Tolerance to climate change of the clonally reproducing endemic Baltic seaweed: is phenotypic plasticity enough?

Running title: climate change tolerance of a clonal Baltic fucoid

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ABSTRACT

To predict the effects of climate change, we first need information on both the current tolerance ranges of species and their future adaptive potential. Adaptive responses may originate either in genetic variation or in phenotypic plasticity, but the relative importance of these factors is poorly understood. Here, we tested the tolerance of *Fucus radicans* to the combination of hyposalinity and warming projected by climate models for 2070-2099. We measured the growth and survival responses of thalli in both current and future conditions, focusing on variations in tolerance among and within different clonal lineages. Survival was 32% lower in future than in current conditions, but the weight and length of the thalli who survived was respectively 267% and 178% higher when exposed to future conditions. The relatively high tolerance to the future conditions suggests that *F. radicans* is likely to persist in its current distributional range, which is limited to the Gulf of Bothia and Estonian coast in the Baltic Sea. Furthermore, this species may be able to expand its distribution southwards and replace its congener *F. vesiculosus*, which, in previous studies, has not tolerated the future conditions as well. In addition, we discovered variation in tolerance to future conditions within one of the clonal lineages, which have been hitherto presumed to lack adaptive variation. The discovery of intra-clonal phenotypic plasticity means that this alga has the potential for adaptive responses to climate change, which may be the key to the future persistence of *F. radicans* in the Baltic Sea.

Key index words: adaptation, Baltic Sea, climate change, clonality, marine seaweed, salinity, temperature, tolerance, plasticity.

Abbreviation: UV, ultraviolet radiation; PCoA, Principal coordinate analysis;

INTRODUCTION

Climate change is currently challenging the persistence of natural populations by causing environmental shifts (Parmesan and Yohe 2003, Harley et al. 2006, Poloczanska et al. 2013, Nadeau et al. 2017). To predict the long-term effects of this, it is of the utmost importance to understand species' adaptive responses to climate change, as these may enable persistence even if the current tolerance range is exceeded. Unless a population can tolerate the novel conditions, through phenotypic plasticity or through the adaptive evolution of tolerance traits, local extinction and a consequent shift in the distribution range are inevitable (Williams et al. 2008, Chevin and Lande 2009, Chevin et al. 2010, Hoffmann & Sgró 2011). Distributional shifts are frequent already (Lenoir and Svenning 2015) and the extinction rate has been predicted to accelerate, with up to one out of every six species going extinct by the end of the century (Urban 2015). Despite the seriousness of the situation, at the present, our ability to predict adaptive responses is poor, and the need for improved predictive power is urgent. Although there has been intense interest in the evolutionary potential for withstanding climate change (reviewed by e.g. Harley et al. 2006, Hoffmann & Sgró 2011, Munday et al. 2013, Reusch 2013, Nadeau et al. 2017), it has been particularly challenging to distinguish whether such potential is truly based on evolutionary changes in allelic composition or instead on the phenotypic plasticity of traits, i.e. a genetic versus an environmental basis for trait variation (Merilä and Hendry 2014).

Two alternative, non-mutually exclusive models for adaptive response have been put forward. In the first, a population can be rescued from extinction by adaptive evolution based on standing heritable genetic variation. Here, phenotypic change is determined solely by a change in allelic frequencies, and any environmentally induced variation (phenotypic plasticity) is thought to hamper the rate of

adaptive evolution by interfering with the selection for the best alleles (e.g., Ghalambor et al. 2007 and references therein). Unfortunately, we currently have very little information about the amount of heritable genetic variation in traits that determine tolerance to climate change (Munday et al. 2013), and it is unclear how relevant this model is. The second model instead proposes that environmentally induced phenotypic plasticity may itself represent the front-line response to improving tolerance in a changing environment. Plasticity may precede adaptive evolution by providing persistence, which buys time for adaptation to occur (Chevin et al. 2010). Furthermore, phenotypic plasticity may even facilitate adaptive evolution, as it may produce beneficial developmental variants that can then be selected for through quantitative genetic changes, a process called genetic accommodation (Schwander and Leimar 2011, Levis and Pfennig 2016). Phenotypic plasticity may be particularly important for long-lived intertidal species in which the change in allele frequencies across generations takes a long time and the plastic responses established during ontogeny and early life are therefore imperative for persistence (Munday et al. 2013).

Genetic variation is considered to form the basis for adaptive responses, but in clonally reproducing organisms, this variation is suppressed through the formation of clonal lineages. However, sexual reproduction is not the only source of phenotypic differences; indeed, individuals within the same clonal lineage may not be genetically homogenous and variation within clones may be less uncommon than we think (Lushai et al. 2003). Studies of the effects of climate change on clonal lineages have revealed substantial variation in plastic responses, for example in corals (Bruno and Edmunds 2016, Caroline E Dubé et al. 2017a) and in macroalgae (Monro and Poore 2009). Loxdale and Lushai (2003) showed how individuals within clonal lineages of *Caenorhabditis elegans* may differ in productivity and life span, two important adaptive responses in the face of environmental changes. In the red-spotted cherry salmon (*Oncorhynchus masou macrostomus*), individuals within clonal lineages vary in their behavioral responses to predation (Iguchi

et al. 2001). The phenotypic variation reported by these studies may be due to genetic variation within clonal lineages; the potential of somatic mutations to explain such variation has been shown in plants (Gill et al. 1995) and aphids (Loxdale and Lushai 2003). In addition to mutational variation, epigenetic mechanisms can generate phenotypic variation among members of the same clonal lineage (Wong et al. 2005). Variation such as somatic mutation and epigenetic variation contribute to differences in phenotypic plasticity within clonal lineages, and, thus, the genetic basis of phenotypic plasticity compromizes the distinction between genetic and phenotypic variation.

Manipulative experiments using model systems (e.g., laboratory mesocosms or small-scale field experiments) represent a useful method to evaluate the impact of climate change on wild marine populations (Benton et al. 2007). In such experiments, individuals are exposed to current and simulated-future climate conditions, and their performance is used to evaluate tolerance. The results provide an estimate of the short-term impact of climate change on the population, but this may be difficult to generalize to natural populations for a number of reasons (Forsman et al. 2016). Most importantly, such estimates do not take into account the genetic variation in tolerance and the potential for adaptive responses that might rescue the population. However, using a suitable experimental design, for example, featuring cloned material, it is possible to gain insights into the genetic variation in tolerance upon which selection can act, i.e. the evolutionary potential (Whitman and Agrawal 2009). Effectively, this tests genetic variation in plasticity with respect to climate change.

In the present study, we investigated how the clone-forming foundation species of the rocky littoral of the Baltic Sea, the brown alga *Fucus radicans* (Fucales, Phaeophyceae), responds to the future combination of hyposalinity and warming projected for 2070-2099

(Meier and Eilola 2011). We specifically assessed the potential for adaptive responses to climate change by evaluating whether there were differences in responses to climate change among different clonal lineages. Finally, for the first time in marine macroalgae, we tested for the existence of variation in phenotypic plasticity within clones to understand how a clonally reproducing species with decreased genetic diversity can respond to climate change.

MATERIALS AND METHODS

Study system

In rocky littoral ecosystems of temperate and subarctic waters, fucoid macroalgae serve as foundation species because they form forest-like habitat structures which host a diversity of organisms. Their occurrence, as well as their genetic diversity, have a fundamental role in shaping the assembly and diversity of the associated communities (Jormalainen et al. 2017). Furthermore, they produce considerable biomass (Eriksson et al. 2006) and are an important sink for carbon dioxide emissions (Viana et al. 2015). In addition, these algae are an important link for the transfer of matter to higher trophic levels (Poore et al. 2012). Thus, changes in environmental conditions which affect the occurrence and abundance of fucoids may have serious repercussions for the functioning of littoral ecosystems (Harley et al. 2012, Mineur et al. 2015, Pereira et al. 2015).

F. radicans is found only in the Baltic Sea; it inhabits most of the Bothnian Sea and Estonian coasts, where the salinity is below the tolerance limits for most marine species (6.5 to 3) (Forslund et al. 2012). This species diverged sympatrically from *F. vesiculosus* approximately 2500 y ago (Pereyra et al. 2009), and the two species are clearly separated genetically (Pereyra et al. 2013). The main factor that determines macroalgal distribution is the salinity gradient, which shapes all biotic interactions; for example, the detrimental

effects of idoteid grazers on algae are ameliorated with decreasing salinity (Bergstrom et al. 2005, Forslund et al. 2012). Furthermore, light availability defines the production and growth of primary producers, and may be of increased importance in sites where *F. vesiculosus* and *F. radicans* live sympatrically (Forslund et al. 2012).

F. radicans reproduces both sexually, through gamete production, and asexually, by producing small adventitious branches that detach from the main thallus and reattach to the substrate; in this way the alga forms a genetically identical clone consisting of several individual thalli (Tatarenkov et al. 2005). Clonal reproduction occurs frequently in the northern parts of the Baltic Sea (Johannesson et al. 2011). A few old dominant clones (such as Clone-4 in Johannesson et al. 2012) are widespread in the Bothnian Sea, covering more than 550 km^2,while the Estonian populations mostly reproduce sexually (Pereyra et al. 2013, Ardehed et al. 2015). A previous study hypothesized that the long-term survival and broad distribution of the clones may be due to their superior fitness and the stability of the Baltic Sea environment over the last few thousand years (Johannesson et al. 2011). However, even if the Bothnian populations of *F. radicans* are well adapted to the current water conditions, their clonality might limit their ability to adapt to changing conditions, as new variation is generally created only by somatic mutation. In light of this, this species' distribution and future persistence may be threatened by the further decline in Baltic salinity that has been projected by Meier and Eilola (2011). Because *F. radicans* is highly ecologically valuable in the northern Baltic Sea, it is important to understand whether this seaweed will be able to adapt to the future environmental conditions.

Sampling

F. radicans was collected on 12 July 2014 from Skagsudde in the Northern Baltic Sea (63°11′21″ N, 19°0′13″ E). A total of 25 thalli were sampled by snorkeling between 0.5 to 2 m in depth, keeping a minimum of 10 m distance among all samples. The thalli were stored in coolers with wet tissue for transportation to the Archipelago Research Institute of the University of Turku. Species were identified by their morphological characteristics (Bergstrom et al. 2005). Each thallus was defined as a single stipe attached to a holdfast (i.e. only one stipe was sampled from each holdfast). The algae were gently flushed with fresh water to wash away grazers and epiphytes, and were stored in a through-flow seawater system at their ambient salinity (5 ± 2) and temperature (15 ± 2 °C) before experimentation.

Experimental set up

We studied the effect of climate change on the performance of *F. radicans* using a manipulative aquarium experiment. Because climate model projections predict that salinity and temperature will vary together, we manipulated these two abiotic factors simultaneously. For current climate conditions, we used the mean summer (June to August) surface seawater temperature and salinity obtained from the Baltic Nest Institute for the Bothnian Sea (http://www.balticnest.org/): 5 and 14°C. Future conditions were those projected to occur by 2070-99 by the model RCAO-ECHAM-A2-REF (Meier et al. 2012): 2.5, 16°C. Summer conditions were used in both cases because this is the period when the growth of Baltic *Fucus* is the highest (Lehvo et al. 2001).

Two aquarium racks, each with 12 aquaria, were constructed to simulate the current and future climate conditions. The aquarium rack had a recirculating water system, in which seawater was pumped continuously from a large head tank (~ 200 L) situated at the base of

the rack to the 12 aquaria (24 L each), from where it returned to the head tank. There, the water was filtered and cleaned first by an acrylic filtration unit (SCHURAN Jetskim 120) that was equipped with a mechanical and biological filter, then by a protein skimmer, and finally by UV radiation. Each head tank was equipped with a chiller/heater to regulate the temperature. We adjusted water salinities for both climate conditions (current and future) by dilution with distilled water. To ensure ad-libitum nutrient availability, we added 3 g of Osmocote® controlled-release fertilizer (NPK 15-9-12+2MgO+trace elements, 2 months) to each rack at the start of the experiment and every second month.

Six LED lamps (Radion ™ XR30w Pro lamp) provided equal light to all aquaria. We used a 17:7 h light:dark rhythm, similar to the average summer light conditions in the Baltic Sea. To mimic the course of the sun, light intensities slowly increased during the day (up to 1200 μmol m^{-2} S^{-1} between 11:00 and 14:00) and decreased in the evenings. During the experiment, we kept the water level and salinity in the aquarium rack constant by adding ion-exchanged water into the head tanks. We checked temperature (daily) and salinity (weekly) to verify that the conditions did not vary over the course of the experiment. We also measured pH weekly to ensure it stayed within the natural range of the Baltic Sea (mean ± SE: 8.31 ± 0.07).

We divided each of the 25 field-sampled thalli into eight similar-sized pieces (initial length, mean ± SE: 6.1 ± 0.07 cm; initial no. of apical meristems: 14.7 ± 0.4; initial wet biomass: 0.45 ± 0.01 g). Four of the thallus pieces were randomly assigned among the twelve aquaria in the current conditions and the other four among the twelve aquaria in the future conditions. To keep the algae at the bottom of the aquaria, each piece was attached to a small ceramic tile. A piece of buoyant foam was used to keep them upright. Once a week, we cleaned the aquaria and removed epiphytes from the algae, then relocated the thallus pieces within the aquarium to avoid micro-

environmental effects. This experiment was conducted together with a similar experiment on *F. vesiculosus* that is described in Rugiu et al. (2018a); *F. vesiculosus* thalli were present in the same aquaria as *F. radicans* and the average algal density was 32.9 ± 0.5 pieces of thallus per aquarium. The two species co-occur also in the sampling site of *F. radicans.*

Molecular multilocus genotyping

We genotyped tissue samples from each of the 25 thalli using microsatellites to assess the number of multilocus haplotypes included in our sampling. Additionally, we genotyped a sample of "Clone-4" which was received as dried tissue from R. Pereyra; this clone is widespread in the northern Baltic Sea (Johannesson et al. 2012) and we wanted to see if it was present in our samples. DNA was extracted from fresh vegetative tissue with a NucleoSpin Plant II kit according to the company's protocol (Macherey Negel). We genotyped the samples using nine microsatellite loci: L20, L38, L58, L85, and L94 (developed by Engel et al. 2003), and Fsp1, Fsp2, Fsp3, and Fsp4 (from Perrin et al. 2007). Two multiplex reactions (the first with Fsp1, Fsp-2, Fsp4, L38, L58, and L94, and the second with Fsp3 and L20) and one single reaction (L85) were used for locus amplification following the PCR protocol found in (Johannesson et al. 2011). The multilocus haplotypes were scored using GENEMARKER version 2.4 (SoftGenetics) with visual inspection, and thalli were considered members of the same clonal lineage if at least seven of the nine markers were present (sometimes all the microsatellites were not resolved, table S1) and 100% of their alleles matched. Throughout the text, we refer to the separate field-sampled thalli that belonged to the same haplotype as ramets, and all the ramets that shared the same haplotype as a clone. PCoA performed with GenAlEx 6.5 (Peakall and Smouse 2012) was used to describe the genetic relationships among thalli based on eigenvalues calculated from microsatellite data.

Measuring algal responses to climate change

We measured the growth rate and survival of algae during the course of the experiment. The initial (day 0) and final (day 140, end of the experiment) size of the thallus pieces were quantified in terms of wet biomass (g WW), length of the major axis (cm), and number of apical meristems. We then calculated the growth gain as the difference between the final and the initial size of each piece. When weighing the algae, we dried the thalli with paper tissue for few seconds to remove excess water. Because there was mortality during the experiment, we only calculated the growth of the thallus pieces that survived the manipulation. As the different growth measures were similar in their responses, we present here growth rate only in terms of wet biomass gain (expressed in g WW) but provide the summary data and analyses for the gain in length and meristems in the supplementary material (Fig. S1, Tables S2-S4).

We checked each piece of thallus weekly for survival. We defined a piece of thallus as dead when more than 90% of its biomass was decayed. Tissue degradation occurred quickly between the weekly observations, starting with reddish spots which rapidly led to disintegration of the thallus (necrosis).

Statistical analysis

The variation in growth gain and survival probability at the end of the experiment was analyzed using generalized linear mixed models implemented in SAS 9.4 procedure GLIMMIX (Kiernan et al. 2012). Normal (growth rate) and binary (survival) distributions were used to estimate the error variances. We used climate change (current and future conditions) as a fixed factor, and haplotype and aquarium as random factors. We checked all possible interactions between random factors and climate change. In addition, for the growth rate analysis we used the initial size as a covariate and tested its interactions with haplotype and climate change. We simplified

the initial model by removing non-significant effects, starting from the higher-order interactions, with the aid of the Akaike Information Criterion (AIC). We used F-statistics to test the significance of fixed effects, and applied the Kenward-Roger approximation (Kenward and Roger 1997) to adjust the degrees of freedom. We tested the significance of both random effects and random-by-fixed effect interactions using X^2-statistics of the likelihood-ratio test (Bolker et al. 2009). Since the multilocus genotyping showed that three different clonal lineages in our experiment were represented by multiple ramets, we estimated the variation in growth rate and survival separately for each of these three haplotypes, using generalized linear modes as described above. In these analyses, we included the random effect of ramet instead of haplotype. This allowed us to test whether the different ramets within the haplotype, grown as distinct entities in the field, varied in their responses to climate change. The means for haplotypes were calculated using the GLIMMIX procedure as the 'best linear unbiased predictors' (BLUPs, Robinson 2008).

RESULTS

Multilocus genotyping

A total of 25 thalli of *F. radicans* were genotyped, and of these, five represented unique multilocus haplotypes (Fig. 1), i.e. haplotypes represented by a single thallus. The other 20 thalli were ramets originating from three different clonal lineages: haplotype *A* (12 ramets), *B* (four ramets), and *F* (four ramets) (Table S1). We determined that the haplotype *A* was the same as the"Clone-4" in Johannesson et al. (2012), the widely spread female clone in the Gulf of Bothnia (Ardehed et al. 2016).

Growth rate and survival under climate change conditions

The growth rate of *F. radicans* was higher in the future conditions (mean ± SE; 0.11 ± 0.02 g) than in current ones (0.03 ± 0.02 g), and depended on the initial size of the alga (Fig. 2, Table 1). The same was also true for the growth rate measured in terms of length gain (mean ± SE; current: 0.23 ± 0.09 cm; future 0.64 ± 0.09 cm), but not in terms of the numbers of meristems, which did not vary between the climate change treatments (Table S2).

The survival of *F. radicans* was compromised by the predicted hyposalinity/warming conditions: only 65% of the algae in future conditions survived to the end of the experiment, compared with 98% of those in current conditions (Fig. 3, Table 1). Different haplotypes varied in their survival but there was no indication of a differential response to climate change (i.e. no climate change-by-haplotype interaction; Fig. 4 Table 1).

Within-clone variation in tolerance to climate change conditions

Using the clonal lineages that were represented by multiple ramets (haplotypes *A*, *B*, and *F*), we examined within-haplotype differences in growth and survival. For two of these haplotypes (*A* and *B*), growth rate (in terms of biomass) was higher in the future conditions than in the current ones, while there were no differences between treatments in the third haplotype (*F*, Fig. 5, Table 2, Table S3-S4). The ramets within haplotype *B* differed in their growth gain regardless of the climate conditions (Table 2), and this within-clone variation explained 69% of the total variance in biomass gain. Ramets within haplotype *F* likewise varied significantly in growth rate (Table 2), with within-clone variation representing 38% of the total variance. Most interestingly, the 12 ramets within haplotype *A*

showed significant variation in their growth response to different climate conditions (Fig. 6a, Table 2), with the factor "ramet" together with the ramet-by-climate change interaction accounting for 57% of the total variance in biomass gain.

Survival of haplotypes *A* and *F* was lower when exposed to future climate conditions, while the survival of haplotype *B* did not differ between climate conditions (Table 3). Within haplotype *B*, only one thallus piece died (in future conditions). In comparison, 96.7% of haplotype *A* survived in current conditions, but only 63% survived in future conditions. As we observed with the growth response, the survival of different ramets within haplotype *A* was affected differently by climate change (Fig. 6b), as indicated by the significant clone-by-climate change interaction effect, which explained 99% of the total variation in survival (Table 3).

DISCUSSION

Effects of climate change on Baltic Sea rockweeds

This study shows that *F. radicans* may tolerate the simultaneous desalination and warming projected for the future of the Baltic Sea. Indeed, although survival was lower when algae were exposed to the future conditions, the thalli who survived grew faster in the future than in the present conditions. This suggests that this species will likely persist in the low-salinity areas of the Baltic Sea despite the effects of climate change.

The increase in growth rate despite the slightly lower survival in future conditions was unexpected. In this respect, the growth response of *F. radicans* differed from that of northern Baltic *F. vesiculosus*, in which similar future conditions negatively affected both growth and survival (Rugiu et al. 2018a). When faced with environmental stress, organisms are generally assumed to alter their gene

expression to decrease resource allocation to growth while increasing allocation to maintenance activities (López-Maury et al. 2008). Thus, stress tolerance should be inversely correlated with growth rate. We suggest that the unforeseen increase in growth under stressful future conditions may result from the fact that we manipulated both the temperature and salinity simultaneously. The future temperature that we used was well within the natural summertime temperature range, and therefore was not in itself stressful. We hypothesize that the main stressor that affected survival in this case was hyposalinity, and that the positive growth response that we observed occurred because the thalli that were able to tolerate this hyposalinity actually benefited from the warmer temperature and grew at a faster rate.

Predicting the future performance of an organism is always challenging because of the multitude of biotic and abiotic factors that may play a role. A separate set of manipulative experiments, similar to those performed here, was conducted with *F. radicans*' coexisting congener *F. vesiculosus* and the crustacean mesograzer *Idotea balthica*. The results indicated that both these species may seriously suffer from the projected future warming/hyposalinity (Rugiu et al. 2018b, 2018a). Furthermore, previous experimental studies showed that the reproduction of *F. vesiculosus* is impaired at salinities below 4, which likely means that this alga will be increasingly sensitive to future salinity changes in this part of the Baltic Sea (Serrão et al. 1996, 1999). Therefore, its distribution is likely to shift southwards by 2070-2099. If *F. vesiculosus* goes extinct or becomes rarer in the Bothnian Sea, the empty habitat left along the rocky shores may provide extra littoral habitat and settlement substrate for *F. radicans*. The mesograzer *I. balthica* is the main grazer of Baltic Sea fucoids (Jormalainen and Ramsay 2009, Forslund et al. 2012, Haavisto and Jormalainen 2014). Where both *Fucus* species co-exist, *I. balthica* is more abundant on *F. radicans*, which it prefers over *F. vesiculosus* in choice experiments (Forslund et al. 2012). This led Forslund et al. (2012) to hypothesize that the southern distributional limit of *F. radicans* is limited mainly by grazing pressure. If *I.*

balthica's distribution shifts southwards, this may further allow the expansion of *F. radicans*' distributional range. In light of *F. radicans*' high degree of tolerance to the projected abiotic conditions and the expected changes in its associated community, it is possible that this rockweed will not only persist, but may even grow faster in the future. Because *F. radicans* appears to be better adapted to deal with future conditions than *F. vesiculosus* is, it has potential to replace *F. vesiculosus* as the dominant habitat-forming rockweed in the areas where the latter goes extinct.

Genetic variation, plasticity, and intra-clonal variation in tolerance to climate change

Clonal reproduction has typically been associated with dispersal to new regions and with the persistence of low-density populations in range-margin habitats, and this is also the case with *F. radicans* (Rafajlović et al. 2017, and references therein). Asexual reproduction is probably an asset in early colonization, but it eventually leads to a decrease in genetic diversity, as a clonal population harbors less standing genetic variation than one that reproduces sexually. Therefore, although clonality may promote the successful establishment of a population, it may ultimately compromise its persistence. Our most interesting finding suggest that *F. radicans* hosts phenotypic variation even within the clonal lineages: ramets within a haplotype responded differently to the climate change conditions. The presence of such intra-clonal variation in phenotypic plasticity may indicate that clonality may not compromise the future persistence of *F. radicans*. Furthermore, it is possible that within-clone phenotypic plasticity represent a more general, previously un-recognized adaptive mechanism of clonally reproducing macroalgae supporting their persistence in changing environment.

The origin of phenotypic variation within a supposedly genetically uniform clonal lineage is an interesting question. There are two possible mechanisms for intra-clonal phenotypic variation. First, contrary to common wisdom, clonal lineages may not be genetically

homogenous and genetic mosaicism may be common. For example, genetic variation has been detected in clonal lineages of aphids (Lushai et al. 2003), the seagrass *Zostera marina* (Reusch et al. 1999) and asexually produced colonies of a hydrocoral species (Dubé et al. 2017a). Because we determined molecular haplotypes based only on nine microsatellites, we were not able in this case to quantify the extent of within-clone somatic mutation. However, because *F. radicans* reproduces asexually through somatic growth and fragmentation of the thallus, we consider it highly likely that this species accumulates somatic mutations. The resulting genetic variation may contribute to this species' adaptive ability, as has been suggested for some coral species (Dubé et al. 2017b).

Second, within-clone variation may arise due to environmental variation, that is, the environmental responses of clones may not be determined by their genotype alone, but also by their environmental history, which results in epigenetic changes (e.g., methylation and histone acetylation) that do not change the genome during ontogenesis (Joyce et al. 2003). Epigenetic mechanisms can lead to differential gene expression among genetically identical individuals (Mather and Jinks 2012, Ong-Abdullah et al. 2015, Evans et al. 2016, Mustonen et al. 2017, Perez et al. 2017, Dubé et al. 2017b). Furthermore, epigenetic variation can also be generated during mitotic cell divisions even in the absence of any specific environmental factors, due to stochastic events during somatic inheritance (Wong et al. 2005). There are no studies on epigenetic variation in clonal rockweeds, but it is certainly possible that this phenomenon may be responsible for intra-clonal variation in the environmental tolerance in *F. radicans*. The effects we found represent previously unknown variation in plasticity for clonal lineages that have been presumed to lack adaptive variation.

Phenotypic plasticity may be the most common adaptive response to climate change (Hoffmann and Sgrò 2011, Stoks et al. 2014, Urban 2015) and may, therefore, help populations to persist and buy time for genetic adaptation over generations (Munday et al. 2013).

Munday et al. (2013) suggested that phenotypic plasticity may be especially important in the response to climate change for marine species that live in highly variable environments such as the intertidal zone, as these species typically already harbor a high level of phenotypic plasticity. Here, we underline the importance of such plasticity in *F. radicans*. The high degree of phenotypic plasticity of Baltic Sea fucoids with respect to salinity has been hypothesized to be the key for their success in colonizing the brackish Baltic Sea, specifically by enabling their spread across the strong salinity gradient. This has been proposed as an example of the so-called plasticity-first scenario for the establishment of a population in marginal habitats (Johansson et al. 2017). Furthermore, Baltic Sea fucoids have been shown to be phenotypically plastic for a number of other traits, such as phlorotannin production (Koivikko 2008), morphology (Sideman and Mathieson 1983, Scott et al. 2001), photosynthetic activity (Russell 1987, Takolander et al. 2017), and induced resistance to herbivory (Jormalainen and Ramsay 2009, Haavisto et al. 2017). Together, this indicates that plasticity represents a major part of the adaptive response of these algae to the highly variable littoral environment. The present study suggests that phenotypic plasticity may promote the persistence of *F. radicans* in the face of environmental changes due to climate change.

The existence of genetic variation is a fundamental precondition for evolutionary adaptation, and genetic variation in tolerance related to climate change has been documented in diverse marine organisms such as sea urchins, mussels, and corals (Pistevos et al. 2011, Sunday et al. 2011, Pespeni et al. 2013, Kurman et al. 2017). Here we found genetic variation among different haplotypes with respect to survival, but not with respect to the response to climate conditions. However, even though we did not find a genetic basis for tolerance to climate change, these results do provide evidence for the existence of genetic variation in fitness-related traits. A previous study of *F. radicans* showed that this species grows better in the salinity of its current northern distributional range (4) than in the salinity of the Baltic Sea entrance (24), and the authors also reported variation in growth rate among ramets of the same clone

(Johansson et al. 2017). Together with our results, this indicates that *F. radicans* is capable of phenotypic plasticity in growth with respect to salinity stress. Furthermore, Johansson et al. (2017) found among-genotype variation in reaction norms (in the formation of adventitious branches) with respect to salinity (4 and 24), i.e. a genotype-by-environment interaction. This indicates the occurrence of genetic variation for plasticity, at least at salinities above those occurring in the current distribution range. Our experiment indicates that this may not be true in salinities lower than the current ambient levels.

In conclusion, our results suggest that the predicted future combination of hyposalinity and warming may have a small negative effect on the survival of *F. radicans*, but may also enhance the growth of the survivors. This species tolerated the projected future conditions better than the closely related *F. vesiculosus*, which is currently more abundant and widely dispersed. We found some evidence for the existence of genetic variation in fitness-related traits. However, phenotypic plasticity in tolerance is likely to be more important than genetic variation for the long-term persistence of *F. radicans* in the face of climate change. Although genetic variation of *F. radicans* is restricted by its asexual reproduction and clonality, the species does show variation in tolerance. In particular, we found intra-clonal variation in tolerance to the projected future conditions, which may provide some degree of adaptive potential and enable the persistence of some of the clonal lineages. In particular, clone *A*, which is widely distributed in the Bothnian Bay, demonstrated a high degree of phenotypic plasticity and tolerance to future climate conditions. We suggest that *F. radicans* may tolerate climate change quite well and, indeed, it may be capable of replacing *F. vesiculosus* as a foundation species in the rocky littoral habitats in the low-salinity regions of the Baltic Sea if the latter becomes extinct.

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Conflict of interest: the authors have no conflict of interest to declare.

LITERATURE CITED

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Table 1. Statistical analyses (generalized linear mixed models) that tested the fixed effect of climate change and the random effects of haplotype and aquarium, and all their interactions, on growth rate (in terms of biomass) and survival of *F. radicans*. The initial size (biomass) was used as a covariate in the analysis of growth. The final statistical models were simplified by removing non-significant interactions based on the AIC.

Source of variation	Growth rate			Survival		
	ndf, ddf	F	P	ndf, ddf	F	P
Fixed Factors						
Climate change	1, 158.7	0.3	0.58	1, 230	22.1	<0.001
Initial size	1, 153.2	12.8	<0.001			
Initial size × Climate change	1, 169.1	7.24	<0.001			
		χ^2	P		χ^2	P
Random Factors						
Haplotype		2.18	0.07		7.4	<0.01
Aquarium		0.95	0.17		0.16	0.34

Table 2. Statistical analyses (generalized linear mixed models) that tested the fixed effect of climate change and the random effects of ramet and aquarium, and all their interactions, on growth rate (in terms of biomass) of *F. radicans*, separately for the clonal lineages A, B and F. Initial size (biomass) was used as a covariate. The final statistical models were simplified by removing non-significant interactions based on the AIC.

Source of variation	Haplotype A			Haplotype B			Haplotype F		
	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P
Fixed Factors									
Climate change	1, 11.2	5.6	<0.05	1, 13.4	29.1	<0.001	1, 12.8	0.04	0.8

Initial size	1, 82.3	0.5	0.5	1,12	18.6	<0.001	1, 13.7	0.01	0.9
Initial size × Climate change									
		X^2	P		X^2	P		X^2	P
Random Factors									
Ramet		1.8	0.1		24.6	<0.001		3.7	<0.05
Ramet × Climate change		2.8	<0.05						
Aquarium		2.3	0.06		1.8	0.1		0.85	0.17

Table 3. Statistical analyses (generalized linear mixed models) testing the fixed effect of climate change and the random effects of ramet and aquarium, and all their interactions, on survival of *F. radicans*, separately for the clones A, B and F. The final statistical models were simplified by removing non-significant interactions based on the AIC.

Source of variation	Haplotype A			Haplotype B			Haplotype F		
	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P
Fixed Factors									
Climate change	1,33.5	9.15	<0.01	1, 30	1	0.3	1, 8	∞	<0.001
		χ^2	P		χ^2	P		χ^2	P
Random Factors									
Ramet		0.0	1		0.0	1		0.0	1
Ramet × Climate change		6.8	<0.01						
Aquarium		0.0	1		0.0	1		0.22	0.64

FIGURE LEGENDS

Figure 1. Principal Coordinate Analysis (PCoA) of molecular genetic variation in the study population of *F. radicans*. Filled circles denote haplotypes with multiple ramets and open circles denote haplotypes represented by a single thallus in our sample. The percentage of explained variation by the PCoA axes is given in parentheses.

Figure 2. The relationship between biomass gain and initial biomass, with separate regression lines for the current (continuous line) and future (dashed line) climate conditions. Squares indicate genotypic means in current conditions; triangles represent genotypic means in future conditions. Mean estimates are calculated by averaging the biomasses of all the pieces of thallus within each haplotype.

Figure 3. Survival curves with 95% confidence intervals for the current (black line) and future (grey line) climate conditions.

Figure 4. Survival probabilities (d) in current (white bars) and future (grey bars) conditions, separately for each haplotype (mean ± SE). Haplotypic estimates were calculated among all the pieces of thalli belonging to each haplotype (x-axis). Numbers on top of the bars indicate the number of pieces of thalli used for each haplotype to calculate the estimates.

Figure 5. Estimates of growth rate (in terms of biomass gain) (mean ± SE) in the current (white) and future (grey) conditions, separately for the haplotypes A, B, and F. Mean values are based on the number of clones within each haplotype. For each treatment, we used N = 12 ramets for the haplotype A and N= 4 ramets for the haplotype B and F. The name of each haplotype is displayed on top of the bar chart.

Figure 6. Variation in growth rate (in terms of biomass gain) (a) and survival probability after 140 days (b) for ramets within the haplotype A exposed to the current and future conditions. Each line represents the mean of a ramet, based on 4 replicated pieces of thalli reared in both the current and future conditions. The reduced number of lines in (b) is due to overlapping of lines.

Figure S1. Estimates (mean ± SE) of length (a) and meristem gain (b) in current (white) and future (grey) conditions for each haplotype. The growth gain of each haplotype is based on the averaged survival among ramets. The number of ramets for each treatment was N= 12 for haplotype A, N = 4 for haplotype B and F. The identity of each haplotype is indicated on the x-axis.

Table S1 showing the multilocus haplotypes determined for the samples of *F. radicans* in this study**.**

Table S2. Results from general linear mixed models (GLMM) that tested the fixed effects of climate change and the random effects of haplotype and aquarium, and all their interactions, on growth rate (in terms of meristem and length gain). Initial size was used as covariate in the analyses. The final statistical models were simplified by removing non-significant interactions based on AIC.

Table S3 Results from general linear mixed models for the haplotypes A, B and F. The model tested the fixed effects of climate change and the random effects of ramet and aquarium on meristem gain. Initial size was used as covariate in the analyses.

Table S4. Results from general linear mixed models for the haplotypes A, B and F. The model tested the fixed effects of climate change and the random effects of ramet and aquarium on length gain. Initial size was used as covariate in the analyses.

Figure 1

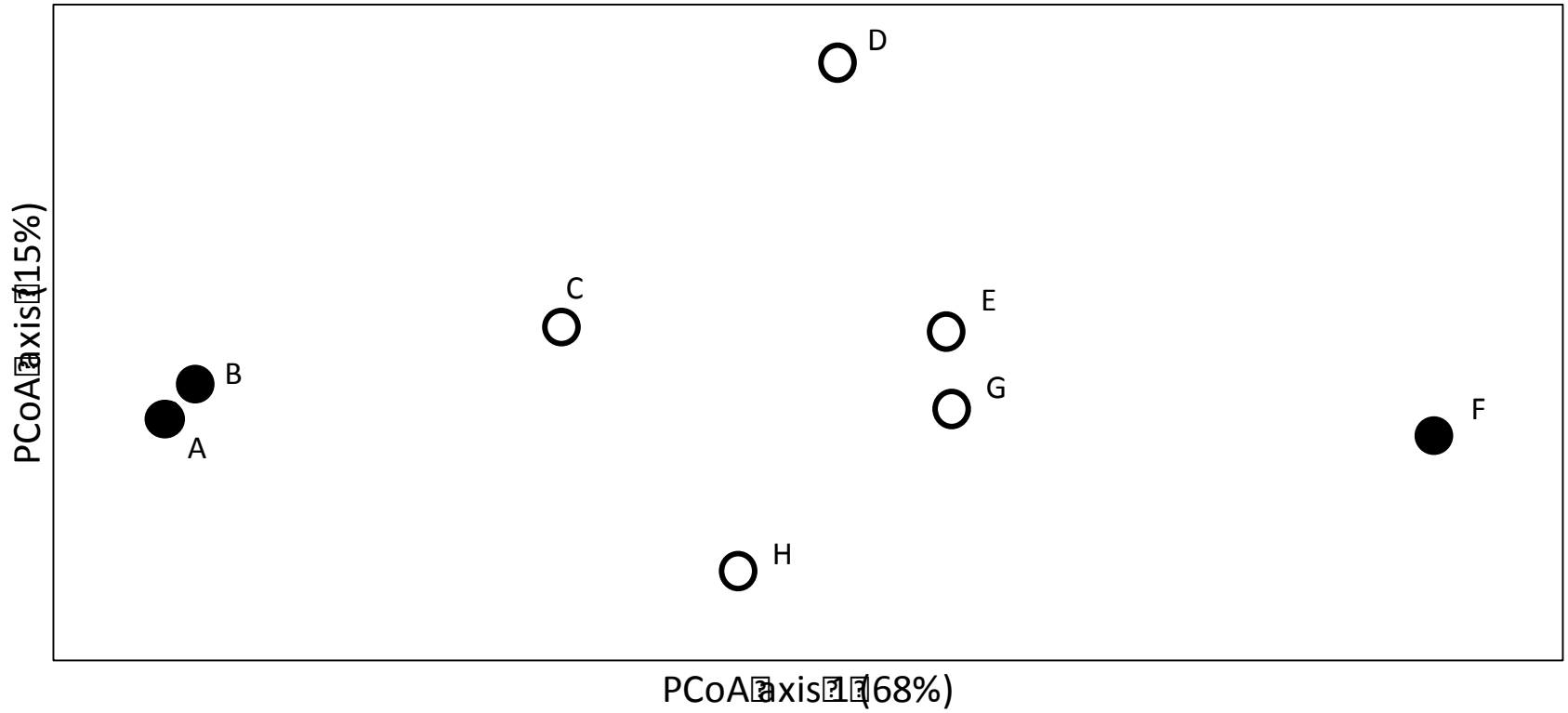


Figure 2

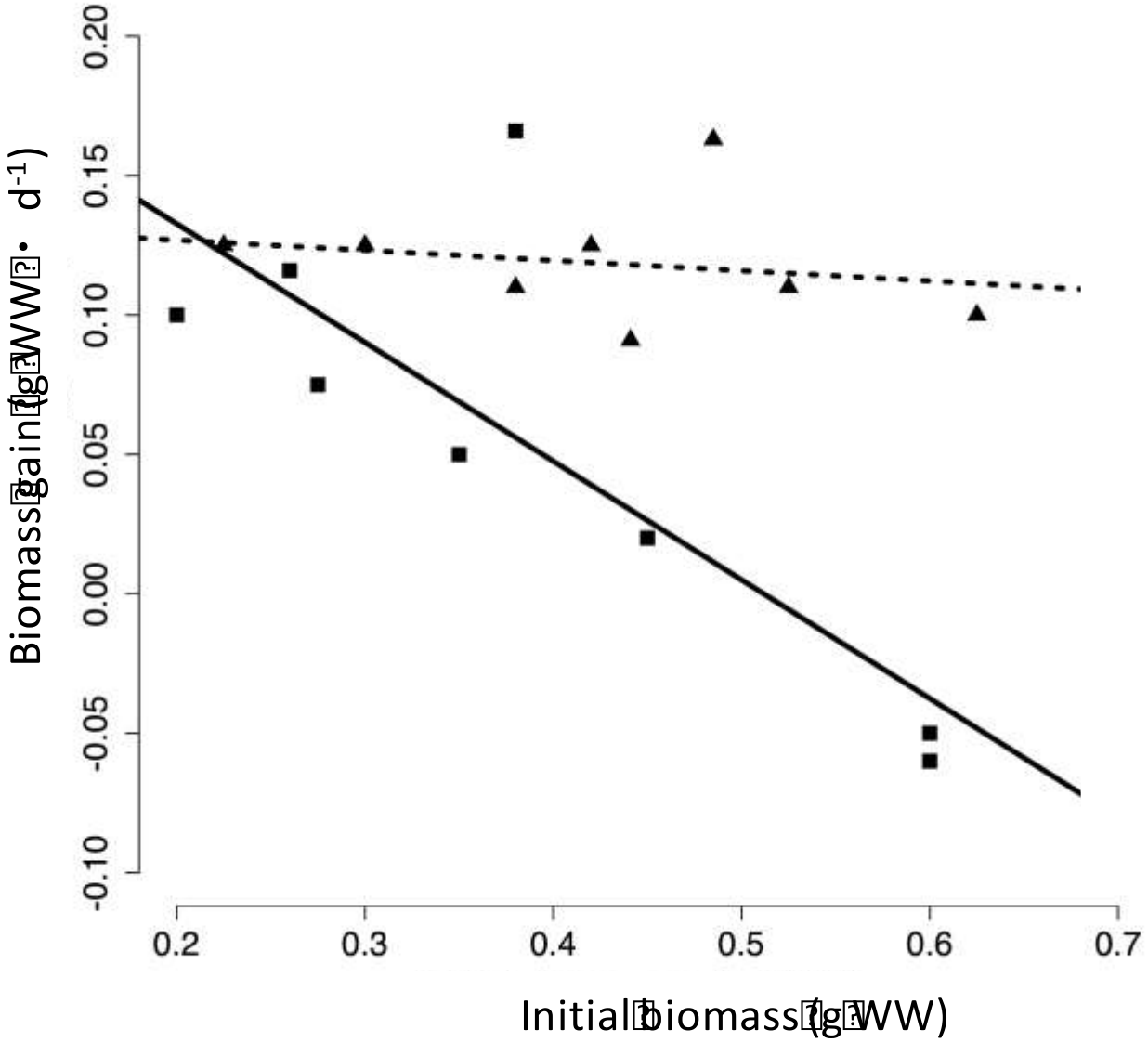


Figure 3

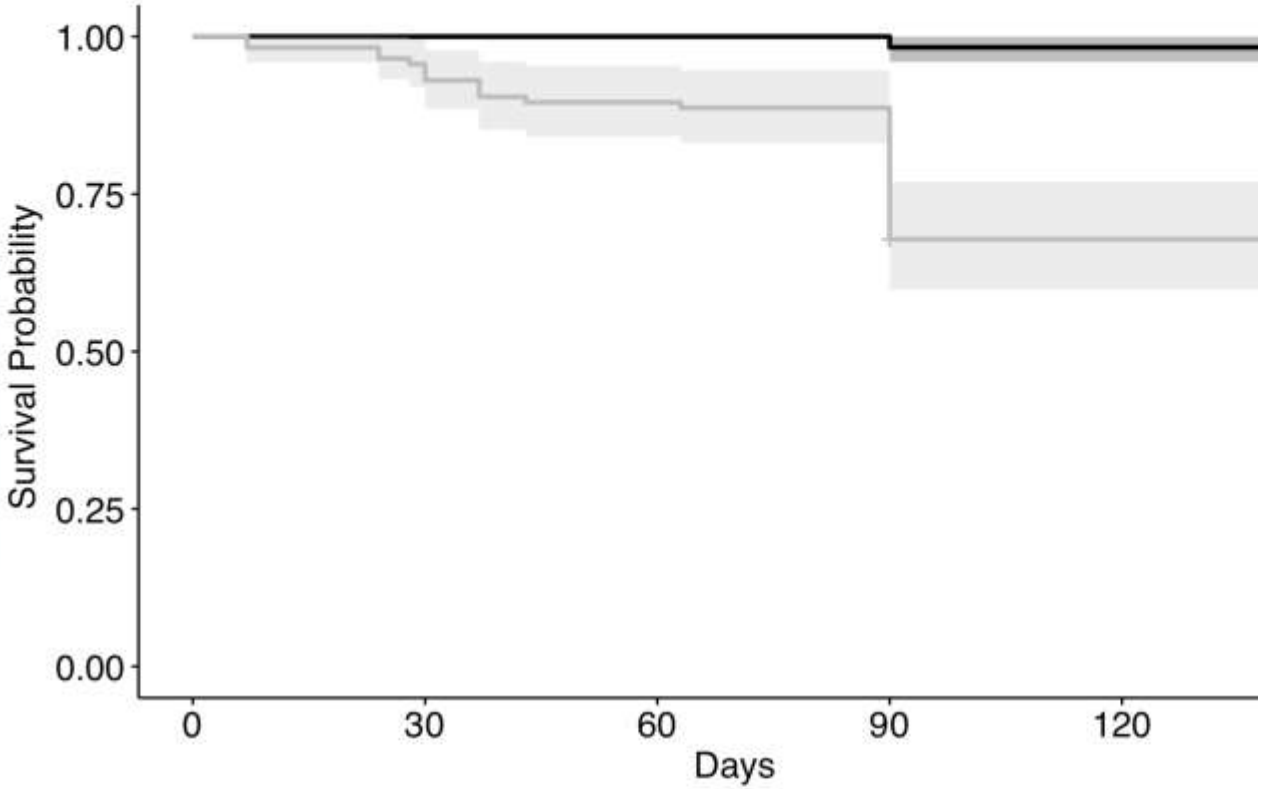
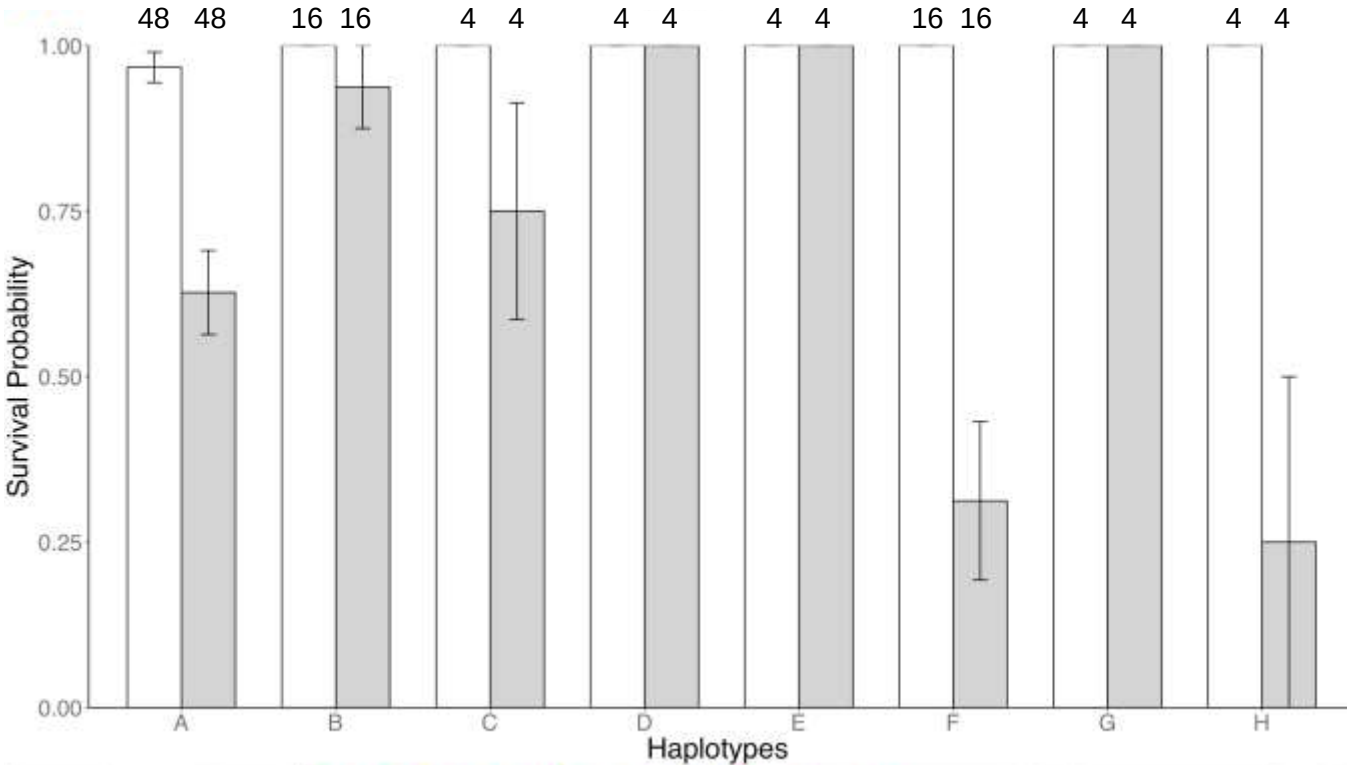


Figure 4


48 48
16 16
4 4
4 4
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16 16
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4 4
1.00
0.75
0.50
0.25
0.00
Survival Probability
A
B
C
D
E
F
G
H
Haplotypes

Figure 5

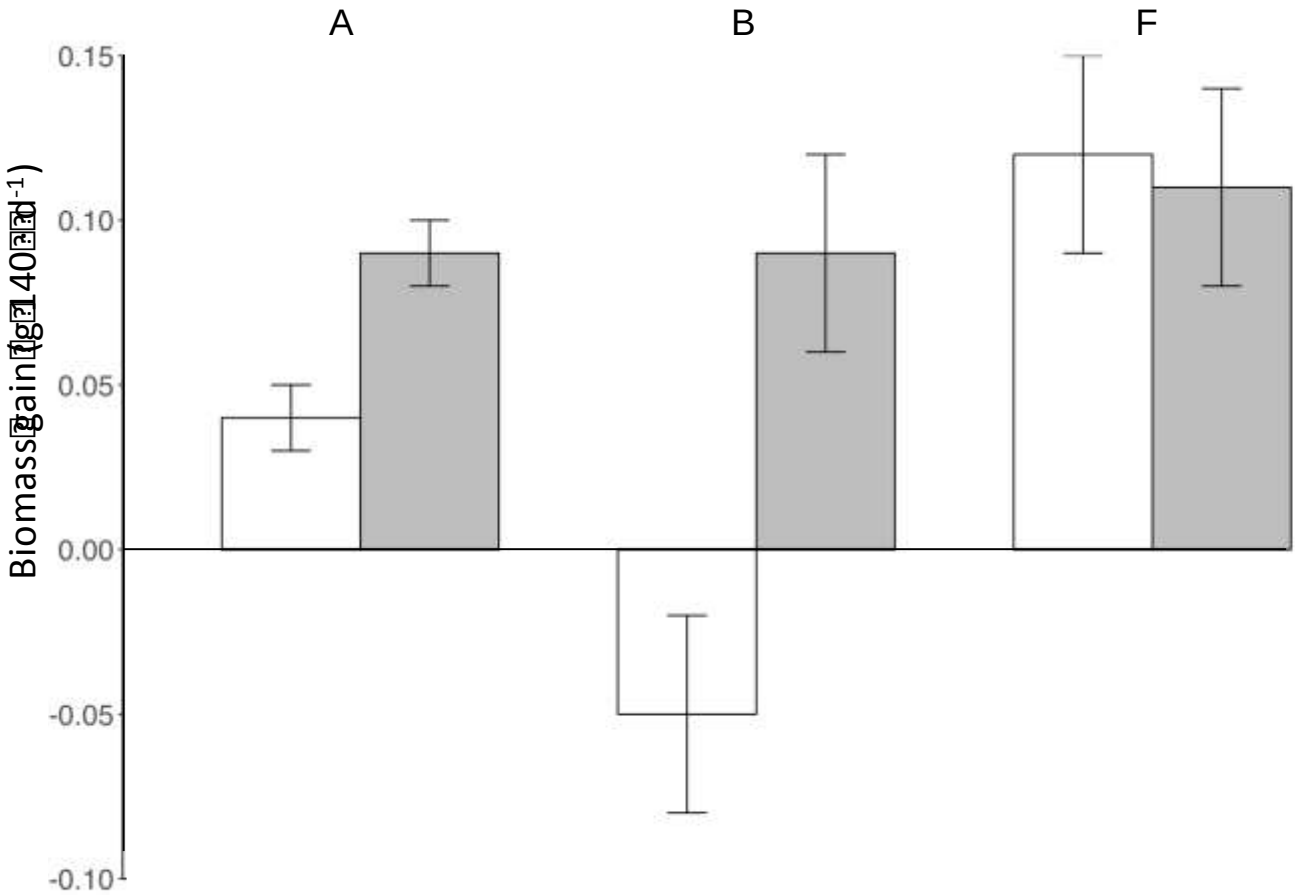
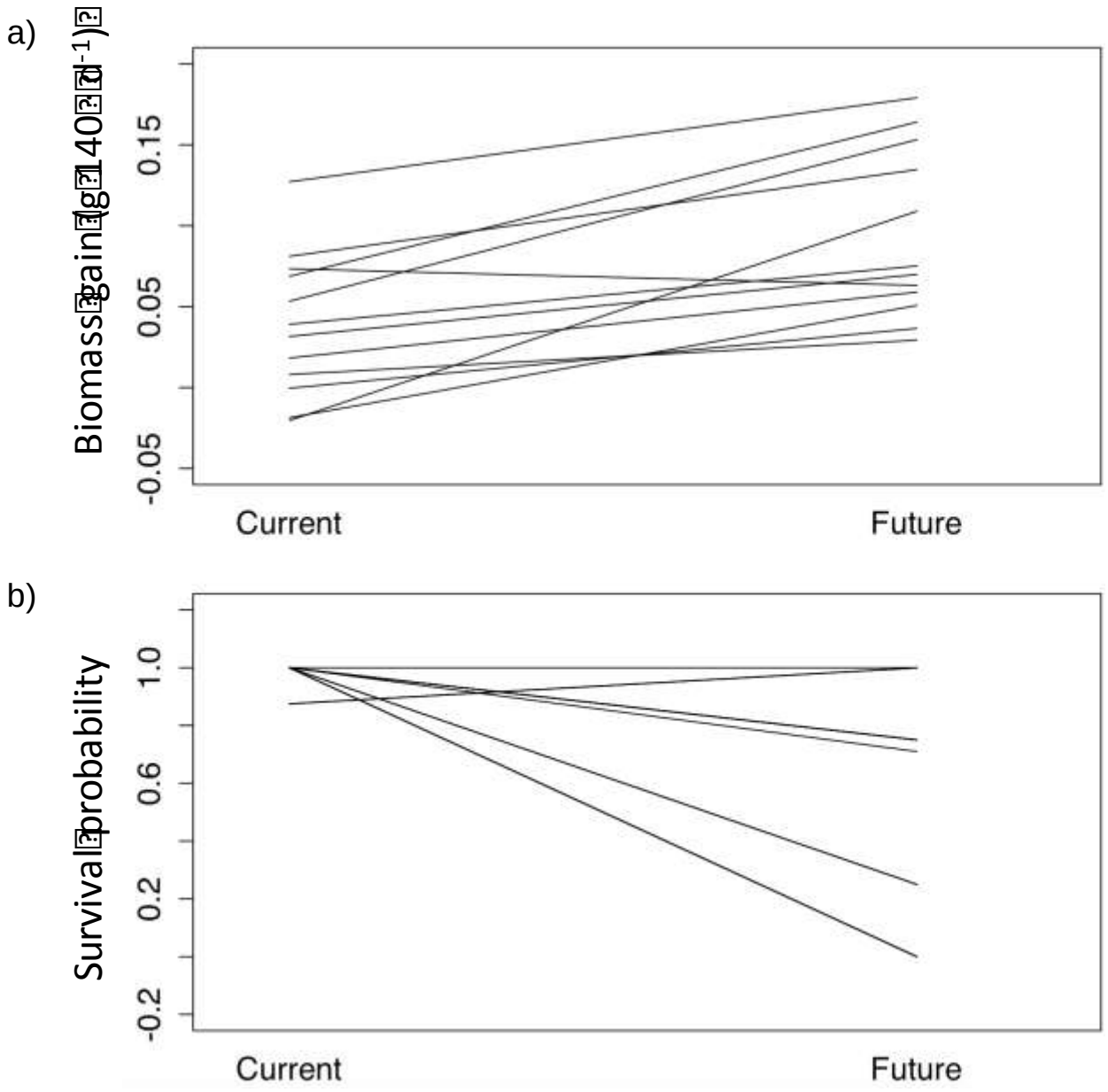
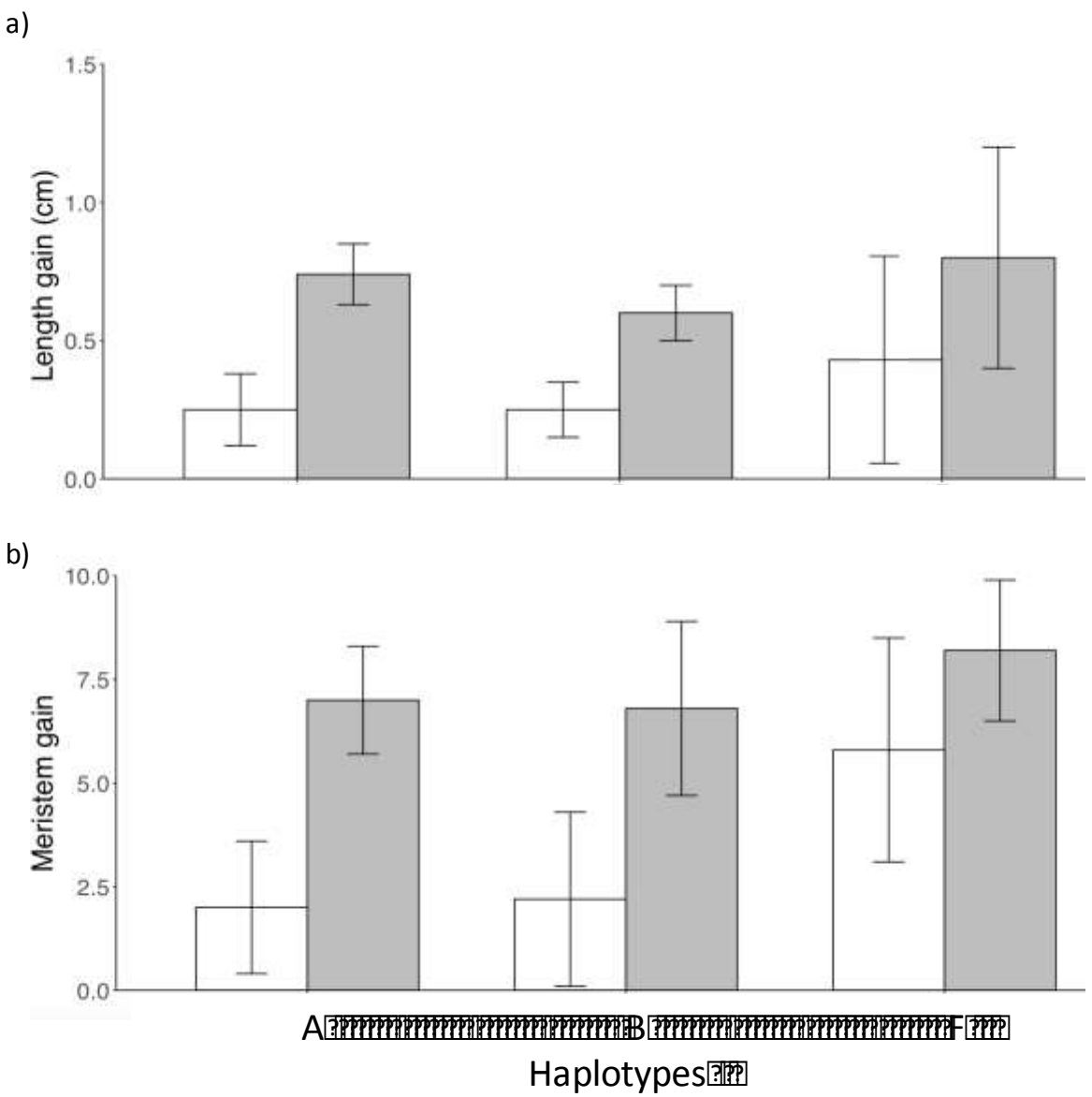


Figure 6


a)
Biomass gain (g g-1 d-1)
-0.05
0.05
0.15
Current
Future
b)
Survival probability
-0.2
0.2
0.6
1.0
Current
Future

Supporting information

Figure S1



Supporting information

Table S1

Haplotype	# thalli	L-85	Fsp-4	L-94	L-38	Fsp-3	L-58	L-20	Fsp-1	Fsp-2
A	12	118 118	129 129	171 171	187 224	122 128	125 129	155 161	147 149	166 205
B	4	118 118	129 129	171 171	187 224	124 128	125 129	155 161	147 149	166 205
C	1	118 118	129 129	171 171	187 224	122 128	125 129	149 164	147 149	0 0
D	1	118 118	129 135	171 177	224 224	124 128	125 125	174 174	147 149	174 174
E	1	118 118	129 129	171 171	224 224	122 128	125 125	0 0	147 149	0 0
F	4	118 120	129 129	171 171	224 224	128 128	125 125	155 155	147 147	166 174
G	1	118 120	129 137	171 171	209 224	128 156	125 125	0 0	147 155	174 205
H	1	116 116	129 129	171 171	224 224	122 128	125 125	155 164	147 147	166 174

Table S3

Source of variation	Haplotype A			Haplotype B			Haplotype F		
	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P
Fixed Factors									
Climate change	1, 20.4	7.3	<0.05	1, 25.3	10.1	<0.01	1, 18	0.6	0.5
Initial size	1, 84.4	8.3	<0.01	1, 27.9	15.8	<0.001	1, 18	0.8	0.4
Initial size × Cl. change									
		χ^2	P		χ^2	P		χ^2	P
Random Factors									
Ramet		0.0	1		8.5	<0.001		0.0	1
Ramet × Cl. change		5.2	<0.05						
Aquarium		0.7	0.4		0.0	1		0.0	1

Table S4

Source of variation	Haplotype A			Haplotype B			Haplotype F		
	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P
Fixed Factors									
Climate change	1, 21.2	12	<0.01	1, 9.9	8.12	<0.05	1,16.7	0.3	0.6
Initial size	1, 62.4	0.6	0.5	1, 9.7	2.4	0.2	1, 17.5	0.7	0.4
Initial size × Cl. change									
		χ^2	P		χ^2	P		χ^2	P
Random Factors									
Ramet		1.36	0.12		4.3	<0.05		0.1	0.8
Ramet × Cl. change									
Aquarium		2.3	0.07		4.6	<0.05		0.0	1