VARIATIONS IN TOLERANCE TO CLIMATE CHANGE IN A KEY LITTORAL HERBIVORE

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Abstract

Changes in global climate patterns are affecting marine ecosystems, challenging species' environmental tolerances, and driving shifts in their distributions. In the Baltic Sea, a brackish water body with low biodiversity, the isopod *Idotea balthica* is a key herbivore species that has a strong top-down effect on habitat-forming macrophytes. Our aim is to understand how the predicted future combination of hyposalinity and warming will affect the survival of this mesograzer throughout the Baltic Sea. By conducting a manipulative aquarium experiment, we simulated future conditions and measured the survival, at different spatial scales, of replicated populations from the entrance, central, and marginal Baltic Sea regions. Overall, the survival rate was strongly affected by the predicted future combination of hyposalinity and warming, but the intensity of the impact varied both among and within regions. Populations from the marginal Baltic Sea responded negatively to climate change. Populations within the entrance varied in their survival responses, with the geographic variation suggesting the existence of spatially distributed genetic variation in tolerance to climate change. In summary, the future combination of hyposalinity and warming is likely to induce a southward shift in the distribution of *I. balthica* in the northeast marginal region of the Baltic Sea. However, the geographic variation in tolerance shown by the entrance populations indicates that, for this Baltic region, the species may contain the potential for future adaptive responses in tolerance to climate change.

Keywords: Global warming, tolerance, Isopoda, desalination, *Fucus*, mesograzer.

INTRODUCTION

Climate change is rapidly modifying marine ecosystems, with impacts already indisputable all over the planet (Dunn et al. 2005, Harley et al. 2006, Hoegh-Guldberg et al. 2007, Poloczanska et al. 2007, Przeslawski et al. 2008, Brierley & Kingsford 2009, Vergés et al. 2014). Changes in many coastal marine areas are projected to include rising surface water temperature and decreasing salinity due to increased precipitation and freshwater run-off (Antonov 2002, Boyer et al. 2005, Meier & Eilola 2011). Ocean warming is already affecting marine ecosystems by provoking the decreased abundance or local extinction of a high number of marine species worldwide (Coma et al. 2009, Harvell et al. 1999, 2004, Knight et al. 2017) as well as shifts in the geographical distribution of species (Hoffman et al. 2011). Two of the primary drivers of these shifts are the reduction in benthic oxygen content in the coastal zones (Altieri and Gedan, 2015) and the modification of species interactions (Helmuth et al. 2006, Harvey et al. 2014, Lenoir and Svenning 2015, Werner et al. 2015 and literature therein). In addition to temperature, seawater salinity is one of the main abiotic factors influencing the survival, growth rate, and reproduction of marine organisms (Qiu and Qian 1999, Normant and Lamprecht 2006, Łapucki and Normant 2008, Torres et al. 2011, Wrange et al. 2014). Due to the all-encompassing nature of climate change, seawater temperature and salinity will change in concert, and synergistic or antagonistic interactions may arise. Because of this, it is important to focus on the combined effects of these stressors (Crain et al. 2008), which have thus far been largely ignored in marine climate change studies (Wernberg et al. 2012).

Climate-driven environmental changes are likely to induce shifts in species' distributional ranges and act as selective pressures for organismal traits. A species facing an environmental change may either tolerate it and persist or go extinct locally (Hoffmann et al. 2011). The short-term persistence of a species during environmental change is therefore determined by its tolerance: the population persists if the experienced environmental change is within its tolerance range. Long-term persistence can be attained through natural selection for increased tolerance, and adaptive evolution occurs if the species contains enough genetic variation in a trait responsible for tolerance (Pauls et al. 2013, Bell and Gonzalez 2009). Hence, to predict the future persistence and distribution of a species under climate change conditions, information about both the species' tolerance and its underlying genetic variation is necessary.

Within their distributional range, species typically show a population structure in which the local populations are isolated from each other to a varying degree. Thus, tolerance and its genetic variation may differ among local populations, which further complicates predictions of the species' response to environmental change (Valladares et al. 2014, Saada et al. 2016). Two different scenarios of population variations in the local environment can be envisioned. First, selective pressures may vary locally among populations (Kawecki & Ebert 2004), and with the passing of time, this process results in populations that are locally adapted and unique in their tolerance traits (Sanford and Kelly 2011, Lamichhaney et al. 2012, Wrange et al. 2014, Defaveri 2014, D'Angelo et al. 2015, Muir et al. 2016). Second, instead of genetic differentiation due to local adaptation, phenotypic plasticity of the tolerance traits may evolve, leading to wide ranges in tolerance to the varying environmental factors. In this case, different local populations are expected to show similarly broad tolerances (Crispo, 2008).

The Baltic Sea provides an excellent model with which to study the combined effects of climate-change-related stressors on populations along an environmental gradient. Biodiversity in the Baltic Sea is strongly shaped by the young age of the sea and pronounced gradients of decreasing salinity and temperature from the North Sea entrance towards the northern and eastern margins (Lass et al. 2008). As climate change progresses in the Baltic

Sea catchment, warming and desalination are predicted to proceed in concert (Meier et al. 2012). While the genetic diversity of Baltic Sea organisms is generally lower than that of their counterparts in the Atlantic, the genetic composition of populations does change along the gradient (Johannesson & Andre 2006), which is expected to reinforce isolation and population differentiation as well as promote local adaptations (Johannesson et al. 2011). As the ability to cope with thermal and osmotic conditions limits the distributions of marine communities (Bonsdorff et al. 2015), Baltic Sea biodiversity is generally very low and ecosystem functions can be dependent on only a few key species (Leidenberger et al. 2012).

One such key species is the isopod *Idotea balthica* (Pallas, 1772), which is one of the predominant herbivores in Baltic Sea littoral ecosystems. Its distribution covers the whole Baltic Sea, and extends to the northern and eastern margins where the low salinity (2.7 PSU) sets the distributional range of this species (Leidenberger et al. 2012). This mesograzer has strong top-down effects, both negative and positive, on populations of habitat-forming macrophytes such as the bladder wrack *Fucus vesiculosus* (Nilsson et al. 2004). Herbivory by this isopod may sometimes remove 60-70% of *F. vesiculosus* biomass (Jormalainen and Ramsay 2009, Haavisto & Jormalainen 2014), and in particular, this herbivory was proposed to be responsible for the decline in *F. vesiculosus* populations off the Finnish coast in the 1970s (Kangas et al. 1982, Haahtela 1984). Furthermore, it has been suggested that herbivory by *I. balthica* limits the southern distributional range of the endemic bladder wrack species *F. radicans* (Gunnarsson & Berglund 2012). On the other hand, *I. balthica* also feeds on filamentous algae (Ravanko 1969, Goecker and Kåll 2003, Orav-Kotta and Kotta 2004), and this may facilitate the growth of *F. vesiculosus* by limiting competition and epibiotism. This isopod species is, thus, a key littoral herbivore capable of affecting the community composition of primary producers and also represents an important link for the transfer of energy and matter in the littoral food web.

Even though the lifespan of *I. balthica* is over one year (Salemaa, 1979) and it experiences the whole seasonality of the Baltic Sea, our knowledge concerning the biology of *I. balthica* in the winter time and its possible vertical migration is still poor (Wood et al. 2014). Temperature plays an important role for the biology of this species, since no moulting occurs during winter, and growth is delayed until spring, when the animals start to grow fast before the breeding season (Salemaa 1979). Climate models from Meier et al (2012) indicate that summer averaged surface seawater temperature will increase by 3-4°C in the Baltic Sea by the 2069-2099. Whether the future summer temperature be within the tolerance range of *I. balthica* is of primary importance for the persistence of this species.

In the present study, we tested for the first time the combined effect of expected future desalination and warming throughout the Baltic Sea on the survival of the herbivore *I. balthica*. Further, this research is focused on the among population variation in tolerance throughout the species' distributional range along the salinity gradient of the Baltic Sea. As a proxy for tolerance to future conditions, we used the difference in survival between current and future conditions. Because the natural salinity and temperature gradients are strong, and the effects of climate change are predicted to vary among different regions of the Baltic Sea, (Meier et al. 2012), we used current and predicted summer averaged conditions that were specific to each region. By testing the tolerance of several populations of this key herbivore to future conditions, we aim to understand if and how the tolerance to climate change vary along the species' distributional range. If such tolerance variation among population is found, this is likely an indication of standing genetic variation that could provide the raw material necessary for adaptation to future conditions.

MATERIALS AND METHODS

Sampling

We sampled a total of eight populations of *I. balthica* between the 6th of May and 25th of June 2015 from the three regions of the Baltic Sea: entrance, central, and marginal (Fig. 1, Table 1). We sampled three populations from the central and marginal regions, while for logistic reasons we were able to sample only two populations from the entrance region. From each population, we collected 60 females and 30 males. Sampling sites of populations were randomly chosen within each region to represent the distributional range of the species along the Baltic Sea salinity gradient. We kept at least 50-km distance between sampling sites in order to include sufficient geographic variability. The isopods were collected from *Fucus vesiculosus* at a depth of 1-3 metres by snorkelling. We placed the samples in polystyrene cooling boxes with seawater and several *F. vesiculosus* thalli as food and habitat, and transported them to the Archipelago Research Institute (University of Turku, Finland) at Seili (60° 14’ N, 21° 58’ E). The isopods from the marginal region were sampled on 6th-8th of May and were introduced into the aquarium racks on the 20th of May. Isopods from the central populations were sampled on 8th-12th of June and were introduced into the wracks on the 15th June. Entrance populations were sampled on 25th of June and went to the aquaria after two days. From the date of collection to the starting of the acclimation in the aquaria, we stored the isopods in their original seawater from the sampling sites in a cold room (15°C).

Experimental setup

The Baltic Sea has a strong salinity gradient, going from 25 PSU near its entrance to the Atlantic Sea to 7.5 PSU in the central region (the Baltic proper), to nearly freshwater in the northern and eastern margins (Feistel et al. 2010). In order to represent this variability, we exposed *I. balthica* to different climate conditions (current and future) using six independent aquarium racks; each rack represented either the current or predicted future conditions of a region (entrance, central, or marginal). The current conditions are calculated by averaging the mean conditions (temperature and salinity) for June, obtained from the Baltic Nest Institute http://www.balticnest.org/). The future expected a conditions are set according to the model by Meier and Eilola 2011, by averaging the June conditions for the years 2069-2099 (Table 2). We used multiple climate drivers simultaneously to better reflect the change due the climate change where salinity and temperature vary in concert. Each aquarium rack had closed water circulation: the seawater was pumped from one head tank at the bottom of the rack to three 54-litre tanks in which isopods were reared in individual containers. From there, water drained back into the head tank, where it was filtered through mechanical and biological filters and a protein skimmer and sterilised by UV rays. A heater/cooler unit situated on each head tank regulated water temperature. The different water salinities for current and future conditions were obtained by adding artificial sea salt to seawater or by diluting it with distilled water. Two LED lamps (Radion ™ XR30w Pro) per tank provided light with a 14:10 h day/night cycle. Peak light intensity was set to 600 μmol m^{-2} s^{-1} from 11:00 to 14:00, and light intensity slowly increased and decreased, respectively, before and after this period. Each tank was provided with a water pump to create water movement and help water oxygenation in the individual containers.

At the start of the experiment, we measured the length of each isopod and placed it individually inside a cylinder-shaped translucent plastic tube (length: 10 cm, diameter: 4 cm). For each population sampled, we exposed half of the isopods to the current conditions, and the other half to the future ones. We observed some cannibalism between the collection and the start of the experiment, therefore, the final number of isopods for some populations was lower (Table 4). Each container was closed at both ends with a mesh-net to allow water exchange. We slowly adjusted the salinity and temperature for the future-conditions treatment over the course of five days to avoid potential hyposalinity and heat shock for the isopods, with no mortality during this acclimation period. We fed isopods with both apical and basal thallus pieces from several individuals of *F. vesiculosus,* changing food in five-day periods. These pieces were randomly distributed *ad libitum* inside each tube as food and substrate. All food algae were freshly collected from a nearby stand (60° 14’ 38.0” N, 21° 59’ 10.2” E). Every two days, isopods were checked to record survival and remove dead individuals. Tanks were cleaned every five days to remove any accumulated faecal pellets. We ended the manipulation experiment after 55 d, at which point about 70% of isopods had died in future conditions.

Statistical analysis

Statistical analyses were conducted with the software SAS 9.4 (Allison, 2010). We performed a regression analysis of survival based on the Cox proportional hazards model (Kalbfleisch and Prentice, 1980) using the PHREG procedure (Rosenberg and Sirkus, 2011). This analysis computes the baseline survivor functions by using the Breslow estimate and performs a Wald Test to test the effect of covariates (climate change, region, population, and sex, and all interactions among these factors) on the survival rate. 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, Littel et al., 2006). The analysis was adjusted for right-censored data (i.e. when some individuals survive until the end of the study). Finally, we obtained the hazard ratio that relates the instantaneous probability of death in future conditions to that in current conditions for different levels of covariates from the Cox regression model, using the PHREG procedure.

RESULTS

Climate change conditions reduced the survival of *I. balthica* (Fig. 2, Table 3). The mean survival time for isopods in future conditions was about 35% lower (mean ± SE: 26.4 ± 2 d) than in the current conditions (40.7 ± 1.9 d). Notably, 96% of the deaths occurred before the midpoint of the experiment (Fig. 2). Survival also varied among regions, populations, and sexes (Table 3). Most interestingly, the responses to climate change varied among isopods that originated from different regions, from different populations within regions, and between sexes, as shown by the significant interactions of climate change with each of these three factors (Table 3).

Because the survival response of *I. balthica* to climate change varied among different regions (climate change-by-region interaction, Table 3, Fig. 2), we calculated the hazard ratios (high, > 1 values indicating increased mortality in future conditions) separately for each region. Isopods from the entrance region had a hazard ratio of 2.45, a value higher than in the central region but lower than in the marginal region (Table 4); these individuals survived on average 48 ± 1.5 d in current conditions and 39.1 ± 2.2 d in future conditions (Fig. 2a). Isopods from the central region exhibited the lowest hazard ratio of the three regions. However, this was caused by the poor survival of two out of three sampled populations in both climate conditions. The third population exhibited a relatively high hazard ratio (Fig. 2b, Table 4). The average value may poorly describe the central region due to the among-population variation in hazard ratios and must be considered with caution. We found the strongest impact of future conditions on survival in the marginal region. There, the hazard ratio was the highest of the three regions (Table 4), with the average survival time in future conditions being less than half of that in the current conditions (current: 43.5 ± 1.5d; future: 19.9 ± 1.6 d; Fig. 2c).

At a population level, the climate change treatment significantly affected the survival rate of five of the eight populations (Table 4, Fig. 3). Notably, populations from the entrance and central regions showed varying responses to future conditions. Among the two entrance populations, only one (M) suffered in the future climate conditions, while the survival of the other (He) did not vary significantly between climate treatments (Fig. 3, Table 4). This population also showed the longest mean survival time of all populations in the experiment (49 ± 1.75 d). From the central Baltic region, the survival of two of the three populations (V and T) did not differ among climate conditions. For the third population (K), the hazard ratio was significantly higher than one (Table 4), with 44% lower mean survival time in future conditions (current: 45.1 ± 2.6 d; future: 29.8 ± 3.2 d). Finally, the future climate conditions affected all the marginal populations: the hazard ratios of all populations were significantly higher than one, and were the three highest values found in this experiment among all populations (Table 4). The mean survival of these three populations (H, R, G) was 52, 49, and 62% lower in future than in current conditions, respectively (H: current: 46.6 ± 2.3 d; future: 22.3 ± 2.8 d; R: current: 44.5 ± 2.8 d; future: 22.8 ± 3 d; G: current: 39.7 ± 2.7 d; future: 15.2 ± 2.3 d).

Sex was a significant predictor of survival (Table 3; mean survival for females: 30.7 ± 0.95 d; males: 33.3 ± 1.5 d). Furthermore, the survival response to climate change differed between the sexes (Fig. 4, Tables 3 and 4): males showed higher tolerance to future conditions than females did (Fig. 4). The survival performance of the sexes was consistent among regions and populations (non-significant climate change-by-sex-by-region and climate change-by-sex-by-population interactions were removed from the final model as described in the methods).

DISCUSSION

This is the first study on the response to climate change of a marine mesograzer in which the combined effect of predicted changes in salinity and temperature in the Baltic Sea is measured. Salinity and temperature are expected to change in concert and the combined effect we detected with our experimental conditions incorporates the possible interactive effects of these changes. Our experiment showed that the combination of hyposalinity and warming will impair the survival of *I. balthica*. This suggests that the expected future conditions will negatively affect the abundance and potentially compromise the persistence of the species' populations. If so, this will weaken the littoral herbivory function in the Baltic Sea unless micro-evolutionary processes over generations will enhance its tolerance to decreasing salinity and increasing temperature.

A review by Leidenberger et al. (2012) suggested that the tolerance of *I. balthica* to a broad range of temperature and salinity conditions is the key to its successful colonisation and broad distribution in the Baltic Sea. The wide salinity tolerance for this species has been partially confirmed by experimental studies such as that of Wood et al. (2014), who showed how Baltic isopods can tolerate a long-term change in salinity from 5 PSU up to a maximum of 10 PSU and vice versa. Furthermore, Hørlyk et al. (1973) showed how a population originating from the entrance of the Baltic Sea could withstand a short-term decrease in seawater salinity from 25 to 7 PSU. However, the results from Hørlyk et al. (1973) also reported a limit to this herbivore's osmoregulatory capability: the isopods were not able to survive a sudden exposure to salinities below 7 PSU. In order to cope with fluctuations in water salinity, adult isopods can plastically adjust their osmotic regulation by altering the number of sodium-potassium pumps located in the pleopods, the respiratory organs (Postel et al. 2000). However, osmoregulation (i.e. the production of extra sodium-potassium pumps) is energetically expensive (Rivera-Ingraham et al. 2017). It may therefore depend on energy availability and involve reallocating resources away from other functions, potentially affecting the population growth rate through decreases in the somatic growth rate or reproduction. In addition, in order to be effective, the plastic osmoregulatory adjustment has to match the speed of the environmental change.

Temperature plays a crucial role in the metabolic activity of aquatic poikilotherms, thereby influencing growth and reproductive rates (Gillooly et al., 2001). For example, the oxygen consumption of *I. balthica* increases with water temperature (Salomon & Buchholz, 2000; Gutow et al 2016). However, the species is able to acclimate in a few hours even to relatively large, sudden changes in seawater temperature (from 5°C to 20°C and vice versa) and can adjust its oxygen consumption accordingly in order to reach a steady metabolic rate (Bulnheim, 1974). Furthermore, higher temperature also leads to higher grazing activity (Gutow et al. 2016). By affecting the ratio between ingestion and metabolic rate, higher temperatures may lead to lower somatic growth-rate (Strong & Daborn, 1980). If metabolic requirements due to increased temperature exceed what is gained by increased consumption, herbivore performance could be hampered (Pörtner, 2001). For example, heat waves have been found to weaken the immunocompetence of these isopods by lowering their phagocytosis activity by up to 50% (Roth et al. 2010). In addition, a minor increase of a few degrees in seawater temperature has been found to impair the survival of Baltic idoteids (Werner et al. 2015).

Climate related environmental changes are multifactorial by nature, and knowledge on the combined effects that includes all possible interactive effects is therefore needed for predicting organismal responses. Our approach does not allow interpretations of the nature of the combined effect (additive vs. interactive), but the combination is likely to involve synergistic effects, as has often been found in other mesograzers. For instance, in the isopods *Sphaeroma hookeri* and *S. rugicauda*, their otherwise robust ability to tolerate hyposalinity stress was reduced when they were also exposed to the natural temperature extremes usually occurring in their habitat (Jansen 1970). Our study species, *I. balthica*, is well-known for its ability to tolerate a wide range of salinity conditions, and the experimental temperatures we used were well within the natural temperature variation experienced by this isopod. We therefore suggest that the simple effects of hyposalinity or warming alone are not able to explain the decrease in survival that we observed, and that an additive or synergetic effect must be responsible. It is likely that the combined costs of acclimation to simultaneous abiotic stressors - i.e. increased energy expenditure for osmoregulation combined with the increased metabolic demands due to the elevated temperature - compromised the tolerance of *I. balthica* and led to its increased mortality.

The effects of climate change on the survival of *I. balthica* varied spatially among populations originating from different regions. The simulated future climate change conditions had a marked negative effect on the survival of one population from the entrance region out of the two sampled, suggesting among-population variation in tolerance for this region. The future conditions had the most severe negative impact on survival of isopods from the marginal region, where all populations responded similarly. In the central region, there was evidence of a negative response to future conditions in one population and of a negative trend in another, though to a smaller extent than in the marginal region. However, two of the central populations survived poorly in both the current and the future conditions. This can be due to the high sensitivity of these two populations towards transportation stress or laboratory conditions (e.g. enclosure into plastic tubes, low water movement, food quality), or alternatively, these populations may already be less tolerant even to the conditions we provided as the current environment. Due to this, the inference about variation in tolerance to future conditions among populations remains uncertain. Based on our results, we hypothesise that the future climate conditions will be particularly harsh for *I. balthica* in the marginal region, where migration from the neighbouring, more saline regions is unlikely to occur, as this would imply a movement of individuals towards a more extreme conditions. Therefore, we expect climate change to result in a southern shift in the northeast range edge of *I. balthica*. The central Baltic Sea populations will be negatively affected as well, but probably less so than the populations from the marginal region. Within the entrance region, some populations may decline as well, but this decline for the less tolerant populations may be compensated by migration from other highly tolerant ones from the same region.

The spatial variability found here in tolerance to climate change could have different explanations. One potential explanation is that populations differ geographically in their tolerance range to environmental stressors, i.e. that *I. balthica* populations have differentiated among the regions sampled here. Another possibility is that the tolerance of isopods does not differ along the Baltic Sea salinity gradient, but the fact that we manipulated the water conditions (both current and future) *ad hoc* for each region might explain the among-region differences in isopod performance i.e. the harshness of the expected future environment will differ among the regions. These two hypotheses are not mutually exclusive, but may both apply. An experiment in which multiple populations of isopods from different Baltic Sea regions were exposed reciprocally to a range of seawater conditions would give greater insights into the role of local differentiation and (potential) local adaptations in explaining differences in tolerance. Here, however, we did observe an indication of genetic differentiation in tolerance to climate change, possibly attributable to local adaptations, from the among-population variation in survival in future conditions. The variation in survival to future conditions among populations from the same region suggests that *I. balthica* has within-region genetic variation in tolerance, and it is likely that there is among-region variation in tolerance too. Since populations within the same region were exposed to the same water conditions, the difference in their survival responses is likely to arise from their intrinsic differences, e.g. different genetic backgrounds. Our results indicate that populations in the entrance region vary in their tolerance, with some populations being better able to tolerate the predicted climate change conditions. The low variability in response to future climate conditions exhibited by marginal populations may suggest that these populations have already gone through strong selection for tolerance to low salinity, which has eroded their variation in tolerance, thus homogenising their response.

Beyond 30 days of the experiment, none of the remaining isopods died under predicted future conditions. This may indicate that genetic variation for the traits related to tolerance to climate change also exists within populations. Since the water conditions used in this experiment are those expected for the years 2070-2099, and *I. balthica* only has a one-year life span, the Baltic Sea populations will have dozens of generations to evolve tolerance limits to adapt to new environmental conditions. The existing within-population genetic variation in tolerance to future desalination/warming, as indicated by our results, might provide the scaffold for a potential adaptive response to climate change.

The combination of desalination and warming decreased the survival of both sexes of *I. balthica*, but with different magnitudes: females were less tolerant of the future climate conditions. Sexes of *I. balthica* differ in habitat choice (Jormalainen & Tuomi 1989a), food consumption (Jormalainen et al. 2001), and assimilation efficiency (Jormalainen et al. 2005). As a general idea, Slatkin (1985) suggested that, owing to different fitness-maximising strategies, resource acquisition for energetic and nutritional demands differs between males and females. For instance, adjusted for their biomass, female *I. balthica* can graze more than twice the amount of algal biomass per day that males can (Salemaa 1987). Our experiment started during the reproductive period, when females invest energy in the development and maturation of ovaries (Jormalainen & Tuomi, 1989b); the differential allocations to reproductive resources by sex have made females more sensitive to stressors than males and led to their higher mortality. It is worth noting that in a species such as *I. balthica*, in which female receptivity to fertilisation is temporally limited and females engage in long incubation of broods, it is female availability that limits the population growth rate. Therefore, the higher sensitivity of females to climate change conditions could be particularly detrimental for populations.

CONCLUSIONS

Our study reveals how the impact of the predicted combination of desalination and warming can increase stress levels over the whole Baltic Sea area, with the result that the tolerance limits of a key littoral herbivore species are exceeded in some populations. The potential decline in herbivore function could then have cascading consequences on ecosystem function, for example through benefitting opportunistic filamentous algae. However, we found variation in tolerance among herbivore populations which may allow the evolution of adaptive responses to climate change and/or recolonization of the sites of extinct populations via migration from more tolerant ones, particularly in the entrance region. Predictive models of future changes in the Baltic Sea ecosystem should, therefore, incorporate among-population variation in tolerance and the potential for adaptive responses. Furthermore, models should take into account the fates of the currently interacting species, as well as potential novel interactions arising with the shifting distribution ranges of other species of the littoral communities.

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COMPLIANCE WITH ETHICAL STANDARD:

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Table 1 Sites, codes and coordinates of each of the sampled population of *I. balthica*.

Region	Site	Population code	Coordinates (N, E)
Entrance	Helsingborg	He	56°00’, 12°43’
Entrance	Malmö	M	61°05’, 21°23’
Central	Trolleboda	T	56°09’, 15°10’
Central	Kivik	K	56° 40’, 16°23’
Central	Västervik	V	57°47’, 16°43’
Marginal	Hanko	H	59°49’, 22°58’
Marginal	Grisslehamn	G	60°05’, 18°49’
Marginal	Rauma	R	61°05’, 21°18’

Table 2. The current and future average summer sea surface temperature (SST) and salinity conditions (SSS). The current conditions are calculated by averaging the mean conditions for June, obtained from the Baltic Nest Institute (http://www.balticnest.org/). The future expected a conditions are set according to the model by Meier and Eilola 2011.

	Current		Future	
Region	SSS (PSU)	SST (C°)	SSS (PSU)	SST (C°)
Entrance	12	14	7	17
Central	7	14	4	18
Marginal	5	11	2.5	14

Table 3. Statistical tests of the effects of Climate change, Sex, Region and Population on survival in *Idotea balthica*. All the fixed factors and their interactions with the Climate change are significant predictors of survival.

Fixed Effect	df	Wald χ^2	P
Climate change	1	9.8	<0.01
Region	2	12.4	<0.01
Population	5	46.4	<0.001
Sex	1	6.2	<0.05
Climate change × Region	2	6.9	<0.05
Climate change × Population	5	11.2	<0.05
Climate change × Sex	1	6.23	<0.05

Table 4. Hazard ratios from the Cox proportional hazards model showing the effects of the different climate conditions on *I. balthica* within each level of the factors Sex, Region and Population. Numbers in square brackets indicate the starting number of isopods used for each environmental condition in each category.

Description	Hazard ratios	95% CI	
Climate change:		lower	upper
Future vs. Current	2.49	2	3.1
Climate change × Region			
Fut. vs. Cur. for Entrance region [90]	2.45	1.37	4.37
Fut. vs. Cur. for Central region [120]	1.65	1.21	2.26
Fut. vs. Cur. for Marginal region [129]	4.64	3.22	6.67
Climate change × Population			
Entrance:			
Fut. vs. Cur. for He [45]	1.24	0.42	3.7
Fut. vs. Cur. for M [45]	3.49	1.74	7.03
Central:			
Fut. vs. Cur. for T [34]	1.03	0.65	1.61
Fut. vs. Cur. for K [46]	3.28	1.66	6.48
Fut. vs. Cur. for V [40]	1.66	0.92	2.98
Marginal:			
Fut. vs. Cur. for H [44]	5.99	3.03	11.85
Fut. vs. Cur. for G [40]	5.21	3	9.02
Fut. vs. Cur. for R [45]	3.78	1.91	7.52
Climate change × Sex			
Fut. vs. Cur. for males [105]	1.97	1.35	2.89
Fut. vs. Cur. for females [234]	2.78	2.13	3.62

Fig. 1. Location of the sampling sites in the Entrance (white dots: He and M), Central (grey dots: T, K and V) and Marginal (black dots: H, G and R) region.

Fig. 2. Survival curves with 95% of confidence intervals showing the effect of different climate conditions for each region separately (a = Entrance, b = Central, c = Marginal).

Fig. 3. Survival curves showing the difference in survival among climate change conditions displayed by population from Entrance (He, and M), Central (T, K and V) and Marginal (H, G and R) region following the decreasing salinity gradient of the Baltic Sea.

Fig. 4. Survival curves (mean ± SE) for female (a) and male (b) *I. balthica* in current and future seawater conditions.

Fig. 1

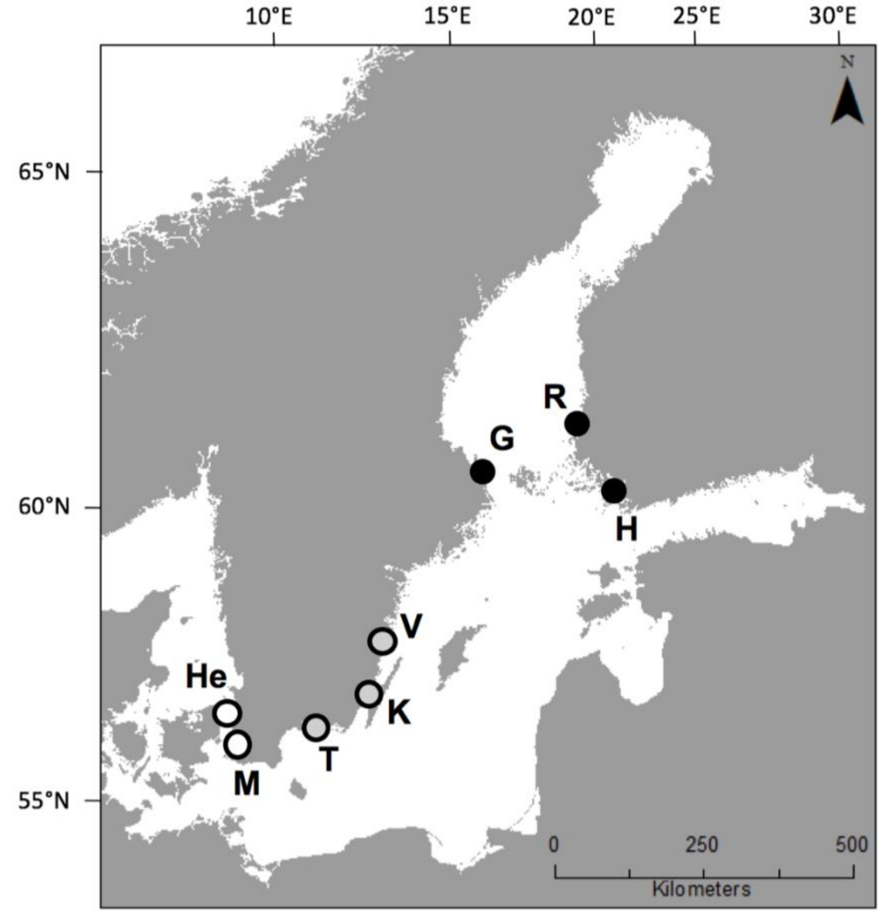

10°E
15°E
20°E
25°E
30°E
65°N
60°N
55°N
N
R
G
H
V
He
K
T
M
0
250
500
Kilometers

Fig. 2

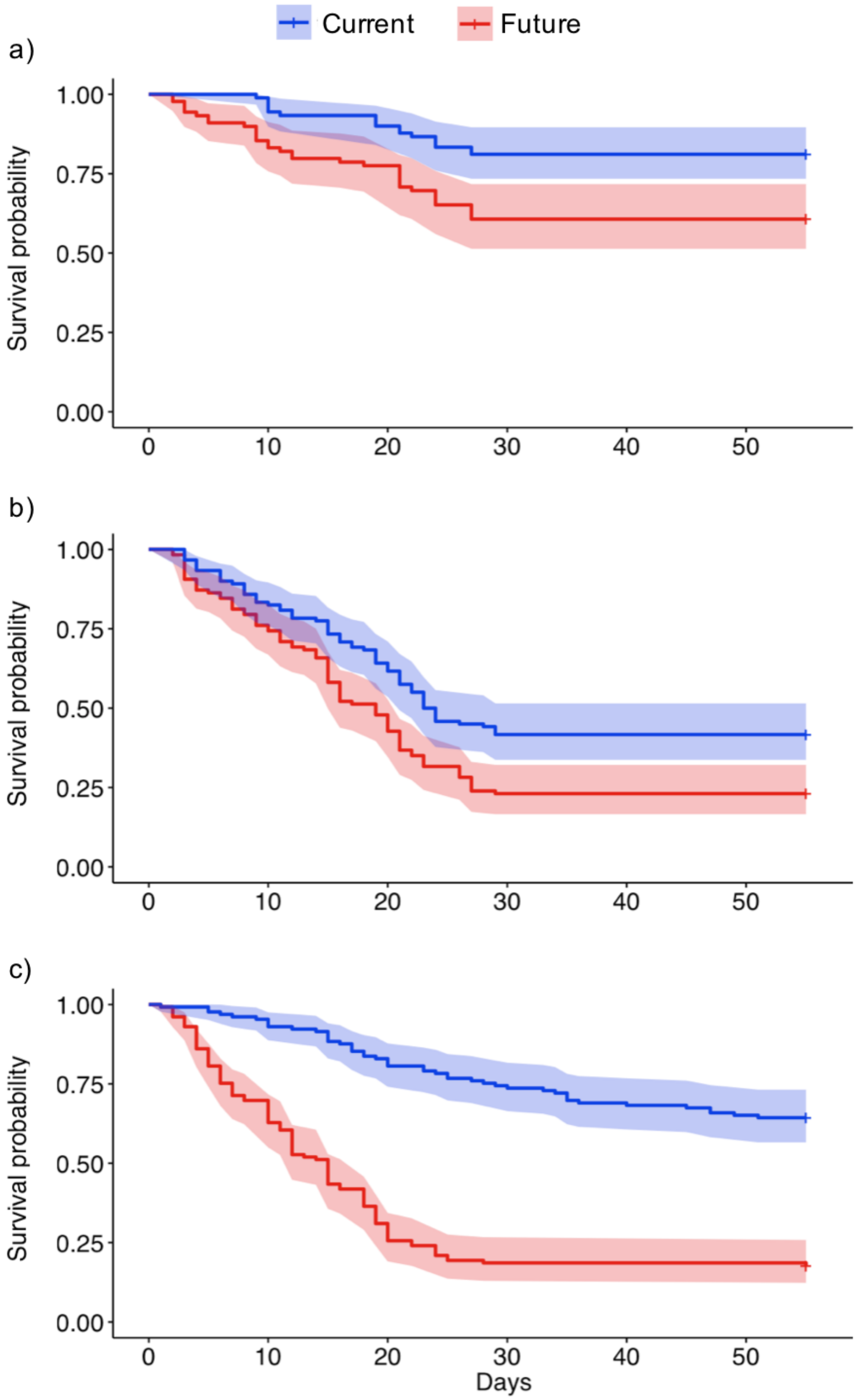
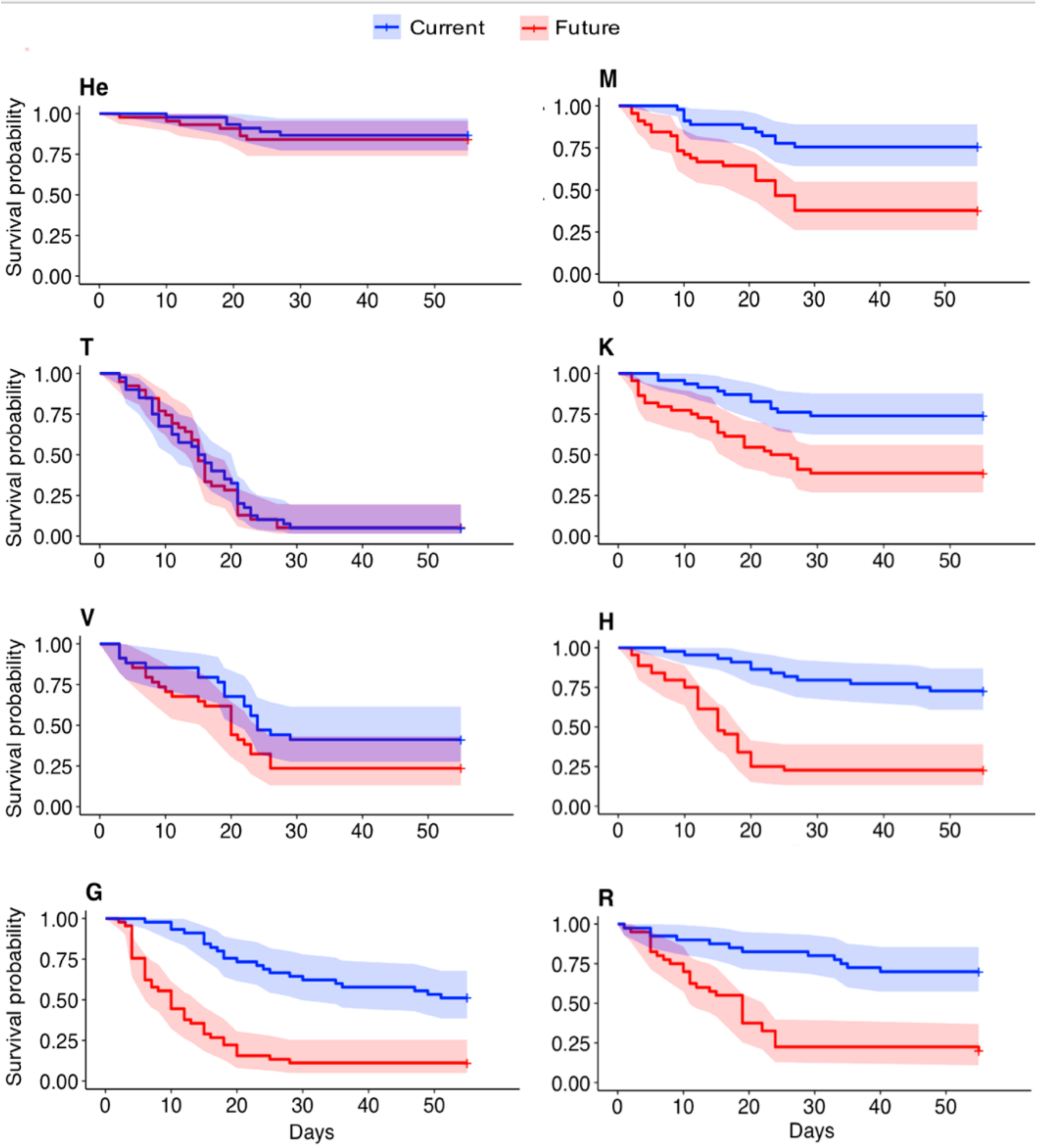

Current
Future
a)
1.00
0.75
0.50
0.25
0.00
Survival probability
0
10
20
30
40
50
b)
1.00
0.75
0.50
0.25
0.00
Survival probability
0
10
20
30
40
50
c)
1.00
0.75
0.50
0.25
0.00
Survival probability
0
10
20
30
40
50
Days

Fig. 3


Current
Future
He
M
T
K
V
H
G
R
Survival probability
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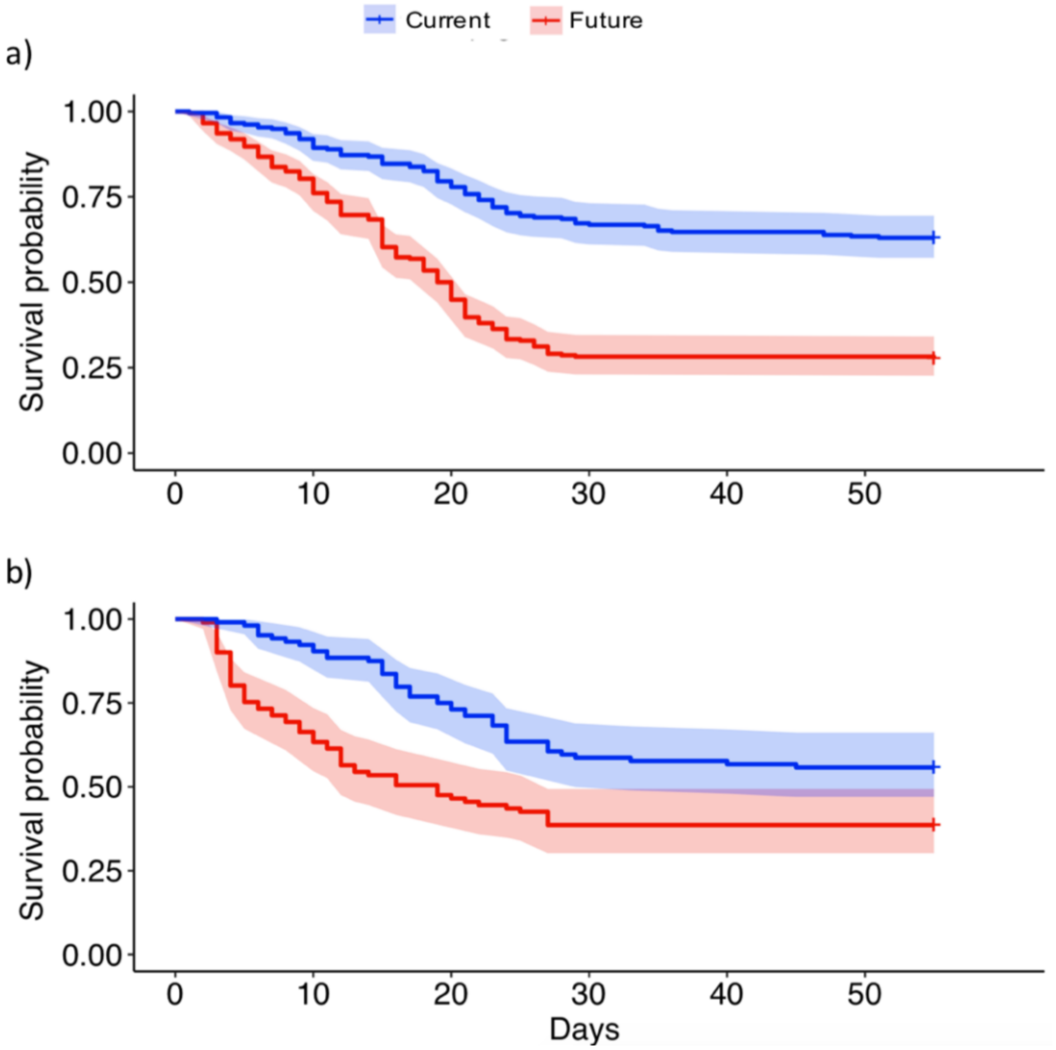
0.75
0.50
0.25
0.00
0
10
20
30
40
50
Days

Fig. 4


Current
Future
a)
Survival probability
1.00
0.75
0.50
0.25
0.00
0
10
20
30
40
50
b)
Survival probability
1.00
0.75
0.50
0.25
0.00
0
10
20
30
40
50
Days