conditions utilized large parts of this energy rich storage carbohydrate to alleviate the cellular hypo-osmolarity and the ion-disequilibrium in order to regulate enzymatic functioning, photosynthetic machinery, and carbon fixation. Consequently, receptacle formation was inhibited due to increased allocation of carbohydrates to maintenance and growth.

By contrast, in current conditions, there was a general trend that multiplication of vegetative meristems slowed because of receptacle formation, which is a consequence of the unavoidable trade-off between producing receptacles or new vegetative tips (Kautsky et al., 1992); each tip can only transform to a receptacle or continue as a vegetative tip. This suggests that under the non-stressful current conditions *Fucus* used storage carbohydrates to initiate and ensure reproduction.

Fucus can reproduce asexually along the northern Gulf of Bothnia at 4 to 6 PSU via the formation of adventitious branches (Tatarenkov et al., 2005; Johansson et al., 2017). These branches fall off and develop rhizoids that reattach them to the substratum, and are thus clonal copies of their mother thallus. Consequently, asexual reproduction gives rise to low genetic diversity (Tatarenkov et al., 2005; Johansson et al., 2017; Rafajlovic et al., 2017). If the formation of adventitious branches is possible also at < 4 PSU, asexual reproduction may promote the persistence of *Fucus* in the projected future environment. Sexual reproduction is known to cease at ~4 to 5 PSU due to polyspermy and subsequent failure of zygote development (Serrão et al., 1996), although some populations may remain sexually recruited down to ~3 PSU (Ruuskanen and Bäck, 2002; Ardehed et al., 2016). Our findings showed that warming together with hyposaline conditions caused cessation of receptacle formation, leading to a nearly complete termination of sexual reproduction. However, it seems that marginal populations with asexual reproduction are favoured under the already ongoing climate forcing factors (Tatarenkov et al., 2005; Johansson et al., 2017; Ardehed et al., 2016).

During the six weeks of experimentation meristem formation and length were unchanged between current (15.1 °C and 5.3 PSU) and future treatments (17.5 °C and 2.7 PSU) and no mortality was observed.

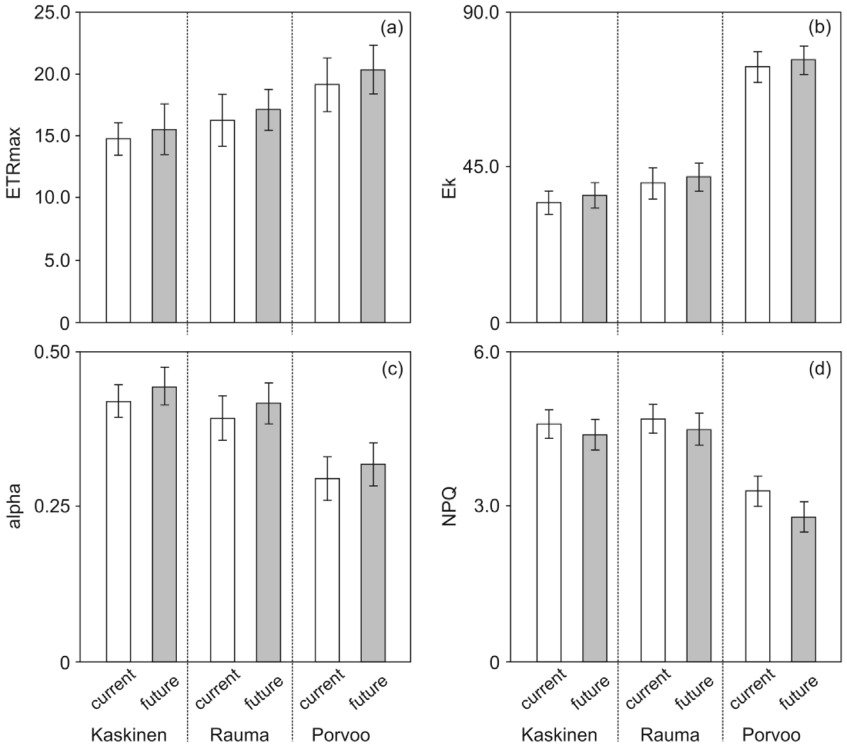

Fig. 5. Photosynthetic responses of *Fucus* from the three different populations grown for 6 weeks under current and future treatments. (a) Maximal electron transport rate, ETR_{max} (b) saturation irradiance, E_k (c) initial slope alpha, and (d) nonphotochemical quenching, NPQ. All photosynthetic responses are based on N = 5 genotypes for Rauma and Porvoo, and on N = 10 genotypes for Kaskinen. Data are mean ± SE.

Indeed, *Fucus* grew and survived well for a period of 7 months when kept under both conditions (Rothäusler et al., 2017). Only the length gain varied among populations with highest length increment in Kaskinen, followed by Porvoo and Rauma. Since all tested populations gained in meristems and length, we suggest that their tolerance to the combination of the applied hyposalinity and warming conditions allowed acclimation and maintenance of growth.

Our results, however, contradict with a recent study, where growth and survival of three marginal populations were drastically hampered under a nearly identical scenario of future temperature (16 °C) and salinity (2.5 PSU) (Rugiu et al., 2018). This inconsistency between the two studies could be due to the fact that different local populations can express distinct tolerances to environmental factors (Nygård and Dring, 2008; Saada et al., 2016; Rugiu et al., 2018), meaning that climate vulnerability can vary among populations. However, we cannot exclude the possibility that minor differences in experimental design (e.g. light and nutrient availability, magnitude of water movement, early vs. late summer) could have generated variable responses to future conditions e.g. by giving rise to synergistic stress effects.

The meristem formation and growth in length varied among genotypes, a result that matches with earlier studies on *F. vesiculosus* kept in common gardens, where genotypic variation in performance has been found (e.g. Rothäusler et al., 2016; Rugiu et al., 2018). Our result is likely to represent standing genetic variation in fitness-related traits but a possibility remains that differences among genotypes include carry-over effects and are thus linked to the environment before *Fucus* was taken into the experiment. However, and more importantly, we found that the meristem formation response to climate change varied among genotypes (climate change-by-genotype -interaction). This may suggest variation in phenotypic plasticity of climate-related traits, which enables *Fucus* to respond adaptively to changing environments.

4.2. Physiological responses under climate change

The expected future changes in seawater conditions did not affect *Fucus* photosynthetic performance responses such as Fv/Fm, ETR_{max}, E_k, α_{ETR}, and NPQ. In contrast, previous studies showed a clear effect of temperature alone (Nygård and Dring, 2008; Graiff et al., 2015) and in combination with hyposalinity (Takolander et al., 2017) on photosynthesis of this species. However, the photosynthetic capacity only declined sharply at temperatures well beyond the optimum (> 27 °C, Graiff et al., 2015), which was amplified in combination with low salinity (4 PSU, Takolander et al., 2017).

Yet, we showed that all of the above mentioned photosynthetic performance responses differed among populations. *Fucus* from Porvoo had the highest ETR_{max} values and photosynthesis became light saturated (E_k) at higher irradiances. In contrast, *Fucus* from Rauma and Kaskinen showed slightly lower ETR_{max} values, and their saturating irradiance of photosynthesis (E_k) was decreased. However, α_{ETR} was higher in the two populations, implying a better efficiency in light harvesting than in the Porvoo population. Consequently, the increase in NPQ, which is the emission of the extra absorbed light energy via heat that was not used during photosynthesis, was necessary in Kaskinen and Rauma to protect the photosynthetic apparatus against light-induced damage. In contrast, *Fucus* from Porvoo exhibited a low NPQ. Therefore, what comes to photosynthetic efficiency, the three populations can cope with the predicted future conditions, as also indicated by the fairly high Fv/Fm values (~0.6). Furthermore, their electron transport was held at a rate sufficient to maintain C assimilation, which is also evident from their ability to grow in length and by producing new meristems.

Herein, genotypes expressed variation in their ETR_{max} values. Similar among genotype variation in ETR_{max} has been found earlier in a range-margin population of *F. vesiculosus* (Rothäusler et al., 2016). These findings suggest that there might be genetic variation within populations in photosynthetic efficiency, a trait closely related to overall performance. As natural selection is assumed to optimize traits, maintenance of variation in fitness-related traits is far from self-evident but here it may be related to the depth gradient and consequent variable irradiance conditions that are always present in the littoral habitat. Existence of variation is necessary for adaptive processes under environmental change.

Overall, *Fucus* needed low to moderate light irradiance to reach maximum photosynthesis. Hence, our data are in agreement with earlier investigations, showing that *Fucus* in brackish waters had lower ETR_{max} and E_k values but similar α_{ETR} values as their Atlantic counterparts (Bäck et al., 1992; Nygård and Ekelund, 2006; Nygård and Dring, 2008; Gylle et al., 2013; Rothäusler et al., 2016). Our study also highlights the existence of geographic variation among populations in photosynthetic performance, which may have emerged due to genetic differentiation or due to plastic responses to differential environmental conditions.

5. Conclusions

We demonstrated in terms of photosynthesis and growth that *Fucus* populations at the margin of their distribution, namely in the Finnish coast of the Bothnian Sea and in the Gulf of Finland, tolerated well the averaged expected summertime future changes in seawater conditions. We also found some evidence of geographic variation in performance as well as genetic variation in tolerance to the forecasted future conditions within the three populations, which suggests that these range-margin populations harbour potential for adaptive responses. Our results are in contrast to a previous study where the survival of marginal *F. vesiculosus* populations was hampered in similar future conditions (Rugiu et al., 2018). These variable results can be explained by small differences in methodological details of the experiments altering the stressfulness of the future conditions.

Yet, cessation of sexual reproduction due to collapsing receptacle production appears to be a major consequence of future conditions. Whether these range-margin populations can persist in the near-future is crucially dependent on their ability to proliferate through asexual reproduction. Ceasing sexual reproduction even with the ability to reproduce asexually is likely to lead to decreased adaptive variation, endangering the persistence of *Fucus* within the northern and eastern margins of the Baltic Sea, which may modify community structure of rocky littoral habitats, as well as diversity and abundance of associated species.

Conflicts of interest

None.

Authors' contributions

ER and VJ conceived, designed, and conducted the experiment. LR analysed the data. ER led the writing of the manuscript; all authors contributed to the text.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.marenvres.2018.09.014.

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