TOLERANCE AND POTENTIAL FOR ADAPTATION OF A BALTIC SEA ROCKWEED UNDER PREDICTED CLIMATE CHANGE CONDITIONS

Luca Rugiu[1], Iita Manninen, Eva Rothäusler, Veijo Jormalainen

Section of Ecology, Department of Biology, University of Turku, FIN-20014, Turku, Finland

[1]Author for correspondence: luca.rugiu@utu.fi

ABSTRACT

Climate change is threating species' persistence worldwide. To predict species responses to climate change we need information not just on their environmental tolerance but also on its adaptive potential. We tested how the foundation species of rocky littoral habitats, *Fucus vesiculosus,* responds to combined hyposalinity and warming projected to the Baltic Sea by 2070-2099. We quantified responses of replicated populations originating from the entrance, central, and marginal Baltic regions. Using replicated individuals, we tested for the presence of within-population tolerance variation. Future conditions hampered growth and survival of the central and marginal populations whereas the entrance populations fared well. Further, both the among- and within-population variation in responses to climate change indicated existence of genetic variation in tolerance. Such standing genetic variation provides the raw material necessary for adaptation to a changing environment, which may eventually ensure the persistence of the species in the inner Baltic Sea.

Keywords: climate change, tolerance, salinity, warming, marine macroalga, distribution, genetic variation, Baltic Sea, adaptation.

1. INTRODUCTION

Climate change is significantly impacting biodiversity and ecosystem functioning worldwide, and by the end of the twenty-first century it may become the most important driver of biodiversity loss and species range shift (Bellard et al. 2012; Poloczanska et al. 2013; Lenoir et al. 2015; Gruner et al. 2016). In the light of the predicted environmental changes, some species may persist by adapting evolutionarily to new conditions but many will shift their distribution with the changing environmental regimes while some may be lost to extinction (Parmesan and Yohe 2003; Perry et al. 2005; Harley et al. 2012; Poore et al. 2016). The challenge for predicting species responses to climate change is to know their environmental tolerances and, in particular, to understand the adaptive potential of tolerance which may rescue populations from local extinction.

Tolerance to a certain range of environmental conditions determines species' geographical distribution (Levins 1968; Banta et al. 2012). Although species are often treated as if they responded uniformly to environmental stress (Banta et al. 2012) populations of broadly distributed species experience distinct gradients of abiotic and biotic factors and typically show phenotypic and/or genotypic differences (Sanford and Kelly 2011, Valladares et al. 2014). The species may adjust its phenotype to the new environmental conditions through phenotypic plasticity (Chevin et al. 2010; Lande 2014; Valladares et al. 2014). Alternatively, populations may differ in traits related to tolerance, and when such variation exists, some of them may be more prone to extinction in the face of widespread environmental alterations such as climate change (Pearson et al. 2000; Hämmerli and Reusch 2002; Kelly et al. 2011; Lamichhaney et al. 2012; Stockwell et al. 2003; Berteaux et al. 2004; Reusch et al. 2005). Our understanding of how tolerance, genetic variation of tolerance and phenotypic plasticity may vary among populations and how it affects species responses to changing environment is still in its infancy.

Here we study variation in tolerance to climate change of a broadly distributed brown alga *Fucus vesiculosus* along the environmental gradient in the Baltic Sea. The Baltic Sea is an ecologically marginal habitat for marine species due to its brackish water nature. The inflow of freshwater from many rivers, together with a poor exchange of seawater with the Atlantic, causes a strong salinity gradient, which decreases from approximately 20 PSU (Practical Salinity Unit) in the southwest, in the Kattegat, to 1 PSU in the north (Rönnberg and Bonsdorff 2004). In addition, the sea surface temperature of the Baltic Sea shows large geographic and seasonal variation. During summer, the temperature exceeds 20°C, while during winter it might drop below zero (Swedish Environmental Protection Agency, 2001). Climate change is predicted to bring changes in surface seawater temperature, salinity, turbidity, and ice coverage and duration (Meier and Eilola 2011; Meier et al. 2012). In particular, a rise in seawater temperature and a remarkable drop in salinity are projected for the years 2070-2099 (Meier et al. 2011), with the biggest absolute change in salinity occurring in the entrance region.

Fucus vesiculosus (hereafter *Fucus*) is the major perennial macrophyte and foundation species in the Baltic Sea littoral (Wikström and Kautsky 2007), where it inhabits the shallow hard-bottom areas (Snoeijs, 1999). It plays a key ecological role by forming a highly structured habitat for many epibionts and other associated organisms (Korpinen et al. 2007), thus providing food and shelter to the benthic community (Lotze et al. 2001). The increased surface seawater temperature and decreased salinity expected for the next century may affect *Fucus* populations in the Baltic Sea both directly and indirectly, possibly causing distributional shifts (Leidenberger et al. 2015, reviewed in Takolander et al. 2017a). Warming has been found to impair survival (Wilson et al. 2015) as well as to speed reproductive maturation with decreasing germination success (Maczassek et al. 2014; Kraufvelin et al. 2012). Warming may also have positive effects on growth of germlings (Steen and Rueness 2004) or adults, and it may benefit *Fucus* indirectly by reducing grazers (Werner et al. 2015; 2016). On the other hand, some indirect effects of warming such as increased consumption rate of herbivorous isopods (Leidenberger, Harding and Jonsson 2012; Gutow et al. 2016; Rothäusler et al. 2017), changes in quality of the thallus as food (Weinberger et al. 2011), or increase of light-absorbing phytoplankton (Alexandridis et al. 2012) may be harmful for *Fucus*. So far, much less is known about the effects of declining salinity on *Fucus*. Bäck et al. (1992a) showed that Baltic *Fucus* evolved higher tolerance to low salinity than its Atlantic counterpart. Laboratory experiments found that salinities lower than 4 PSU are a physiological boundary for reproductive efficiency of *F. vesiculosus*, and this would therefore limit the distribution of this species (Serrão et al. 1999; Serrão et al. 1996a, b). However, *Fucus* individuals have been found in salinity down to 2 PSU in the Bothnian Sea, Gulf of Finland, and the White Sea. This is possibly due to periodic salinity fluctuations during their reproductive period or a localised higher salinity (Ruuskanen and Bäck, 2002, Ardehead et al. 2016). A decrease in salinity between 6 and 3 PSU in the Gulf of Finland was associated with a decrease in thallus size Baltic of *F. vesiculosus* (Ruuskanen et al. 1999).

Even though *F. vesiculosus* experiences different gradients of salinity and temperature across the Baltic Sea, experimental studies seldom account for this interactive effect, and typically only a single environmental factor has been manipulated (Wernberg et al. 2012; Forsman et al. 2016). In the present study, we exposed Baltic *Fucus* to a long-term climate change experiment (140 days) to test if it has the potential to tolerate and adapt to the projected simultaneous summer-time future temperature and salinity conditions expected for the years 2070-2099 in the Baltic Sea (Meier et al. 2011). Based on these climate projections, we tested the following hypotheses: (i) Populations originating from the entrance, central and marginal regions of the Baltic Sea are differently affected by the predicted future conditions of their region: the expected future shift in salinity and temperature for the entrance region can be within the tolerance range but for the populations in the central and marginal regions it may be challenging to tolerate the predicted combination of warming and low salinities. (ii) Populations within regions may vary in their responses to future conditions due to their local differentiation. Such among-population variation represents either geographic genetic variation or phenotypic plasticity in tolerance, both of which may enhance persistence through dispersal from the more tolerant populations. (iii) Populations may harbor within-population variation in tolerance. Also such variation can be based on standing genetic variation or individual variation in phenotypic plasticity. Within population variation indicates potential for adaptive responses to climate change. Given the important role of Baltic *Fucus*, this information is essential in evaluating the consequences of global climate change on rocky littoral communities within this basin.

2. MATERIALS AND METHODS

2.1 Sampling of Fucus

We collected *Fucus vesiculosus* from three different regions – entrance, central, and marginal – of the Baltic Sea (Fig. 1, Table 2) in summer 2014. Within each of these region, we randomly sampled three populations, and from each population we collected 25 individuals. Herein, one individual is defined as all the apical tips of a thallus growing from a single stem attached to a holdfast. We detached the individual in at least 5 m distance between each other to ensure the uniqueness of samples (see Supporting Information for more details). We only genotyped two populations from the marginal region where clonality has been previously recorded to ensure that they were different genotypes (for the analyses see Tables S1, S2 and S3). For the rest of the populations (from the entrance and central regions), the distance between samples collected and the fact that we were detaching only one stem from one holdfast ensured the uniqueness of the genotypes. Individuals were collected by snorkeling and at all sites they were detached in the range between 0.5 to 2m depth.

From 27th to 28th June 2014, we collected the marginal populations, while the central populations were gathered between the 2nd and 3rd of July. On the 3rd and 4th of July, we collected the entrance populations. All individuals were kept in coolers between wet paper tissues to avoid dehydration and transported to the Archipelago Research Institute (University of Turku) at Seili (60° 14’ N, 21° 58’ E), where they were carefully rinsed with freshwater to remove associated grazers and epiphytes. Then, we stored the algal individuals in their native salinities until the experiment started.

2.2 Fucus preparation for the experiment

Once our sampling was complete we split each algal individual (N = 25 per population and region) into eight similar sized branches (we hereafter refer to one branch as a ramet - initial length, mean ± SE: 7.1 ± 0.05 cm; initial # of apical meristems: 8.7 ± 0.16; initial wet weight (WW): 0.99 ± 0.02 g). Four of the branches were distributed randomly among the aquaria in the current conditions, and the other four among the aquaria in the future conditions, so that each aquarium contained a mix of 25 ramets (Fig. 2a). Epiphytes were rinsed from experimental algae when necessary to avoid competition for nutrient availability and light. Micro-environmental effects were accounted for by randomly relocating the algae within each aquarium each week. In order to avoid flotation of the ramets, a small ceramic weight was attached individually with a cable tie to each ramet. To prevent any damage, we fixed a piece of a plastic mat between the cable tie and the ramet. We first started to prepare the marginal populations (11th and 12th of July), then the central populations (12th and 13th July) and finally the entrance populations (15th and 16th of July).

At the starting point all aquaria were set up with current conditions. After all the ramets have been introduced in their respective aquaria racks, we simultaneously shifted the temperature and salinity of all future aquaria within one day. The experiment started for all populations on the 23rd of July and ended on 10th of December.

2.3 Experimental setup

We examined the effects of different temperature and salinity conditions on the performance of *Fucus* in an indoor aquarium experiment. Because climate change typically involves simultaneous shifts in several abiotic factors (IPCC Climate Change, 2007), we focused on the combined effects of hyposalinity and increased temperature. These are the main environmental factors that determine the structural and functional characteristics of aquatic biota, and they covary regionally, both currently and in the future projections.

We used six aquarium racks (each consisted of 12 aquaria) to expose, separately, the algal material from each region to two different climate conditions, the current and predicted future (Table 1, Fig. 2b). We used summer conditions because during this period *Fucus'* growth rate is up to three times faster than in the winter (Lehvo et al. 2001). We extended the duration of the experiment further than the natural duration of the Baltic summer to detect the long-term influence of the future conditions. The long term exposure to hyposalinity/warming may evidence patterns of among- and /or within population variation in performance that may not be evidenced by short term experiments. In order to apply a realistic setup, the current conditions within each region were based on the average summertime salinity and temperature conditions of the sampling sites within the three regions (Table 2). The data on future (2070-2099) changes in summer salinity and temperature for Baltic coastal areas come from the model RCAO-ECHAM-A2-REF from Meier et al. (2011). The data on current surface seawater temperature and surface salinity have been averaged from the mean values for June to August for each region (http://www.balticnest.org/).

Each aquarium rack consisted of a bottom tank (~ 300L) and 12 aquaria (24 L each), which were connected to each other via recirculating water system. Seawater was pumped from the bottom tank individually to each aquarium, from where it flowed back into the bottom tank. Before it was pumped up, the seawater was cleaned first by an acrylic filtration unit (SCHURAN Jetskim 120) equipped with a mechanical and biological filter, then by a protein skimmer, and finally by UV radiation. To regulate the desired water temperature, each bottom tank was equipped with a chiller/heater. We obtained the region-specific water salinities for both climate conditions (current and future) by adding artificial sea salt to seawater or by dilution with distilled water. To ensure ample 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.

Each shelf contained four aquaria, which received artificial light from two LED lamps (Radion ™ XR30w Pro lamp). We used a 17:7 h light:dark rhythm, which was similar to the average summer light conditions in the Baltic Sea. The light level slowly increased in the mornings, reached a maximum intensity (1200 µmol m^{-2} S^{-1}) at the aquarium water surface between 11:00 and 14:00, and then slowly decreased in the evenings to darkness.

During the experiment, we kept the water level and salinity in the aquarium system constant by adding ion-exchanged water. We monitored temperature (daily) and salinity (weekly) to ensure that conditions remained at the desired levels (Table 1). We also measured pH weekly to ensure it stayed within the natural range of the Baltic Sea (mean ± SE: 8.31 ± 0.07).

2.4 Measuring responses

We measured the growth rate and survival of *Fucus* as a proxy for sensitivity to environmental changes, since they are dependent on the ratio between respiration and photosynthetic activity and they give an overall estimate of the algal performance (Karsten, 2008). Growth rate was measured as a change in wet biomass (g WW), in length along the major axis (cm), and in the number of apical meristems during the 140 d experiment. Therefore, each ramet was measured at the beginning and at the end of the experiment. For the growth rate in terms of biomass, we gently dried the ramets between paper tissues before determining their initial and final weight. As there was mortality during the experiment, the growth measures refer to growth of the survivors after 140 days. Therefore, we measured the growth rate of the most tolerant individuals. As the different growth rate measures lead to similar conclusions, we present here only the biomass gain rate (expressed as g WW / 140 d), but give the summary data and analyses for the length and meristem gain rate in supplementary material (Figure S1, S2 and S3, Tables S4-S5).

We recorded survival throughout the experiment and at the end. We checked the ramets weekly and defined as dead those with > 90% of the thallus area showing necrosis. When an individual started to degenerate, >90 % necrosis typically proceeded relatively quickly, between the weekly observations. Survivors didn’t show dead thallus parts. Survival was expressed as the probability of being alive at the end of the experiment. Growth rate and the survival probability of each individual was calculated as the average of N = 4 ramets in the future and N = 4 ramets in the current conditions. These means were calculated using the Glimmix procedure as the ‘best linear unbiased predictors’ (BLUPs), which are considered the best estimates for random factors (Robinson, 2008).

2.5 Statistical analysis

We analyzed the variation in growth rate (length, number of apical meristems, and biomass) using a general linear mixed model within populations separately for each region. A normal distribution was used for the error variance, and the analyses were implemented using the procedure GLIMMIX in SAS 9.4 (SAS Institute Inc. 2013). The fixed factor in the model was climate change (future and current conditions). Random factors were population, individual within population, aquarium, and all the possible interactions between these factors and climate change. The aquarium was included as a random factor to capture possible variations in growing conditions among aquaria within a rack (e.g. lighting, position effect, water through-flow). In the analyses of growth rate, we used the initial size as a covariate and tested all of its interactions with the fixed factor. We then simplified the model by removing non-significant effects, starting from the higher-order interactions, with the aid of the Akaike Information Criterion (AIC). The significance of fixed effects was tested using F-statistics, with the denominator degrees of freedom estimated by the use of the Kenward-Roger approximation (Kenward and Roger 1997). The significance of the random effects and the random-by-fixed effect interactions was tested by X^2-tests of the differences in the 2×log likelihood value of that factor included versus excluded from the model (likelihood ratio test, Littell *et al.*, 2006).

The survival probability (after 140 days) was analyzed using a generalized linear mixed model, with survival as a binary response variable (alive, dead). This model was similar to that described above for the growth rate analyses.

3. RESULTS

3.1 Growth performance among regions under climate change conditions

Populations originating from different regions varied in their biomass gain in the current conditions of their respective region: entrance populations grew the most, followed by the central and marginal populations (Fig.2). The entrance populations tolerated the future conditions well: there was no overall difference in biomass gain between current and future conditions (Fig. 3, Table 3). In contrast, future conditions were harsh for the central region populations that grew less compared to their counterparts in the current conditions (Fig. 3, Table 3). Similarly, biomass gain of the populations from the marginal region was strongly hampered by the future conditions (Fig. 3, Table 3).

3.2 Variation among populations and individuals in growth responses to climate change

Within the entrance region, the biomass response to climate change varied among populations (Fig. 3, Table 3). Algae from the population G tolerated the future conditions the best, gaining similar amounts of biomass in both climate conditions, while for the populations B and S, the difference between climate conditions was more pronounced (25% and 16% respectively; Fig. 3). In the central region, we found no differences among populations in their biomass response to climate change, but, in the marginal region, we found such variation (Fig. 3, Table 3): The population R was the least tolerant to climate change and grew 98% less when exposed to future conditions, while the decrease in growth in future conditions was 80% for the population P and 70% for the population H.

We found pronounced among-individual variation in biomass gain in entrance and marginal populations as indicated by the significant among-individual variance component (Table 3). Most interestingly, individuals in the central populations varied in their growth response to climate change (Fig. 4, Table 3) indicating that different individuals expressed varying tolerance to future conditions. It is worth to note that the despite the among-individual variation in tolerance remained also the after strong mortality selection during the experiment (similar among-individual variance in both the climate change conditions in Fig. 4).

3.3 Effects of future climate change conditions on survival of Fucus across the Baltic Sea regions

Fucus originating from the entrance region survived well in both the current and future conditions indicating high tolerance to future conditions (Fig. 5, Table 4). Instead, survival of *Fucus* originating from the central region and even more that from the marginal region was hampered by their future conditions (Fig. 5, Table 4). Only 34% of *Fucus* ramets from the central region and 23% from the marginal region survived until the end of the experiment in the future conditions.

Marginal populations varied in their survival responses to climate change (Fig. 5, population-by-climate change interaction in Table 4). Furthermore, within the marginal populations individuals responded differently to climate change (individual-by-climate change interaction in Table 4). Individuals within entrance and central regions varied in their survival but not in their survival response to climate change (Table 4).

4. DISCUSSION

4.1 Climate change effects on algal growth and survival

Our results show that the tolerance of *Fucus* populations to their projected future conditions varies along the Baltic Sea. Populations from the entrance region tolerated future conditions well, maintaining their growth and survival unchanged between current and future conditions. This suggests that their future hyposalinity and warming is within the current range of tolerance of the populations at the Baltic Sea entrance. Instead, future climate conditions had a pronounced negative effect on survival of populations from the central region and an even a more severe impact on those from the marginal region. Moreover, the growth reduced to about fifth of that in the current conditions in populations from the central region, and almost completely ceased in the marginal ones. We suggest that while the populations at the Baltic Sea entrance are likely to tolerate well the future conditions, those from the central and marginal regions of the Baltic Sea are faced with serious challenges and are unlikely to persist in the current distributional range unless their tolerance cannot adapt evolutionarily with the environmental change.

The negative effects of low salinity on seaweed performance have been attributed to the inability to maintain osmotic balance (cell turgor pressure) and to keep a positive ratio between photosynthesis and respiration (Hellebust 1976). Low salinity (≤ 2 PSU) is known, for instance, to damage the cellular structures responsible for protein synthesis and energy metabolism (Tropin et al. 2003). Low mannitol contents have been found in response to low salinity and combination of high temperature and hyposalinity in *F. vesiculosus* (Munda and Kremer, 1977; Takolander et al. 2017b), as this compound is also used for osmoregulation (Groisillier et al. 2014; Munda and Kremer, 1977). Negative effects of hyposalinity on *Fucus* growth have been found in experimental studies. For instance, Bäck et al. (1992b) showed that Baltic *Fucus* from the marginal region in the Gulf of Finland could grow and survive in salinities from 6 to 12 PSU, but that salinity extremes (1.5, 34, and 45 PSU) reduced both growth and survival. *Fucus* from the marginal region has also been reported to tolerate short-term (26 h) exposure to hyposalinity (2.5 PSU) without any signs of photoinhibition or damage to the photosynthetic machinery (Rothäusler et al. 2016). Moreover, there is also evidence on local adaptation to local salinity (Johansson et al. 2017): a reciprocal transplant experiment indicated that *F. vesiculosus* from the Atlantic and Baltic Sea grows better in their local than in foreign salinity (respectively 24 and 4 PSU). However, Serrão et al. (1996b) showed that sperm motility and fertilization success of *F. vesiculosus* decreases sharply in salinity below 5PSU, suggesting that early life stages might be most important for the persistence of the species at extremely low salinity.

Temperature plays an important role in algal physiology because it controls the photosynthetic rate (Raven and Geider 1988), which affects the rate of carbon fixation by RuBisCO (Sukenik, Bennett and Falkowski 1987). Warming temperatures become stressful for plants when they affect the balance between protein denaturation and the action of heat-shock proteins and the higher production of proteins (Csikász-Nagy and Soyer 2008). Moderately warm temperatures enhanced growth in *Ascophyllum nodosum* (Keser et al. 2005) and *F. vesiculosus* from the western Baltic Sea where it grew and survived well in temperatures ranging from 5 to 26°C, with a damaging effect on the photosynthetic system only at temperatures >26°C (Graiff et al. 2015). A similar result was reported for eastern Atlantic populations of *F.vesiculosus* (Russell 1987), in which high water temperature affected the sensitivity of the photosynthetic machinery. However, Al-Janabi et al. (2016) found that the effects of temperature changes on Baltic *Fucus* germlings depend on the season: a 5 °C increase in natural temperature enhanced the growth in early summer, but it caused a severe mortality in late summer. Warming may also be responsible for temporal changes in receptacle maturation such as shown for *F. vesiculosus,* under experimental conditions (Graiff et al. 2017) but also *in situ* (Kraufvelin et al. 2012). Indeed, if warming will increase the duration of the reproductive period of *Fucus,* it is possible that enhanced window for recruitment may help buffering the losses caused by hyposalinity/warming, at least in the regions where low salinity is not limiting fertilization.

Because climate change modifies several abiotic factors simultaneously, we designed our experiment to detect only the combined effect of the predicted future temperature and salinity combinations in the Baltic Sea, not to separate the single factor effects. The combined effect of future seawater salinity and temperature may be simply additive, or it may involve antagonistic or synergistic interactive effects. A meta-analysis of multi-stressor studies by Wahl et al. (2011) found that for *Fucus* spp. the combined effects were on average additive. For instance, a short term (8 days) manipulative experiment conducted with *F. vesiculosus* showed that low salinity slowed down the recovery of growth and photosynthetic performances after an exposure to high water temperature (Takolander et al. 2017b). Interactive effects may occur and are of course important, but, if present, they are included in our combined effect. Further, while our experiment was designed to measure the tolerance of *F. vesiculosus* to the averaged expected changes in seawater conditions, climate change effects will also enhance climate variability (e.g. frequency and intensity of heat and cold waves, Vasseur et al. 2014). For instance, Graiff et al. (2015) showed that *Fucus* is able to acclimate to higher temperature only if there is enough acclimation time.

4.2 Potential of Fucus *to adapt to future conditions*

The potential for adaptive responses to the predicted future salinity/temperature conditions was indicated by among-individual variation in performance, and, especially by the differential responses of individuals to climate change. The among-individual variation might have different explanations. That we cloned and reared replicated ramets of each individual in common garden conditions entails that the differences we found among clones do represent genetic differences in plasticity. However, a possibility remains that differences among clones include some carry-over effects from the original environment of the sampled individuals, the clonal mothers. It is difficult to judge the relevance of such carry-over effects but even if they contributed to variation detected among individuals (i.e. affect the main effect of individual) we find highly unlikely that they would do differently so in current and future conditions (i.e. affect the individual-by-climate change interaction). Thus, we consider the among-individual variation in responses to climate change to represent genetic variation in reaction norms, i.e. variation in phenotypic plasticity of traits responsible for tolerance. A high degree of such within-population variation in quantitative traits that are closely related to fitness is considered to be the core component of adaptive evolution, allowing the species persistence in a changing environment (Pigliucci 2005; Wrange et al. 2014).

The observed among-population variation in growth and survival within regions likely indicates variation in tolerance to climate change at a regional spatial scale, within both the entrance and marginal regions of the Baltic Sea. Within the entrance region, all populations survived equally well in current and future salinity/temperature conditions, but *Fucus* from the G population were the most tolerant to future conditions, with the least decrease in growth. The populations from the marginal region differed in their responses to climate change, both in survival and growth. Given the strong spatial genetic structuring (Tatarenkov et al. 2007; Pereyra et al. 2013; Ardehed et al., 2016) and reduced dispersal capacity of Baltic *Fucus* (Serrão et al. 1996b), we consider it likely that such among-population variation within region might represent genetic differentiation in plasticity. Intra-specific geographic variation in tolerance to climate change, such as found here and also in the Atlantic *F. serratus* and *F. vesiculosus* (Pearson et al. 2009; Jueterbock et al. 2014; Saada et al. 2016), means that some populations are more vulnerable than others to climate change. The tolerant populations may provide local persistence assurance through acting as sources for floating thalli that may disperse and generate gene flow over long distances (Rothäusler et al. 2015).

Further, the significant individual-by-climate change interaction in growth of entrance and central populations and in survival of marginal populations suggests the existence of genetic variation in phenotypic plasticity. Also other studies have found individual-by-environment -interactions in quantitative traits of *Fucus* indicating genetic variation in plasticity to different environmental conditions, such as growth responses to light or nutrient regimes (Jormalainen and Honkanen 2004) or phlorotannin responses to herbivory and depth distribution (Jormalainen and

Ramsay 2009). In our study, those individuals from the entrance and central regions that survived in future conditions until the end of the experiment also showed genetic variation in plasticity of growth (individual-by-climate change -interactions), with the variation in growth remaining also in future conditions after mortality. Upon this variation in plasticity, natural selection can alter the reaction norms of growth.

5. Conclusion

Our results imply that the projected increase in temperature and decrease in salinity will be challenging for *Fucus* populations, particularly in the central and marginal regions of the Baltic Sea. There, the abundance of *Fucus* is likely to decline unless populations cannot respond by adaptive evolution of tolerance. Our experiment with almost instant exposure to future conditions represents an extreme scenario. The future conditions we used are a projection for the end of this century (2070-2099) so *Fucus* will be confronted with a gradual change taking place over several generations. We found indications of phenotypic plasticity and genetic variation in tolerance of *Fucus* to the projected future conditions, both within and among the Baltic Sea populations, suggesting potential for adaptive responses exists. Thus, adaptive increase of tolerance may provide persistence in the face of climate change. However, our data just documents the potential for adaptation but does not allow estimations whether the speed of adaptation can match the rate of change. Furthermore, the fate of *Fucus* populations in the Baltic Sea will strongly depend on how the biotic interactions within the entire associated community, such as with the competing macro-and microalgae and grazers, will respond to climate change. Further research on such community responses is needed.

Authors' Contributions

VJ, LR and E.R. conceived and designed the experiment. All authors performed the experiment. LR analyzed the data. LR led the writing of the manuscript; all authors contributed to the text.

Acknowledgments

We are grateful to J. Sjöroos, T. Salo, K. Gagnon, and C. Duffner for helping with the setup and sampling of the experiment. Meri Lindqvist is acknowledged for the help with *Fucus* genotyping. We are also thankful to the Archipelago Research Institute of the University of Turku for the use of their facilities and logistical help. This study was funded by BONUS, the EU joint Baltic Sea research and development program, project BAMBI and the Academy of Finland grant decision number 273623.

Conflicts of interest: none.

References

Al-Janabi, B., I. Kruse, A. Graiff, U. Karsten, and M. Wahl. 2016. Genotypic variation influences tolerance to warming and acidification of early life-stage *Fucus vesiculosus* L. (Phaeophyceae) in a seasonally fluctuating environment. Mar. Biol. **163**: 1–15. doi:10.1007/s00227-015-2804-8

Alexandridis, N., A. Oschlies, and M. Wahl. 2012. Modeling the effects of abiotic and biotic factors on the depth distribution of *Fucus vesiculosus* in the Baltic Sea. Mar. Ecol. Prog. Ser. **463**: 59–72. doi:10.3354/meps09856

Allison L. Perry, P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate Change and Distribution Shifts in Marine Fishes. Science. **308**: 1912–1915. doi:10.1126/science.1111322

Ardehed, A., D. Johansson, L. Sundqvist, E. Schagerström, Z. Zagrodzka, N.A. Kovaltchouk, L. Bergström, L. Kautsky, M. Rafajlovic, R.T. Pereyra, K. Johannesson. 2016. Divergence within and among seaweed siblings (*Fucus vesiculosus* and *F. radicans*) in the Baltic Sea. PLoS One **11**: 1–16. doi:10.1371/journal.pone.0161266

Bäck, S., J. C. Collins, G. Russel. 1992a. Comparative ecophysiology of Baltic and Atlantic *Fucus vesiculosus*. Mar. Ecol. Prog. Ser. **84**: 71–82. doi:10.3354/meps084071

Bäck S., J.C. Collins, G. Russell. 1992b. Effects of salinity on growth of Baltic and Atlantic *Fucus vesiculosus*. Br. Phycol. J. **27**:39–47

Banta, J. a., I. M. Ehrenreich, S. Gerard, L. Chou, A. Wilczek, J. Schmitt, P. X. Kover, and M. D. Purugganan. 2012. Climate envelope modelling reveals intraspecific relationships among flowering phenology, niche breadth and potential range size in *Arabidopsis thaliana*. Ecol. Lett. **15**: 769–777. doi:10.1111/j.1461-0248.2012.01796.x

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. **15**: 365–377. doi:10.1111/j.1461-0248.2011.01736.x

Berteaux, D., D. Reale, M. A. G., and B. Stan. 2004. Keeping Pace with Fast Climate Change : Can Arctic Life Count on Evolution? Integr. Comp. Biol. **44**: 140–151.

Chevin, L. M., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. PLoS Biol. **8**: e1000357. doi:10.1371/journal.pbio.1000357

Csikász-Nagy, A., and O. S. Soyer. 2008. Adaptive dynamics with a single two-state protein. J. R. Soc. Interface **5**: 41–47. doi:10.1098/rsif.2008.0099.focus

Feistel R., S. Weinreben, H. Wolf, S. Seitz, P. Spitzer, B. Adel, G. Nausch,B. Schneider and D. Wright. 2010. Density and absolute salinity of the Baltic Sea 2006–2009. Ocean. Sci. **6**:3–24

Forsman, A., H. Berggren, M. Åström, and P. Larsson. 2016. To What Extent Can Existing Research Help Project Climate Change Impacts on Biodiversity in Aquatic Environments ? A Review of M ethodological Approaches. J. Mar. Sci. Eng. 75. doi:10.3390/jmse4040075

Graiff, A., M. Dankworth, M. Wahl, U. Karsten, and I. Bartsch. 2017. Seasonal variations of *Fucus vesiculosus* fertility under ocean acidification and warming in the western Baltic Sea. Bot. Mar. **60**: 239–255. doi:10.1515/bot-2016-0081

Graiff, A., D. Liesner, U. Karsten, and I. Bartsch. 2015. Temperature tolerance of western Baltic Sea *Fucus vesiculosus* – growth, photosynthesis and survival. J. Exp. Mar. Bio. Ecol. **471**: 8–16. doi:10.1016/j.jembe.2015.05.009

Groisillier, A., Z. Shao, G. Michel, S. Goulitquer, P. Bonin, S. Krahulec, B. Nidetzky, D. Duan, C. Boyen, T. Tonon. 2014. Mannitol metabolism in brown algae involves a new phosphatase family. J. Exp. Bot. **65**: 559–570. doi:10.1093/jxb/ert405

Gruner, D. S., M. E. S. Bracken, S. A. Berger, B. K. Erikkson, L. Gamfeldt, B. Matthiessen, S. Moorthi, U. Sommer, H. Hillebrand. 2016. Effects of experiemental warming on biodiverstiy depend on ecosystem type and local species composition. Oikos **126**:8-17. doi:10.1111/oik.02986

Gutow, L., I. Petersen, K. Bartl, and K. Huenerlage. 2016. Marine meso-herbivore consumption scales faster with temperature than seaweed primary production. J. Exp. Mar. Bio. Ecol. **477**: 80–85. doi:10.1016/j.jembe.2016.01.009

Hämmerli, A., and T. B. H. Reusch. 2002. Local adaptation and transplant dominance in genets of the marine clonal plant *Zostera marina*. Mar. Ecol. Prog. Ser. **242**: 111–118. doi:10.3354/meps242111

Harley, C. D. G., K. M. Anderson, K. W. Demes, J. P. Jorve, R. L. Kordas, T. A. Coyle, and M. H. Graham. 2012. Effects of climate change on clobal seaweed communities. J. Phycol. **48**: 1064–1078. doi:10.1111/j.1529-8817.2012.01224.x

Hellebust, J. A. 1976. Osmoregulation. Annu. Rev. Plant Physiol. Plant Mol. Biol. **27**: 485–505.

IPCC 2007. Climate Change 2007, Synthesis Report. A Contribution of working groups I, II, and III to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK

Johansson, D., R. T. Pereyra, M. Rafajlović, and K. Johannesson. 2017. Reciprocal transplants support a plasticity-first scenario during colonisation of a large hyposaline basin by a marine macroalga. BMC Ecol. **17**: 14. doi:10.1186/s12898-017-0124-1

Jormalainen, V., and T. Honkanen. 2004. Variation in natural selection for growth and phlorotannins in the brown alga *Fucus vesiculosus*. J. Evol. Biol. **17**: 807–820. doi:10.1111/j.1420-9101.2004.00715.x

Jormalainen, V., and T. Ramsay. 2009. Resistance of the brown alga *Fucus vesiculosus* to herbivory. Oikos **118**: 713–722. doi:10.1111/j.1600-0706.2008.17178.x

Jueterbock, A., S. Kollias, I. Smolina, J. M. O. Fernandes, J. A. Coyer, J. L. Olsen, and G. Hoarau. 2014. Thermal stress resistance of the brown alga *Fucus serratus* along the North-Atlantic coast: acclimatization potential to climate change. Mar. Genomics **13**: 27–36. doi:10.1016/j.margen.2013.12.008

Karsten, U. 2008. Defense strategies of algae and cyanobacteria against solar ultraviolet radiation. In Amsler, C. D. [Ed.] Algal Chemical Ecology. Springer, Springer Berlin Heidelberg, Germany, pp. 273–95.

Kelly, M. W., E. Sanford, and R. K. Grosberg. 2011. Limited potential for adaptation to climate change in a broadly distributed marine crustacean. Proc. R. Soc. B **279**: 349–356. doi:10.1098/rspb.2011.0542

Kenward, M. G., and J. H. Roger. 1997. Small Sample Inference for Fixed Effects from Restricted Maximum Likelihood. Biometrics **53**: 983–997.

Keser, M., J. T. Swenarton, and J. F. Foertch. 2005. Effects of thermal input and climate change on growth of *Ascophyllum nodosum* (Fucales, Phaeophyceae) in eastern Long Island Sound (USA). J. Sea Res. **54**: 211–220. doi:10.1016/j.seares.2005.05.001

Korpinen, S., T. Honkanen, O. Vesakoski, A. Hemmi, R. Koivikko, J. Loponen, and V. Jormalainen. 2007. Macroalgal communities face the challenge of changing biotic interactions: review with focus on the Baltic Sea. Ambio **36**: 203–211.

Kraufvelin, P., A. T. Ruuskanen, S. Bäck, and G. Russell. 2012. Increased seawater temperature and light during early springs accelerate receptacle growth of *Fucus vesiculosus* in the northern Baltic proper. Mar. Biol. **159**: 1795–1807. doi:10.1007/s00227-012-1970-1

Lamichhaney, S., A. M. Barrio, N. Rafati, G. Sundström, C.-J. Rubin, E. R. Gilbert, J. Berglund, A. Wetterbom, L. Laikre, M. T. Webster, M. Grabherr, N. Ryman, L. Andersson. 2012. Population-scale sequencing reveals genetic differentiation due to local adaptation in Atlantic herring. Proc. Natl. Acad. Sci. U. S. A. **109**: 19345–50. doi:10.1073/pnas.1216128109

Lande, R. 2014. Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. J. Evol. Biol. **27**: 866–875. doi:10.1111/jeb.12360

Lehvo, A., S. Bäck, and M. Kiirikki. 2001. Growth of *Fucus vesiculosus* L. (Phaeophyta) in the

Northern Baltic Proper: Energy and Nitrogen Storage in Seasonal Environment. Bot. Mar. **44**: 345–350.

Leidenberger, S., R. De Giovanni, R. Kulawik, A. R. Williams, and S. J. Bourlat. 2015. Mapping present and future potential distribution patterns for a meso-grazer guild in the Baltic Sea. J. Biogeogr. **42**: 241–254. doi:10.1111/jbi.12395

Leidenberger, S., K. Harding, and P. R. Jonsson. 2012. Ecology and distribution of the isopod genus *Idotea* in the Baltic Sea: key species in a changing environment. J. Crustac. Biol. **32**: 359–381. doi:10.1163/193724012X626485

Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography. **38**: 15–28. doi:10.1111/ecog.00967

Levins, R. 1968. Evolution in Changing Environments. Princeton University Press, Princeton.

Lynch,

Littell R.C., G.A. Milliken, W.W. Stroup, R.D. Wolfinger, O. Schabenberger. 2006. SAS for mixed models. 2nd ed.Cary,NC. SAS Institute Inc.

Lotze, H. K., B. Worm, and U. Sommer. 2001. Strong bottom-up and top-down control of early life stages of macroalgae. Limnol. Oceanogr. **46**: 749–757. doi:10.4319/lo.2001.46.4.0749

Maczassek, K. Effects of sequential stressors on survival of young life stages of the bladder wrack *Fucus vesiculosus* L. Doctoral dissertation. University of Kiel.

Meier, H. E. M., and K. Eilola. 2011. Future projections of ecological patterns in the Baltic Sea. Oceanografi **207**.

Meier, H. E. M., R. Hordoir, H. C. Andersson, C. Dieterich, K. Eilola, B. G. Gustafsson, a. Höglund, and S. Schimanke. 2012. Modeling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961–2099. Clim.

Dyn. **39**: 2421–2441. doi:10.1007/s00382-012-1339-7

Munda, I. M., B.P. Kremer. 1977. Chemical composition and physiological properties of fucoids under conditions of reduced salinity. Mar. Biol. **42**: 9–15.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**: 37–42. doi:10.1038/nature01286

Pearson, G. a., A. Lago-Leston, and C. Mota. 2009. Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. J. Ecol. **97**: 450–462. doi:10.1111/j.1365-2745.2009.01481.x

Pearson, G., L. Kautsky, and E. Serrão. 2000. Recent evolution in Baltic *Fucus vesiculosus:* reduced tolerance to emersion stresses compared to intertidal (North Sea) populations. Mar. Ecol. Prog. Ser. **202**: 67–79. doi:10.3354/meps202067

Pereyra, R. T., C. Huenchuñir, D. Johansson, H. Forslund, L. Kautsky, P. R. Jonsson, and K. Johannesson. 2013. Parallel speciation or long-distance dispersal? Lessons from seaweeds (*Fucus*) in the Baltic Sea. J. Evol. Biol. **26**: 1727–37. doi:10.1111/jeb.12170

Pigliucci, M. 2005. Evolution of phenotypic plasticity: where are we going now? Trends Ecol. Evol. **20**: 481–6. doi:10.1016/j.tree.2005.06.001

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D.S. Schoeman, P.J. Moore, K. Brander , J. F. Bruno, L.B. Buckley , M.T. Burrows, C.M. Duarte, B.S. Halpern, J. Holding, C.V. Kappel , M.L. O’Connor, J.M. Pandolfi, C. Parmesan, F. Schwing, S.A. Thompson, A.J. Richardson. 2013. Global imprint of climate change on marine life. Nat. Clim. Chang. **3**: 919–925. doi:Doi 10.1038/Nclimate1958

Poore, A. G. B., S. E. Graham, M. Byrne, and S. A. Dworjanyn. 2016. Effects of ocean warming and lowered pH on algal growth and palatability to a grazing gastropod. Mar. Biol. **163**: 1–11. doi:10.1007/s00227-016-2878-y

Raven, J. A. and R. J. Geider. 1988. Temperature and algal growth. New Phytol. **110**: 441–61.

Reusch, T. B. H., A. Ehlers, A. Hämmerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. PNAS **102**: 2826–2831.

Robinson, G. K. 2008. That BLUP is a good thing: the estimation of random effects. Stat. Sci. **6**: 15–32. doi:10.1214/ss/1177011926

Rönnberg, C., and E. Bonsdorff. 2004. Baltic Sea eutrophication: Area-specific ecological consequences. Hydrobiologia **514**: 227–241. doi:10.1023/B:HYDR.0000019238.84989.7f

Rothäusler, E., F. Haavisto, and V. Jormalainen. 2017. Is the future as tasty as the present? Elevated temperature and hyposalinity affect the quality of *Fucus* (Phaeophyceae , Fucales) as food for the isopod *Idotea balthica*. Mar. Biol. **164**: 207. doi:10.1007/s00227-017-3237-3

Rothäusler, E., J. Sjöroos, K. Heye, V. Jormalainen, and C. Hurd. 2016. Genetic variation in photosynthetic performance and tolerance to osmotic stress (desiccation, freezing, hyposalinity) in the rocky littoral foundation species *Fucus vesiculosus* (Fucales, Phaeophyceae). J. Phycol. **52**: 877–887. doi:10.1111/jpy.12455

Röthausler, E., Corell H., Jormalainen V. 2015. Abundance and dispersal trajectories of floating *Fucus vesiculosus* in the Northern Baltic Sea. Limnol. Oceanogr. 60: 2173-2184

Russell, G. 1987. Spatial and environmental components of evolutionary change: interactive effects of salinity and temperature on *Fucus vesiculosus* as an example. Helgoländer Meeresuntersuchungen **41**: 371–376. doi:10.1007/BF02366199

Ruuskanen, A., S. Bäck, and T. Reitalu. 1999. A comparison of two cartographic exposure methods using *Fucus vesiculosus* as an indicator. Mar. Biol. **134**: 139–145. doi:10.1007/s002270050532

Ruuskanen, A., and S. Bäck. 2002. Morphological changes in submerged *Fucus vesiculosus* (L) (Phaeophyta) along the salinity gradient of the River Keret estuary, Russia. Sarsia **87**: 185–188. doi:10.1080/003648202320205265

Saada, G., K. R. Nicastro, R. Jacinto, C. D. McQuaid, E. A. Serrão, G. A. Pearson, G. I. Zardi, and D. Schoeman. 2016. Taking the heat: distinct vulnerability to thermal stress of central and threatened peripheral lineages of a marine macroalga. Divers. Distrib. **22**: 1060–1068. doi:10.1111/ddi.12474

Sanford, E., and M. W. Kelly. 2011. Local Adaptation in Marine Invertebrates. Annu. Rev. Mar. Sci **3**: 509–537. doi:10.1146/annurev-marine-120709-142756

SAS Institute Inc., 2013. SAS/STAT® 9.2 User's Guide. SAS Institute Inc., Cary.

Serrão E.A., L. Kautsky, T. Lifvergren and S. H. Brawley. 1996a. Gamete dispersal and pre-recruitment mortality in Baltic *Fucus vesiculosus*. Phycologia Suppl. **36**: 101–102

Serrão, E. A., L. Kautsky, and S. H. Brawley. 1996b. Distributional success of the marine seaweed *Fucus vesiculosus* L . in the brackish Baltic Sea correlates with osmotic capabilities of Baltic gametes Oecologia. **107**: 1–12.

Serrão, E. A., S. H. Brawley, J. Hedman, L. Kautsky, and G. Samuelson. 1999. Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. J. Phycol. **35**: 254–269.

Serrão, E. A., L. Kautsky, and S. H. Brawley. 2016. Distributional Success of the Marine Seaweed *Fucus vesiculosus* L . in the Brackish Baltic Sea Correlates with Osmotic Capabilities of Baltic Gametes Published by : Springer in cooperation with International Associatio. **107**: 1–12.

Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. Proceedings of the National Academy of Sciences USA 105:8974–8979.

Steen, H., and J. Rueness. 2004. Comparison of survival and growth in germlings of six fucoid species (Fucales, Phaeophyceae) at two different temperature and nutrient levels. Sarsia **89**: 175–183. doi:10.1080/00364820410005818

Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation

Contemporary evolution meets conservation biology. TRENDS Ecol. Evol. **18**: 94–101. doi:10.1016/S0169-5347(02)00044-7

Sukenik, A., J. Bennett, and P. Falkowski. 1987. Light-saturated photosynthesis - Limitation by electron transport or carbon fixation? BBA - Bioenerg. **891**: 205–215. doi:10.1016/0005-2728(87)90216-7

Takolander, A., M. Cabeza,E. Leskinen., 2017a. Climate change can cause complex responses in Baltic Sea macroalgae: a systematic review. J. Sea Res. **123**:16–29.

Takolander, A., E. Leskinen, and M. Cabeza. 2017b. Synergistic effects of extreme temperature and low salinity on foundational macroalga *Fucus vesiculosus* in the northern Baltic Sea. J. Exp. Mar. Bio. Ecol. **495**: 110–118. doi:10.1016/j.jembe.2017.07.001

Tatarenkov, A., R. B. Jonsson, L. Kautsky, and K. Johannesson. 2007. Genetic structure in populations of *Fucus vesiculosus* (Phaeophyceae) over spatial scales from 10 m to 800 km. J. Phycol. **43**: 675–685. doi:10.1111/j.1529-8817.2007.00369.x

Tropin, I. V., N. V. Radzinskaya, and G. M. Voskoboinikov. 2003. The influence of salinity on the rate of dark respiration and structure of the cells of brown algae thalli from the barents sea littoral. Biol. Bull. **30**: 40–47. doi:10.1023/A:1022063426675

Valladares, F., S. Matesanz, M. B. Araujo, L. Balaguer, M. Benito-Garzóon, W. Cornwell, E. Gianoli, M. van Kleunen, D.E. Naya, A.B. Nicotra, H. Poorter, M. A. Zavala. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol. Lett. **17**: 1351–1364. doi:10.1111/ele.12348

Vasseur, D. A., J. P. Delong, B. Gilbert, H.S. Greig, C.D.G. Harley, K.S. McCann, V. Savage, T.D. Tunney, M.I.O Connor. 2014. Increased temperature variation poses a greater risk to species than climate warming. Proc. R. Soc. B 20132612.

Wahl, M., V. Jormalainen, B.K. Eriksson, J.A. Coyer, M. Molis, H. Schubert, M. Dethier, R. Karez, I. Kruse, M. Lenz, G. Pearson, S, Rohde, S. A. Wikström, and J.L. Olsen. 2011 Chapter Two - Stress

Ecology in *Fucus*: Abiotic, Biotic and Genetic Interactions. Michael, L. (ed.) Advances in Marine Biology, Academic Press, pp. 37- 105.

Weinberger, F., S. Rohde, Y. Oschmann, L. Shahnaz, S. Dobretsov, and M. Wahl. 2011. Effects of limitation stress and of disruptive stress on induced antigrazing defense in the bladder wrack *Fucus vesiculosus*. Mar. Ecol. Prog. Ser. **427**: 83–94. doi:10.3354/meps09044

Wernberg, T., D. A. Smale, and M. S. Thomsen. 2012. A decade of climate change experiments on marine organisms: Procedures, patterns and problems. Glob. Chang. Biol. **18**: 1491–1498. doi:10.1111/j.1365-2486.2012.02656.x

Werner, F. J., A. Graiff, and B. Matthiessen. 2015. Temperature effects on seaweed-sustaining top-down control vary with season. Oecologia **180**: 889–901. doi:10.1007/s00442-015-3489-x

Werner, F. J., A. Graiff, and B. Matthiessen. 2016. Even moderate nutrient enrichment negatively adds up to global climate change effects on a habitat-forming seaweed system. Limnol. Oceanogr. **61**: 1891–1899. doi:10.1002/lno.10342

Wikström, S. A., and L. Kautsky. 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuar. Coast. Shelf Sci. **72**: 168–176. doi:10.1016/j.ecss.2006.10.009

Wilson, K. L., L. M. Kay, A. L. Schmidt, and H. K. Lotze. 2015. Effects of increasing water temperatures on survival and growth of ecologically and economically important seaweeds in Atlantic Canada: implications for climate change. Mar. Biol. **162**: 2431–2444. doi:10.1007/s00227-015-2769-7

Wrange, A.-L., C. André, T. Lundh, U. Lind, A. Blomberg, P. J. Jonsson, and J. N. Havenhand. 2014. Importance of plasticity and local adaptation for coping with changing salinity in coastal areas: a test case with barnacles in the Baltic Sea. BMC Evol. Biol. **14**: 156. doi:10.1186/1471-2148-14-156

Table 1. Average summer sea surface temperature (SST) and salinity (SSS) for current and future conditions within the three regions. Current conditions were calculated by averaging the monthly means from June to August obtained from the Baltic Nest Institute (http://www.balticnest.org). The future expected conditions were set according to the model of Meier et al. (2012).

Region	Current		Future	
	SSS (PSU)	SST (C°)	SSS (PSU)	SST (C°)
Entrance	22	18	17	21
Central	7	16	4	20
Marginal	5	14	2.5	16

Table 2. Seawater surface salinity (SSS, Feistel et al. 2010) and seawater surface temperature (SST, Siegel et al. 2008) (mean ± SD) for the summer period (June to August). Salinity and temperature means for each site were averaged for observations from open water and coastal areas for the regions targeted by our sampling. The number of individuals sampled for each population is corrected after the genotyping.

Region	Population	Coordinates (N, E)	SSS (PSU)	SST (°C)	# Individuals
Entrance	B	56°31’, 10°38’	23±11	17±3	25
Entrance	G	57°07’, 12°12’	24±7	17±3	25
Entrance	S	56°19’, 12°45’	24±7	17±3	25
Central	O	56°11’, 16°23’	7.3±2.5	16±4	25
Central	V	57°41’, 16°43’	6.8±1.5	17±4	25
Central	K	55°41’, 14°13’	7.7±2.5	16±3	25
Marginal	H	61°41’, 17°31’	5±3	13±3	21
Marginal	R	61°08, 21°18’	5.5±3	13±3	23
Marginal	P	60°08’, 22°17’	6.3±3.5	15±2	25

Table 3. Results from general linear mixed models that tested the fixed effects of climate change and the random effects of population, individual, and aquarium on biomass gain for each region. Initial size was used as a covariate in the analyses.

Source of variation	**Entrance**			**Central**			**Marginal**		
	ndf, ddf	**F**	**P**	**ndf, ddf**	**F**	**P**	**ndf, ddf**	**F**	**P**
Fixed Factors									
Cl. change	1, 2.82	3.1	0.18	1, 43	42.8	<0.001	1, 4.4	15.2	<0.05
In. size	1, 472	113	<0.001	1, 311	0.19	0.67	1, 321	12.9	<0.001
In. size × Cl. Change									
		χ^2	**P**		**χ^2**	**P**		**χ^2**	**P**
Random Factors									
Population		0.52	0.24		0.86	0.35		-	1
Individual		18.8	<0.001		0.01	0.91		40.6	<0.001
Population × Cl. Change		5.12	<0.05		-	1		18.9	<0.001
Individual × Cl. Change		0.47	0.25		8.24	<0.01		-	1
Aquarium		7.71	<0.05		-	1		0.5	0.48

Table 4. Generalised mixed model statistics for the probability of survival at 140 days, displayed separately by region.

Source of variation	**Entrance**			**Central**			**Marginal**		
	ndf, ddf	**F**	**P**	**ndf, ddf**	**F**	**P**	**ndf, ddf**	**F**	**P**
Fixed Factors									
Cl. change	1, 2	0.14	0.74	1, 2	62.4	<0.05	1, 2	90.7	<0.05
		χ^2	**P**		χ^2	**P**		χ^2	**P**
Random Factors									
Population		1.31	0.25		1.85	0.16		0.55	0.46
Individual		4.83	<0.05		60.7	<0.001		0.74	0.4
Population × Cl. Change		-	1		1.18	0.27		3.40	<0.01
Individual × Cl. Change		-	1		-	1		31.9	<0.001
Aquarium		-	1		-	1		-	1

Figure 1. Location of *Fucus* sampling sites in the marginal (black dots: H, R, and P), central (grey dots: V, O, and K) and entrance (white dots: S, B, and G) regions. Summertime (average values from June to August) sea surface salinities and temperatures for each Baltic region are indicated as average values for years 1990-2008, obtained from Siegel et al. (2008). Different letters denote the different populations sampled within a region.

Figure 2. Schematic illustration of the experimental design. Fig. 2a. Schematic of the experimental design, detail about pseudo-replication of each genotype in multiple ramets. Fig. 2b shows how we distributed each population in the aquarium racks.

Figure 3. Growth rate (g WW / 140 d, mean ± SE, adjusted for the average initial size of algae) for *Fucus* populations in current and future conditions displayed by region. The biomass gain of each population is based on the individual estimate of each survivor. The number of individuals was N=25 for every population except for H (N=21) and R (N=23) The identity of each population is indicated on the x-axis. Asterisks above denote the degree of significance indicated by the general linear model (*$p < 0.05$, **$p<0.01$, ***$p<0.001$)

Figure 4. Individual estimates for growth rate (g WW/ 140d) in current and future conditions for the central populations. Lines connect the average of each individual (N=35) in the two conditions. The individual average was calculated averaging 1to 4 ramets for each condition.

Figure 5. Survival estimates (mean ± SE) for *Fucus* populations after 140 days in current and future conditions, separately by region. The survival of each population is based on the individual estimate, obtained from the average of N = 4 ramets for each condition. The number of individuals was N= 25 for every population except for H (N=21) and R (N=23).

Figure 1

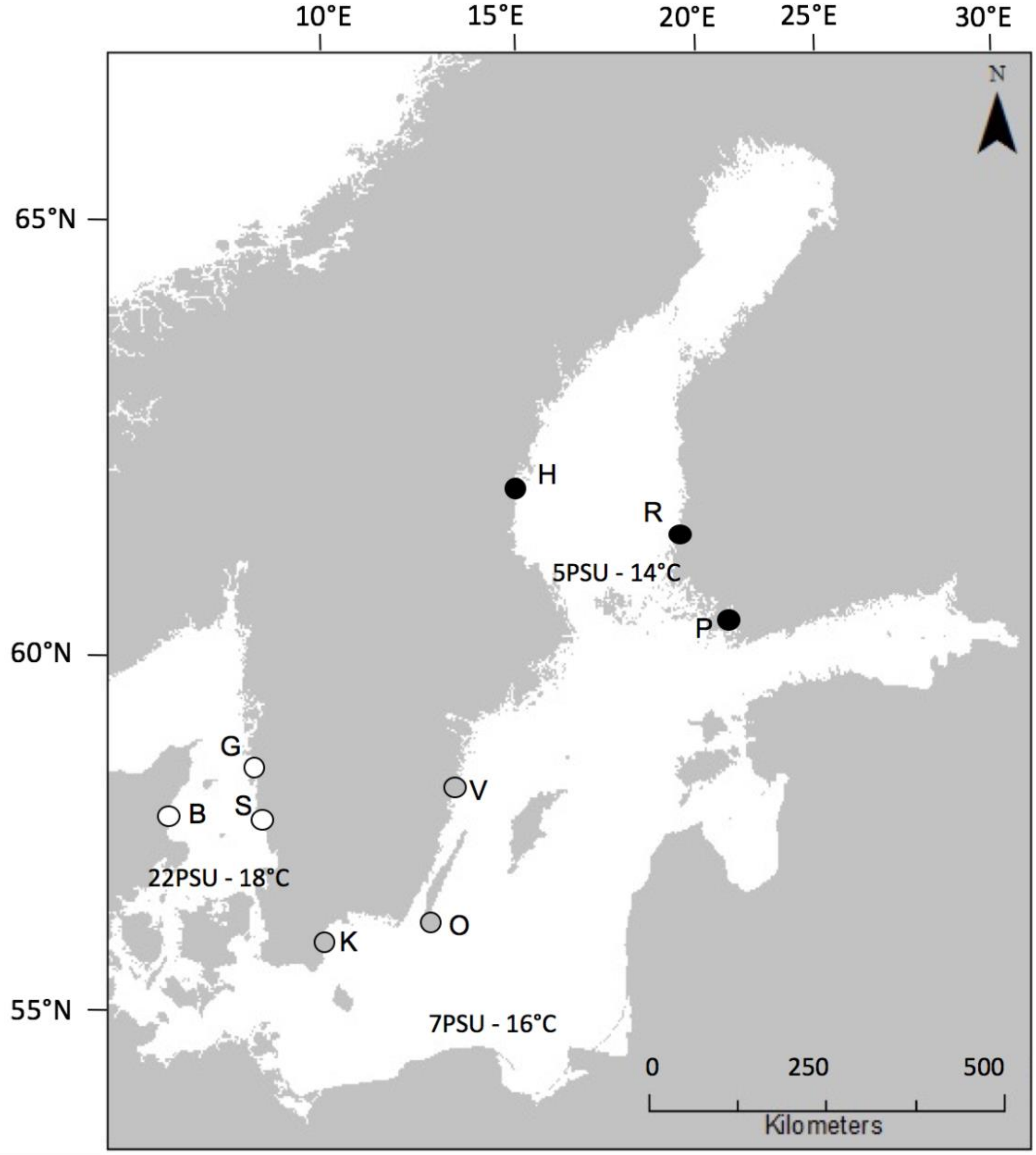

10°E
15°E
20°E
25°E
30°E
65°N
60°N
55°N
N
H
R
P
5PSU - 14°C
G
S
B
V
22PSU - 18°C
O
K
7PSU - 16°C
0
250
500
Kilometers

Figure 2

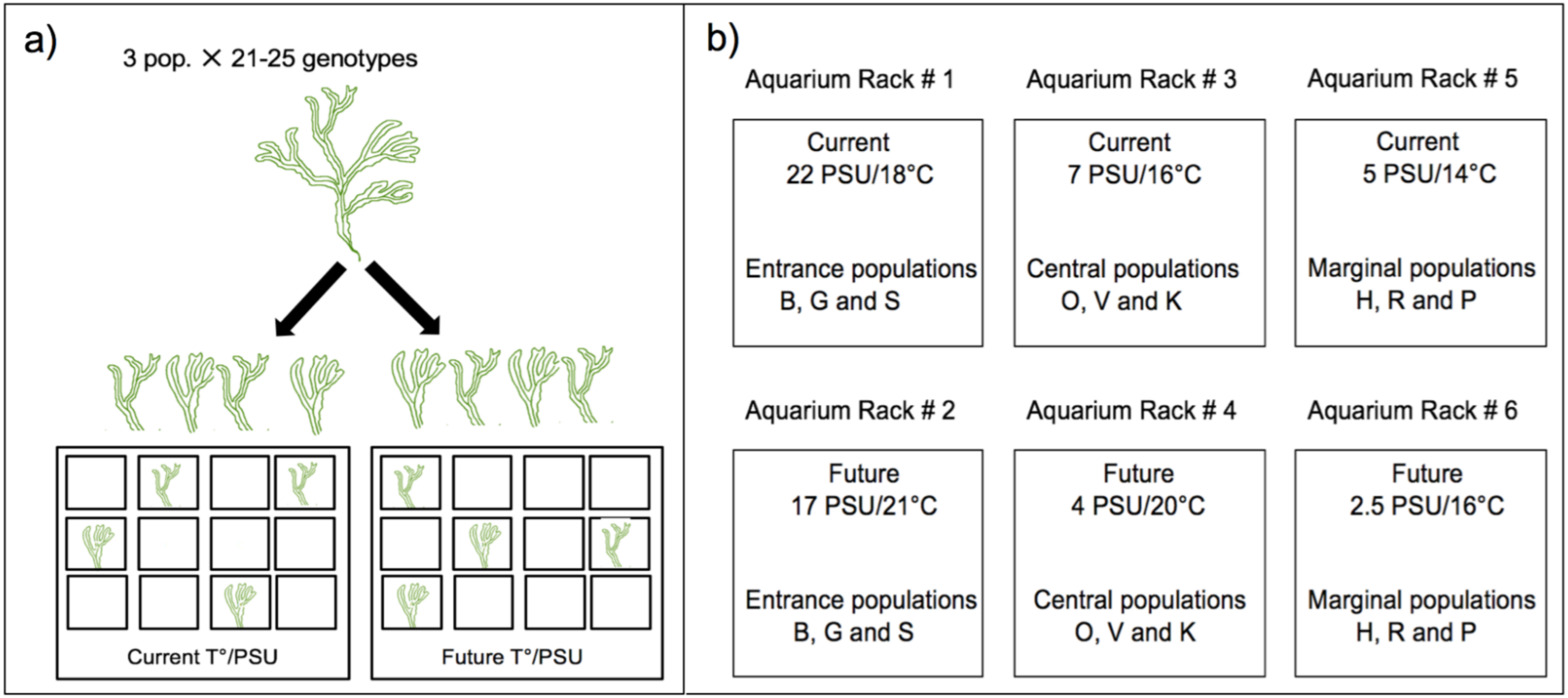

a)
3 pop. × 21-25 genotypes
Current T°/PSU
Future T°/PSU
b)
Aquarium Rack # 1
Current
22 PSU/18°C
Entrance populations
B, G and S
Aquarium Rack # 3
Current
7 PSU/16°C
Central populations
O, V and K
Aquarium Rack # 5
Current
5 PSU/14°C
Marginal populations
H, R and P
Aquarium Rack # 2
Future
17 PSU/21°C
Entrance populations
B, G and S
Aquarium Rack # 4
Future
4 PSU/20°C
Central populations
O, V and K
Aquarium Rack # 6
Future
2.5 PSU/16°C
Marginal populations
H, R and P

Figure 3

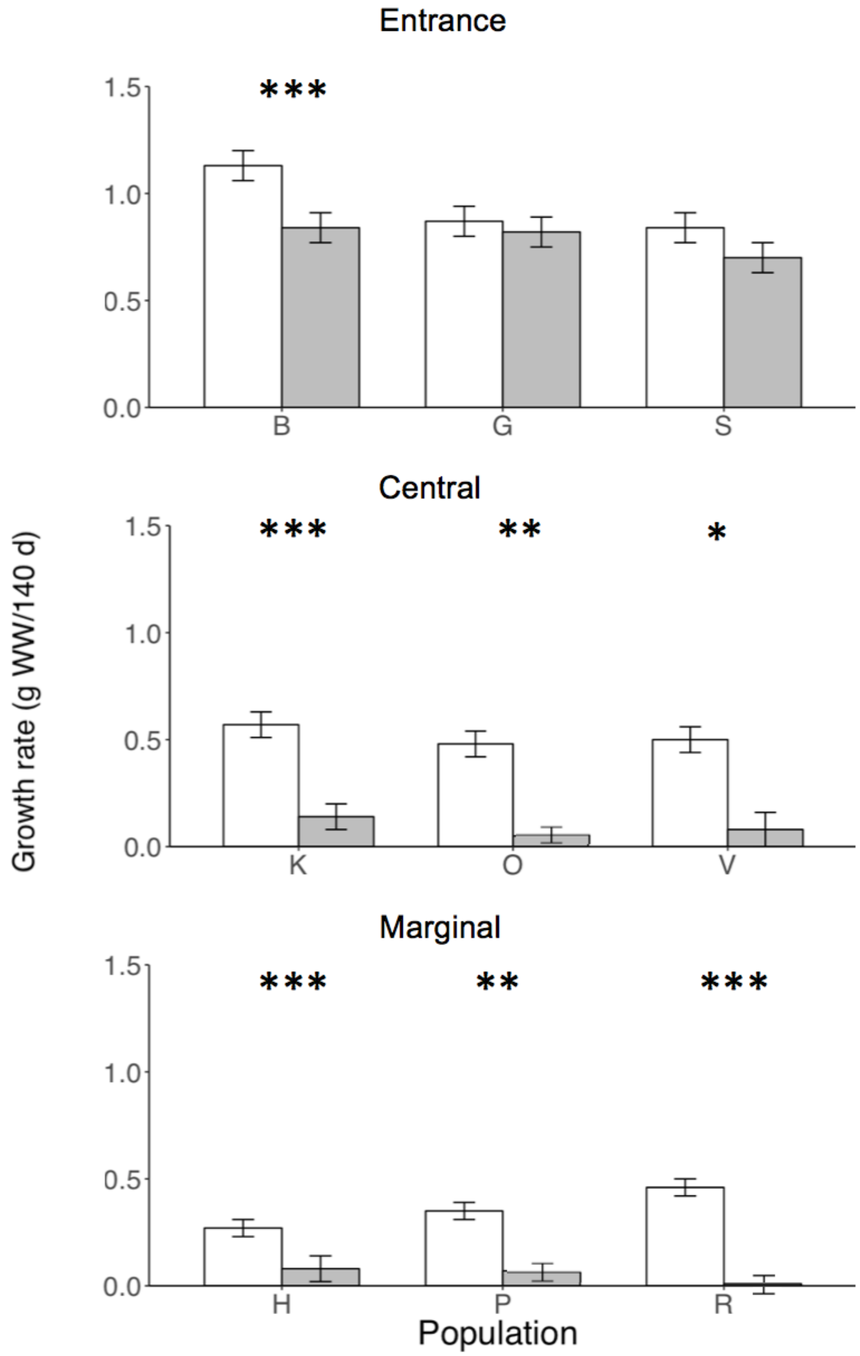

Entrance
Central
Marginal
Growth rate (g WW/140 d)
Population
1.5
1.0
0.5
0.0
***
**
*
B
G
S
K
O
V
H
P
R

Figure 4

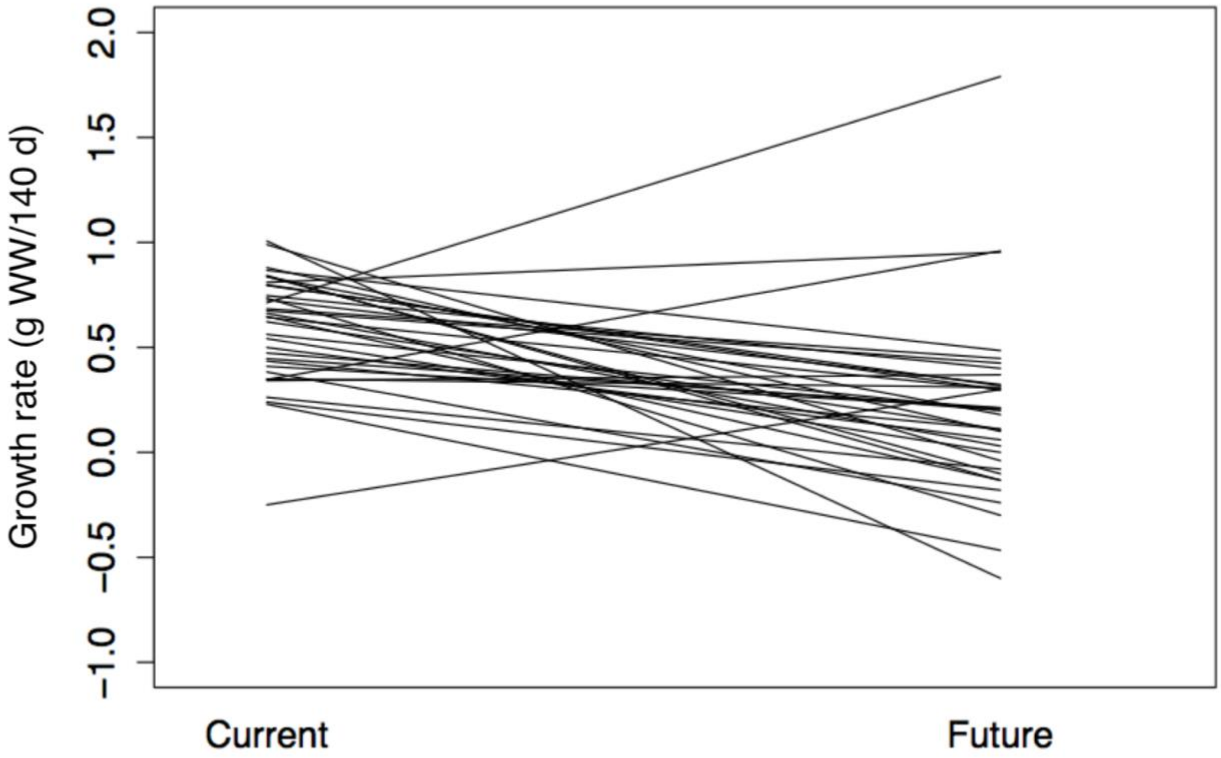
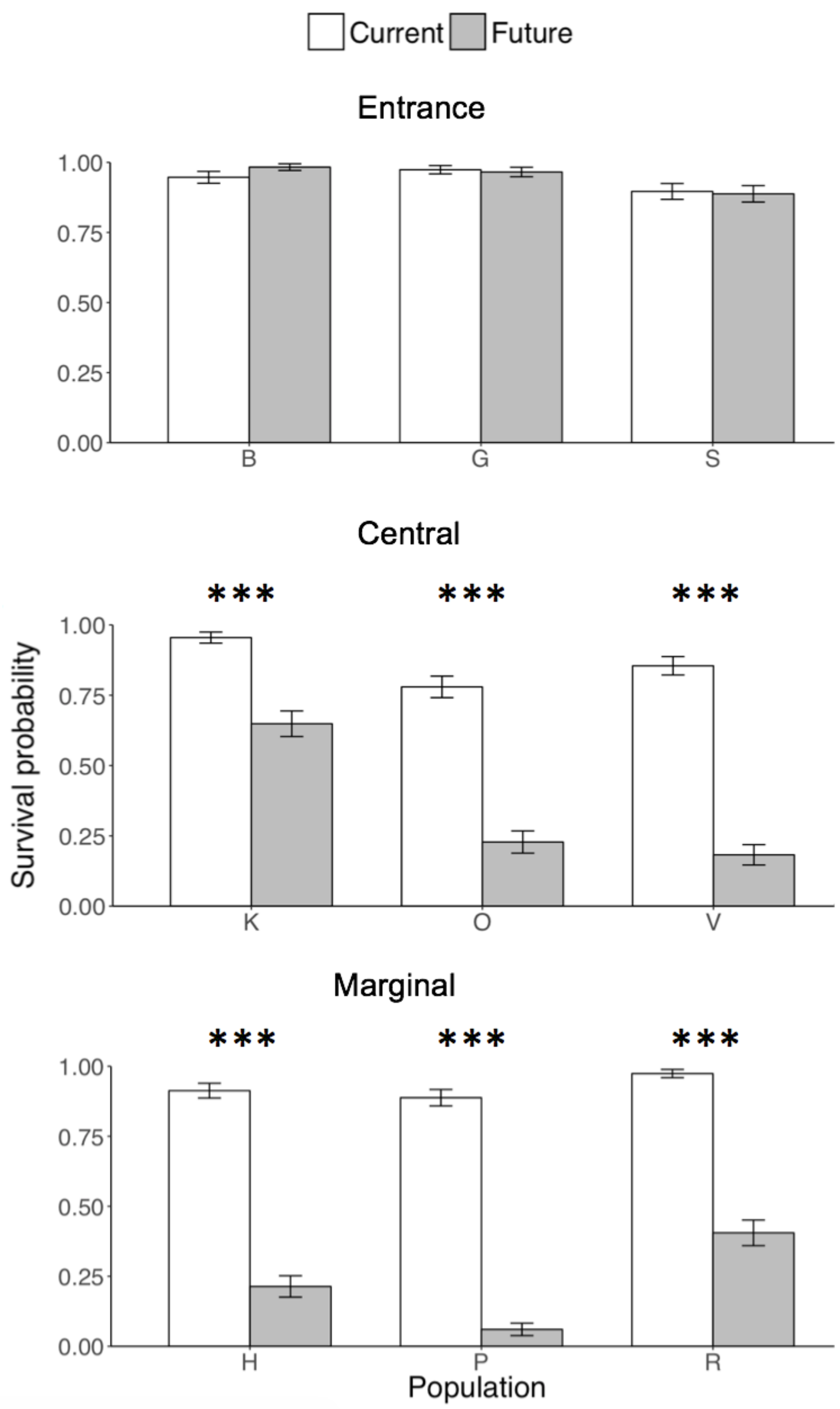


Figure 5


Current
Future
Entrance
1.00
0.75
0.50
0.25
0.00
B
G
S
Central
***
***
***
K
O
V
Marginal
***
***
***
H
P
R
Survival probability
Population