The meaning of genetic diversity
on the example of the bladder wrack *Fucus vesiculosus* L.

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1 Summary

Over the last decades, *Fucus vesiculosus*, an ecologically important macroalga in the German Baltic Sea, has shown a massive retreat from the deeper zones of its former distribution presumably due to low light co-acting with other potential stressors such as high temperature, fouling, and grazing (Wahl et al 2011). In shallow water *F. vesiculosus* may be exposed to high water temperatures during summer seasons. Intensity and frequency of heat waves are expected to increase due to climate change which could potentially affect all fucoid life stages. Early life stage processes (fertilization, germination) are often considered particularly sensitive to stress. If the mortality caused by a first heat wave in a genetically diverse population selects for stress resistance, we would expect the survivors to be less sensitive to a second heat wave or possibly even to other stressors like feeding pressure.
In the present study, the mortality of early post-settlement stages of *F. vesiculosus* under thermal stress and the sensitivity of survived recruits against a proximate stressor (feeding pressure, second heat wave) were analysed by laboratory experiments. The mortality of early fucoid life stages at 25°C, compared to their mortality at 15°C was significantly higher. Regrettably, the ensuing assessment of feeding impact by *Idotea baltica* and *Hydrobia ulvae* on the surviving germlings could not be analysed since the two consumer species unexpectedly avoided feeding on the young stages of *F. vesiculosus*.
During the second thermal stress experiment fucoid offspring which was genetically preselected by high temperature (first heat wave: 25°C) differed not significantly in sensitivity from fucoid offspring without prior stress.

2 Backround

Global climate change will affect marine ecosystems in several ways. The semi-enclosed Baltic Sea is characterized by its glacial development including species adapted to cold water conditions. Therefore strong ecological impacts are expected due to future global warming. The RADOST project (Regional Adaption Strategies for the German Baltic Sea Coast) aims to develop adaptation strategies for the Baltic coastline of Mecklenburg-Western Pomerania and Schleswig-Holstein. The Agency for Agriculture, Environment and Rural Areas of Schleswig-Holstein (LLUR) is one among 17 partners within the project. The key aspects of their project activities include the development of concepts to protect the remaining populations of the bladder wrack (*Fucus* *vesiculosus*) and to re-establish the bladder wrack where it is locally vanished. Detailed management strategies of coastal ecosystems require scientific knowledge about the impact of climate change on marine macrophytes in the Baltic Sea. The investigation in 2011 analysed the sequential stress effects of raising water temperature (thermal stress) and subsequent feeding pressure or a second heat wave on the survival of early post-settlement stages of *F. vesiculosus* by laboratory experiments. The study was financed by the RADOST project.

3 Introduction

Macrophyte communities are important habitats for many organisms in shallow coastal zones and basic links in marine nutrient and carbon cycles (Carr 1989, Duggins et al. 1989, Arrontes 1999, Worm 2000, Lotze et al. 2001, Berger et al. 2004, Wikström & Kautsky 2007). In the Baltic Sea, the most common canopy-forming and wide spread species is the bladder wrack *Fucus vesiculosus* (Torn et al. 2006), which has shown a massive retreat from the deeper zones of its former distribution and now seems to appear mainly in the shallow water zone (Vogt & Schramm 1991, Fürhaupter et al. 2003, Torn et al. 2006). This decline is caused by loss of hard substrata (Karez & Schories 2005, Vogt & Schramm 1991), increased grazing pressure (Schaffelke et al. 1995), sedimentation and eutrophication (Vogt & Schramm 1991). Although the bladder wrack tolerates low salinity (Torn et al. 2006) *F. vesiculosus* populations in the eastern parts of the German Baltic coast declined recently (Fürhaupter et al. 2006, Schories et al. 2006). Which reasons lie behind this recent decline remains unclear. One possible reason for this phenomenon could be the impact of climate change (BACC 2008), which represents additional threats to the populations of the bladder wrack. Increasing thermal stress and enhanced feeding pressure on adults or early life stages of *F. vesiculosus* could be the consequences. Among other things the abundance of *Fucus* algae is controlled by post-settlement events (Pearson & Brawley 1996, Johnson & Brawley 1998, Berndt et al. 2002). One example for a post-settlement event is a strong rise in water temperature after reproduction which could significantly reduce the germination success of fucoid zygotes. To assess the consequences of a single high temperature pulse on the survival of early bladder wrack stages laboratory experiments were performed. A follow-up question was, whether the surviving genotypes would exhibit a different sensitivity to a second stress, feeding or rather a second heat wave in this case.

We first tested the hypothesis that (1) moderate thermal stress (one pulse of high temperature) reduces the survival of the early life stages of *F. vesiculosus*. We further hypothesized that (2) fucoid offspring which was preselected by high temperature differs in sensitivity to feeding pressure or to a second heat wave from fucoid offspring without prior stress (but having experienced random mortality).

4 Materials and methods

4.1 Sampling

Fertile tips (receptacles) from spring/summer reproducing *F. vesiculosus* individuals were collected in a water depth of 0.5-1.5 m at Bülk in June 2011 (Fig. 1). Bülk is an exposed sampling site in the outer Kiel Fjord (54°27.327 N, 10°11.977 E) with mainly hard substrate and a varying salinity between 14-19 (hourly measurements from April-December 2009 in a water depth of 0.5-1.5 m, by a CTD logger; Star-Oddi, Reykjavik, Iceland).

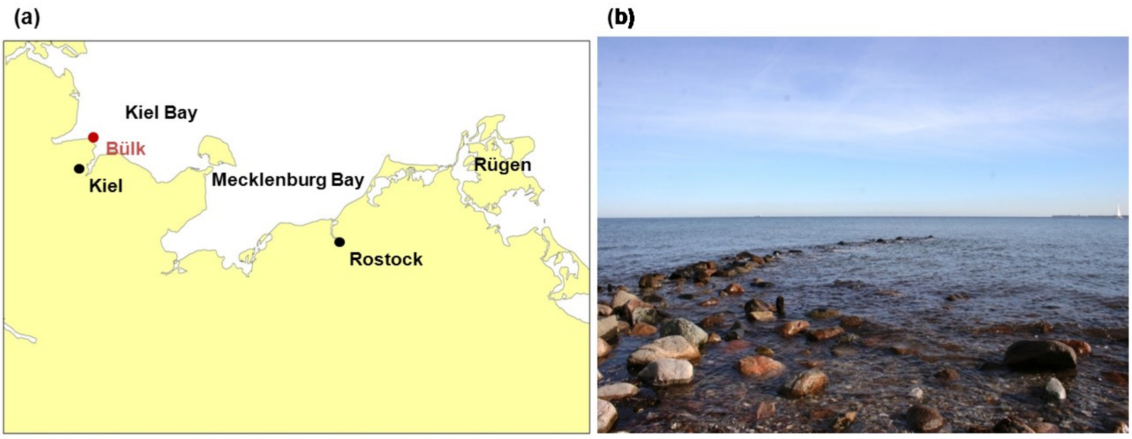

Fig. 1. Location Bülk of the German Baltic Coast where fertile individuals of *Fucus vesiculosus* were collected (a), an exposed area with mainly hard substrate (b).

In previous studies we found out that the reaction of fucoid offspring to thermal stress is related to genetic effects (Maczassek 2009). In the present, the effect of thermal stress on fucoid survival as a potential selective agent for stress resistance was tested. To warrant genetic diversity in each experimental germling population, we used random mixtures of fucoid zygotes from different set of parents. For this purpose receptacles from 60 different *F. vesiculosus* individuals (4 receptacles per *F. vesiculosus* individuals; number of males and females are unknown) were collected in the field. Because *F. vesiculosus* gametes disperse 0.5-2 m from the adult plants (Serrão et al. 1997), a distance of 2 meters between the different fertile *F. vesiculosus* individuals was kept.

4.2 Production of the fucoid zygotes

The following method to produce fucoid zygotes is based on a previous study by Karez (1997) and on our experience from former investigations of early fucoid life stages (Maczassek 2009).

The gamete release was induced in the lab by first washing the receptacles with fresh water and by then keeping them dry in the dark at a constant temperature of 15°C. After 5 days fertile tips were transferred into 15°C seawater from the Kiel Fjord with a salinity of 16 and exposed to light (200 µmol $m^{-2}s^{-1}$) for a duration of 5 h. During this period gamete release and fertilisation took place (Fig. 2).

Fig. 2. Gamete release of *Fucus vesiculosus*.

Fucoid embryos were collected with a glass pipette and stored in a beaker glass. Homogenized fucoid zygotes suspension was transferred into 6-well plates (1000 µl zygote suspension/well) using an Eppendorf pipette. 8 ml of filtered seawater (0.2 µm membrane filter/cellulose acetate) from Kiel Fjord was added. Only fertilized eggs attach to the substrate (Ladah et al. 2003). To remove unfertilized eggs the wells were rinsed three times with filtered seawater 24 hours later.

4.3 Thermal stress on *Fucus vesiculosus* (first heat wave)

4.3.1 Thermal treatment of early fucoid life stages

Average densities of early fucoid life stages were determined by counting 7 visual fields in each well with an inverted microscope (10 x). Well plates with known initial germling density were placed into water baths of two different temperatures (25°C, 15°C) for 4 days. Both treatments were replicated 6 times (Fig. 3) and during the experiment water was exchanged daily.

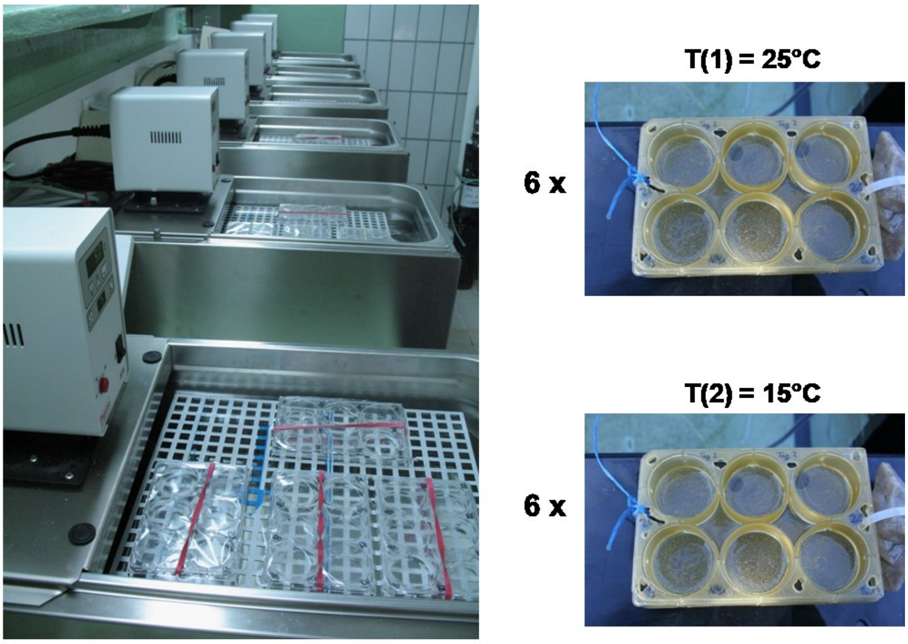

Fig. 3. Thermal treatment. Fucoid zygotes cultured in 6-well plates, placed into water bathes with 2 different temperatures (25 °C, 15 °C; n = 6).

In former experiments 60-100% of early fucoid stages died after an incubation at 25°C for 5 days (Maczassek 2009). In the present experiment a water temperature of 25°C and an exposure time of four days were assumed to be sublethal but represented thermal stress for early fucoid life stages. In contrast, 15°C was observed as an optimal temperature for germination (Maczassek 2009) and growth (Lüning 1985) of *F. vesiculosus*. Therefore, in our experiment 15°C was supposed to be the optimal incubation temperature for young stages of *F. vesiculosus* and will be referred to as “optimal temperature”.

After the thermal treatment of 4 days the number of surviving fucoids (Fig. 4a) in their early life stages was counted.

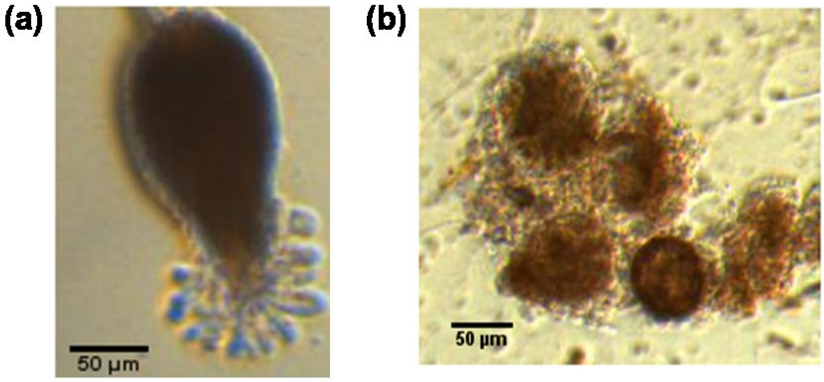

Fig. 4. Early fucoid life stages (4 days old) which survived (a) and which died (b) after a thermal treatment of 4 days at 25 °C.

4.3.2 Analyses

Mortality (%) was calculated according to the formula:

$$\text{Mortality (\%) of early fucoid life stages} = \frac{(\text{Initial number} - \text{number of survied early fucoid life stages}) \times 100}{\text{Initial number of early fucoid life stages}}$$

To standardize the density of germlings in the wells for the subsequent feeding experiments the number of germlings in the 15°C treatment were adjusted to the mean number of germlings of the 25°C treatments by removing surplus young *F. vesiculosus* individuals with a forceps. In contrast to the other treatment group, this mechanical and random "mortality" did not select for any stress resistance among the *Fucus* genotypes.

The mortality of early fucoid life stages at 25°C, compared to their mortality at 15°C (%, transformed with arcsine transformation) was analyzed with an One-way ANOVA (Statistica; Table 1). The transformed data were normally distributed and homoscedasticity was found.

4.4 Growth of early fucoid life stages

Marine isopods are known as consumers of adult *F. vesiculosus* (see discussion). In order to determine the feeding pressure on young life stages of *F. vesiculosus* we intended to provide an "attractive" biomass of the germlings (length ≥ 1 mm) for the isopods. For this reason, we incubated fucoid early life stages after the thermal stress experiment at a constant temperature (15°C) with filtered seawater (exchanged daily) and at a constant light intensity of 106 µmol $m^{-2}s^{-1}$ (16h:8h light:dark cycle) to let them grow.

4.5 Feeding pressure on *Fucus vesiculosus*

Isopods and snails are known to be efficient grazers of young recruits of *F. vesiculosus* (Korpinen et al. 2007). In this study the isopod *Idotea baltica* and the snail *Hydrobia ulvae* were used for the feeding pressure experiments. 25 individuals of *I. baltica* (1–2 cm body length) and 30 *H. ulvae* (3-5 mm shell height) were collected in a *Zostera marina* bed in Falckenstein, Kiel Fjord (54.40608° N 10.194249° E) with a hand brailer while snorkelling.

For the pilot study and the feeding pressure experiment (4.5.1 and 4.5.2) several of the sampled animals were taken randomly. 12 individuals of *I. baltica* and 12 individuals of *H. ulvae* were placed individually into aquariums with a salinity of 16 and a temperature of 15°C for 3 days.
For both experiments (for every temperature treatment 6 replicates) one well was occupied with one isopod (pilot study) or one snail (feeding pressure experiment) per replicate and a second well without grazer was used as control. These treatments were exposed to a light intensity of 100 µmol $m^{-2}s^{-1}$ (16h:8h light:dark cycle) and to filtered seawater from Kiel Fjord with a salinity of 16 and a temperature of 15°C. Daily, water was exchanged and the density of fucoids was determined.

4.5.1 Pilot study

After a recovery period of 4 months, fucoid offspring was < 1 mm (see results, Table 1). A pilot study was conducted to find out if the grazers feed on the germlings. To determine feeding pressure we estimated the initial densities of the fucoid offspring (from both treatments) before isopods were transferred into the wells and after termination of the experiments. After 5 days of observation we could not find grazing patches neither in the wells with the isopods nor in the controls. So we conclude that *I. baltica* did not consume the fucoid offspring. The same pilot study was done with *H. ulvae*. Here little grazing patches were found. We thus decided to conduct the feeding experiment with this snail.

4.5.2 Feeding pressure experiment

The initial density of young *F. vesiculosus* in each well was determined. Water was exchanged every day and controlled for early fucoid life stages. This control was necessary to ensure that the changing density of fucoid offspring was a result of feeding pressure and not caused by mechanical removal of the snail or by water change. After 2 weeks the density of residual *Fucus* offspring was counted.

4.6 Thermal stress on *Fucus vesiculosus* (second heat wave)

After a recovery period of 5 months (1 month after the feeding experiments) sensitivity of fucoid offspring with (25°C) and without (15°C) prior stress to a second heat wave (25°C) was tested. During the last 4 weeks of recovery period young *F. vesiculosus* was kept outside in aquaria (salinity: 16), were water temperature decreased. So before experiment was started a water temperature of 8°C (hourly measurements for 7 days) was measured. Thus 8°C was chosen as the control treatment.

First the average initial density of young *Fucus* was determined. Then wells were placed into water baths with two different temperatures (25°C, 8°C) for 2 weeks. Both treatments were replicated 6 times and during the experiment water was exchanged daily.

Fucoid offspring which died during thermal stress experiment dispersed like mentioned above (4.3.1; Fig. 4b). So after the thermal treatment of two weeks, the number of surviving *F. vesiculosus* individuals was counted.

5 Results

5.1 Thermal stress on *Fucus vesiculosus* (first heat wave)

Mortality increased significantly ($p = 0.000105$; $F = 38.05$) with temperature (Fig. 5; Table 1, 2). After 4 days the mean mortality of early fucoid life stages was 26% (25°C) compared to 9% mortality (15°C).

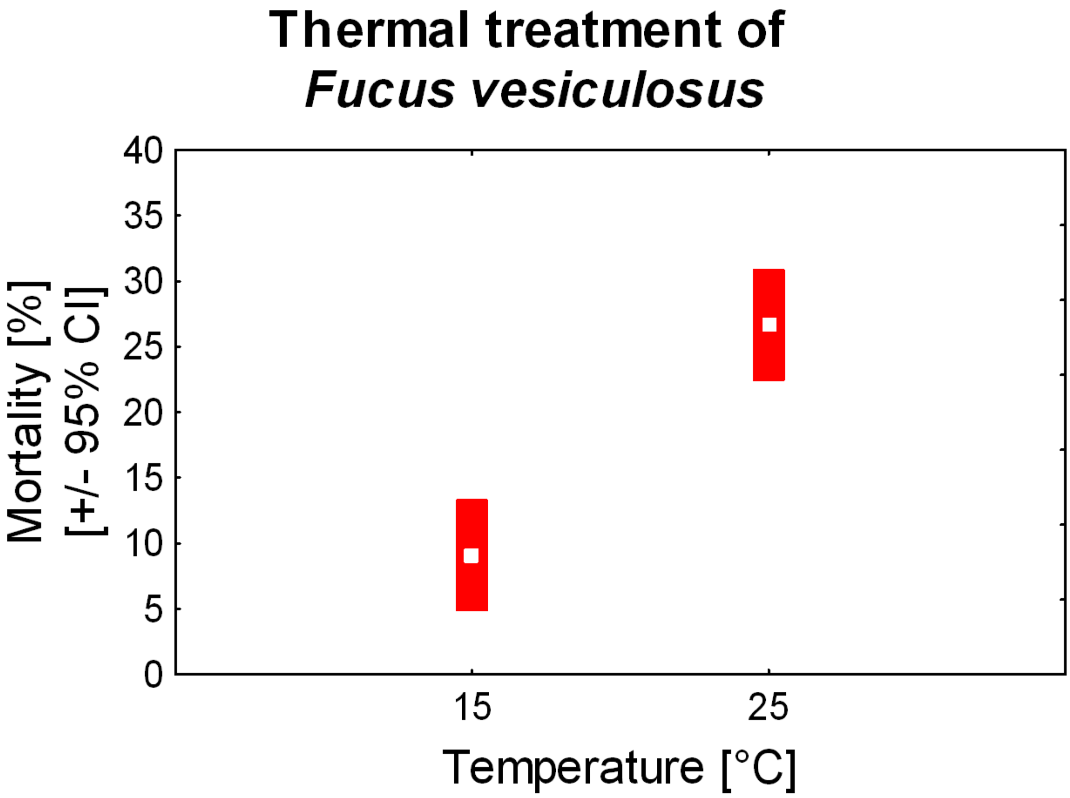

Fig. 5 Thermal stress on *F. vesiculosus* (first heat wave). Mortality of five days old fucoid offspring (%, mean ± 95% CI, n = 6) under two different temperatures (15 °C, 25 °C).

Table 1. Number of *Fucus vesiculosus* individuals (mean ± SD, n = 6) before and after a thermal treatment of 4 days at 25°C (red colomn) and 15°C (green colomn).

Number of young *F. vesiculosus* individuals			
before thermal treatment at 25°C	after thermal treatment at 25°C	before thermal treatment at 15°C	after thermal treatment at 15°C
534 ± 25	391 ± 24	451 ± 156	407 ± 124

Table 2. One-way ANOVA (Thermal Stress Experiment) for the effect of two different temperatures (15 °C, 25 °C) on the mortality of early fucoid life stages.

Effect	*df*	MS	*F*	*p*
Temperature [°C]	1	0.04595	38.08	0.000105
Error	10	0.00121		

5.2 Growth and feeding pressure experiment

Table 3 shows the length of fucoid offspring at various times. After an incubation period of 4 months (after the heat stress treatment) no differences in growth were observed. Early fucoid life stages reached a mean size of 274 µm at 15°C and 278 µm at 25°C. During the feeding pressure experiment with *H. ulvae* - in contrast to the pilot study - no grazing patches were observed and no difference in germling density was found (Fig. 6, Table 4; even in the controls mortality was found).

Table 3. Size of *Fucus vesiculosus* (µm, mean ± SD, n = 60) at different life stages and different time periods of incubation. Per thermal treatment from every replicate, or rather in 6 different wells, 10 *Fucus* individuals were measured. Red column represents the fucoid offspring which was icubated at 25 °C and green column incubation at 15 °C during the first thermal stress experiment.

Age of fucoid offspring and time periods of incubation	Size of *Fucus vesiculosus*	
24 hours old fucoid offspring (before thermal treatment at 25 °C and 15 °C)	77 ± 10	75 ± 9
5 days old fucoid offspring (after a thermal treatment of 4 days (25 °C, 15 °C)	83 ± 11	84 ± 13
125 days old fucoid offspring (after a thermal treatment of 4 days (25 °C, 15 °C) and a following incubation of 4 months at 15 °C)	215 ± 35	215 ± 39

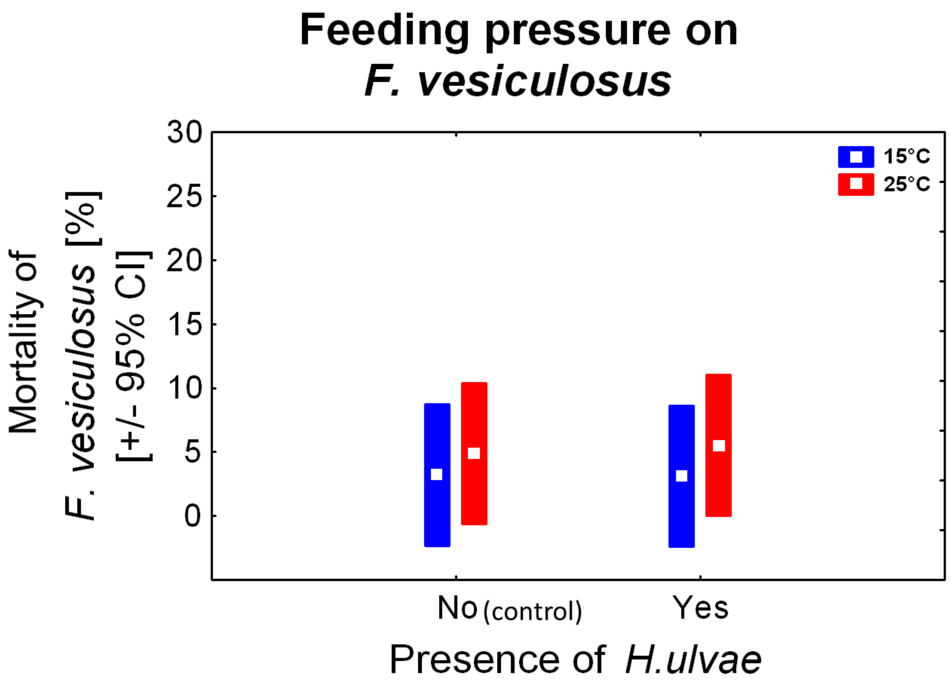

Fig. 6 Feeding pressure experiment. Mortality of 125 days old fucoid offspring (%, mean ± 95% CI, n = 6) by *H. ulvae* after 2 weeks of grazing (at 15°C). Early fucoid life stages were treated for 4 days with 25°C (thermal stress) and 15°C (optimal temperature). After this thermal treatment they were incubated for 3,5 months at 15°C (revovery period). At both treatments (presence and no presence of *H. ulvae*) mortality was found.

Table 4. Number of *Fucus vesiculosus* individuals (mean ± SD, n = 6) before and after the feeding pressure experiment by *H. ulvae*. Red column represents the fucoid offspring which was icubated at 25 °C and green column incubation at 15 °C during the first heat wave experiment.

Number of young *F. vesiculosus* individuals				
before	after	before	after	feeding pressure
165 ± 25	157 ± 24	150 ± 13	144 ± 14	no (control)
155 ± 18	146 ± 20	152 ± 14	146 ± 19	yes

5.3 Thermal stress on *Fucus vesiculosus* (second heat wave)

During the second thermal stress experiment fucoid offspring which was preselected by high temperature (25°C) differed not significantly in sensitivity from fucoid offspring without prior stress (15°C). At both, preselected and unselected fucoid offspring, mortality (45% – 50%) was independent from temperature (Fig. 7, Table 5).

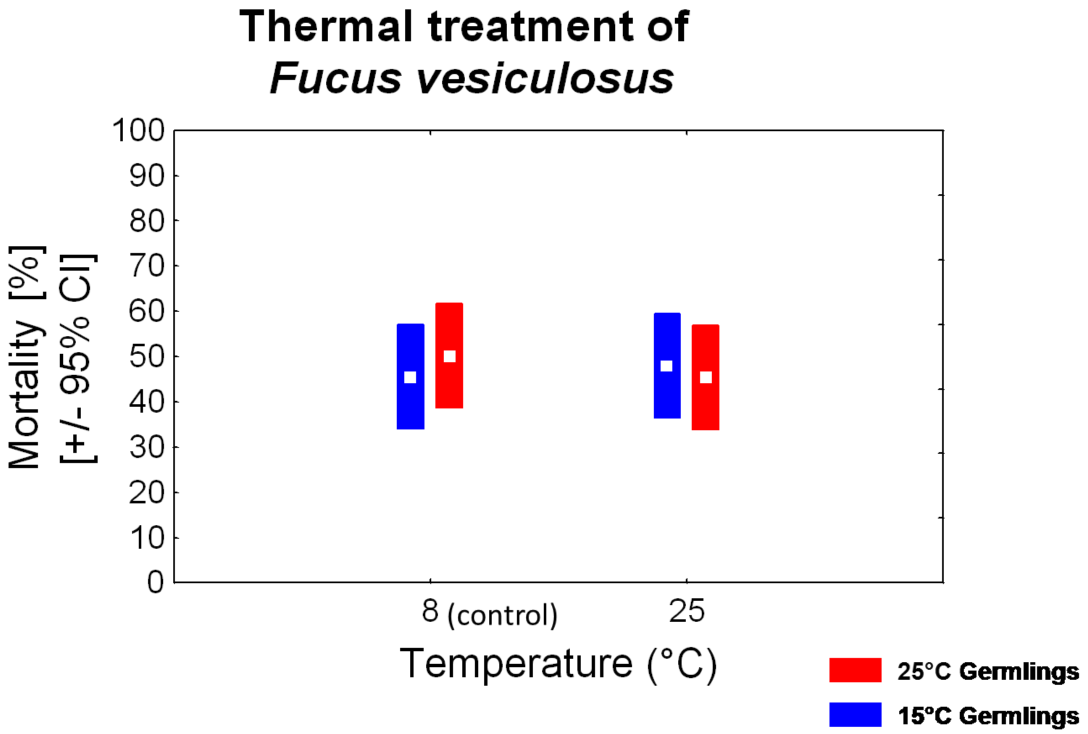

Fig. 7 Thermal stress on *F. vesiculosus* (second heat wave). Mortality of 169 days old fucoid offspring (%, mean ± 95% CI, n = 6) after a recovery period of 5 months and a following thermal treatment of 2 weeks at 8°C (control) and 25°C (thermal stress). Before the recovery period early fucoid life stages were treated for 4 days with 25°C (thermal stress) and 15°C (optimal temperature).

Table 5. Number of *Fucus vesiculosus* individuals (mean ± SD, n = 6) before and after the second heat wave experiment. Red column represents the fucoid offspring which was icubated at 25 °C and green column incubation at 15 °C during the first heat wave experiment.

Number of young *F. vesiculosus* individuals				
before	after	before	after	**second heat wave**
188 ± 26	99 ± 33	208 ± 29	116 ± 50	**no (control/8°C)**
180 ± 13	97 ± 12	174 ± 19	86 ± 13	**yes (25°C)**

6 Discussion

6.1 Thermal stress on *Fucus vesiculosus* (first heat wave)

The mortality of early fucoid life stages was almost three times higher at 25°C than at 15°C. This result is conform to our previous studies were early post-settlement stages were affected negatively by a temperature of 25°C (Maczassek 2009) and supports our first hypothesis that thermal stress has a negative effect on survival of young fucoid stages (*F. vesiculosus*).

Lüning (1984) reported an upper survival temperature of 28°C for adult *F. vesiculosus* (1 week exposure) whereas in our experiments even 25°C had a strong negative effect on fucoid offspring. If this is not an inter-population difference (North Sea versus Baltic Sea), this may suggest that early fucoid life stages are more sensitive to heat stress than adult *F. vesiculosus*. Post-settlement processes confine the abundance of fucoid species (Brawley & Johnson 1991, Pearson & Brawley 1996, Serrão et al. 1996, Johnson & Brawley 1998, Berndt et al. 2002). The stress treatment applied was not unnatural since during summer we repeatedly measured temperatures up to 25°C in shallow water depth where *Fucus* individuals occur. Furthermore it might be that an increase of intensity and frequency of heat waves due to climate change leads to water temperatures which are even higher than 25°C. So we assume that recruitment success and therefore the abundance of *Fucus* beds in shallow waters could be threatened by warm summer seasons.

6.2 Growth and feeding pressure on *Fucus vesiculosus*

We hypothesized that young *F. vesiculosus* which is genetically preselected by high temperature, may be more or less sensitive to feeding pressure or a second heat wave than fucoid offspring without stress. During feeding pressure experiments with *I. baltica* no consumption of early fucoid life stages was observed. All previous studies about the feeding pressure on *F. vesiculosus* by isopods were performed with adult *F. vesiculosus* (Schaffelke et al. 1995, Karez et al. 2000, Jonne et al. 2006, Råberg & Kautsky 2008, Ringelhan 2008, Petrowski 2010, Roth et al. 2010, Yun et al. 2010) and which size of *F. vesiculosus* germlings is preferred by *I. baltica* is unknown. In our study early fucoid life stages were still smaller than 1 mm 4 months after settlement, although fucoid offspring were reared under controlled conditions, like filtered seawater (no diatoms and no grazers), optimal temperature (15°C) and constant light intensity. So it might be that fucoid germlings were too small to be “attractive food” for *I. baltica*. Higher growth rates of *Fucus* germlings are known in nature (McLachlan et al. 1971). Although during the pilot study grazing patches were observed, no consumption of fucoid offspring by *H. ulvae* was measurable in the main experiment. During the pilot study water was exchanged every day, but not controlled for early fucoid life stages. So it could be that the grazing patches during the pilot study are caused by mechanical removal of the snail.

The question whether genetic preselection by thermal stress affects the sensitivity of *Fucus* germlings to grazing must remain unanswered for the moment since consumption under the experimental conditions was nil. Whether the mortality caused by thermal stress leads to a genetic shift in the surviving population is analyzed at the moment. Only if such a shift happens and if susceptibility to grazing differs among genotypes (which is unknown so far) can we expect an interaction between heat-driven mortality and grazing impact. We are confident that our ongoing investigation will elucidate this question in the near future.

6.3 Thermal stress on *Fucus vesiculosus* (second heat wave)

Results do not confirm our hypothesis that fucoid offspring which is genetically preselected by thermal stress differs in sensitivity from *F. vesiculosus* offspring without prior stress. But nearly 50% of fucoid recruits which were already stressed by a first heat wave survived a second heat wave. This fact does not confirm our assumption that warm summer seasons could have a negative effect on survival of fucoid recruits. But in this case it has to be noticed that the second heat wave was tested on 5 months old fucoid offspring, first heat wave on 1 day old fucoid offspring. We already mentioned above that the upper survival temperature for adult *F. vesiculosus* is 28°C (Lüning 1984). So it could be that preselected as well as unselected fucoid offspring was less sensitive to second heat wave because of their higher age. Therefore further experiments concerning to genetically preselection should be made (see also 6.2).

6.4 Outlook

Besides feeding pressure and thermal stress other factors exist which could influence the development of fucoid recruits. Desiccation for example negatively affects early post-settlement stages of algae in open areas (not sheltered by parental canopy) (Brawley & Johnson 1991). Other environmental stressors can be low salinity, high light intensity and intensive UV radiation. On the biotic side, parasitism, diseases and epibiotism can be stressful at the individual and the population level. Especially during warm summer seasons in shallow waters UV radiation, light intensity and heat waves could have negative synergetic effects on survival of young fucoid offspring. In a newly constructed outdoor benthocosm facility (Fig. 8) the impact of multiple stressors on adult and young *Fucus* will be investigated in the coming years.

Fig. 8. Benthocosmen at the Kiel Fjord.

If a stressor through genetically differential mortality leads to a shift in genetic diversity and composition of a population we may expect the subsequent impacts of other stressors will be affected. The interactive action of multiple biotic and abiotic stress as an important ecological scenario to be expected in the course of climate change.

The mortality of fucoid offspring which was found even in the controls (5.2, Table 4; 5.3, Table 5) might be caused by the long period (4 months) *F. vesiculosus* individuals were kept indoors (because of low light for example). We assume that during outdoor benthocosm experiments culturing of *Fucus* algae will be more successful than by indoors.

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