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REPORT

Effects of sequential stressors on survival of young life stages of the bladder wrack *Fucus vesiculosus* L.

Kerstin Maczassek

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REPORT

EFFECTS OF SEQUENTIAL STRESSORS ON SURVIVAL OF YOUNG LIFE STAGES OF THE BLADDER WRACK *FUCUS VESICULOSUS* L.

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Marine Benthic Ecology

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Inhalt

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. Global warming may increase abiotic as well as biotic pressures and exacerbate environmental conditions in coastal ecosystems. The present study focussed on the effects of single or subsequently combined stressors on survival and palatability of juvenile *F. vesiculosus*. Fucoid offspring were exposed to high temperature and/ or feeding pressure. Feeding preference of *Idotea baltica* was quantified in a pellet assay calculated as an odds ratio. High temperature significantly impaired the survival of juvenile fucoids. Neither single nor combined stress considerably influenced the feeding preference of *I. baltica*. Surprisingly *I. baltica* strictly avoided pellets with juvenile *F. vesiculosus* compared to adult *F. vesiculosus*. Avoidance tended to be less pronounced in juvenile fucoids previously stressed by high temperature. Obviously grazing does not induce anti-herbivore defence, but rather the young plants appeared constitutively well-protected against isopod feeding. These results contradict the prevailing opinion that juvenile *F. vesiculosus* is more susceptible to herbivore grazing than adult *F. vesiculosus*.

2 Background

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), which financed the present study in cooperation with the State Agency for Agriculture, Environment and Rural Areas Schleswig-Holstein, 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 18 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.

3 Introduction

Macrophyte communities build important habitats for many organisms in shallow coastal zones and basic links in marine nutrient and carbon cycles (Carr 1989, Duggins et al. 1990, Arrontes 1999, Lotze et al. 2001, 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). In the Western Baltic Sea *F. vesiculosus* has shown a massive retreat from the deeper zones of its former distribution and is now limited to the upper subtidal (Vogt & Schramm 1991, Torn et al. 2006). This decline is caused by loss of hard substrata (Vogt & Schramm 1991, Karez & Schories 2005), sedimentation and eutrophication (Vogt & Schramm 1991, Schaffelke et al. 1995, Pedersén & Snoeijs 2001). Also grazing pressure can significantly reduce the abundance of *F. vesiculosus* in the Baltic Sea (Korpinen et al. 2007). Increasing consumption by the isopod *Idotea baltica*, the most important herbivore of *F. vesiculosus* (Korpinen et al. 2010), was discussed to be one possible reason for the declining populations (Salemaa 1987, Schaffelke et al. 1995, Engkvist et al. 2000).

‘Resistance to grazing can be constitutive (stable in intensity) or regulated, i.e. deployed in the presence of grazers and reduced when grazing stops’ (Weinberger et al. 2011). Rohde et al. (2004) found that direct feeding of *I. baltica* as well as feeding on neighbouring plants induced chemical defence in *F. vesiculosus.* The authors suggested that not physical damage alone triggers defence induction and that waterborne cues are emitted by the grazer or the consumed conspecific. These findings were confirmed later by a study of Haavisto et al. (2010). Anti-herbivory defence in *F. vesiculosus* can be impaired by environmental factors. For example nutrient enrichment increases the amount of unsolvable sugars but simultaneously reduces the content of feeding deterrents and the physical toughness of the thallus. Thus it was suggested that eutrophication may potentially improve the nutritional quality of *F. vesiculosus* for *I. baltica* (Hemmi & Jormalainen 2002). Moreover, Weinberger et al. (2011) mentioned that ‘thermal stress may either impact *F. vesiculosus* directly or affect its biotic interactions (Wahl et al. 2010), e.g. by provoking changes in its palatability or antifeeding protection’.

Upward shifts in water temperature by approximately 10°C inhibit inducible defence in adult *F. vesiculosus* algae (Weinberger et al. 2011). Furthermore temperatures in summer (> 15°C) lead to increasing grazing rates of *I. baltica* and thus stimulate biotic stress in Baltic Sea *Fucus* (Wahl et al. 2011).

Due to climate change temperature will increase during the coming decades (Meier 2006, Neumann 2010). *I. baltica* is well adapted to temperature changes (Bulnheim 1974) and may survive the predicted extreme environmental changes in the Baltic Sea due to its evolutionary potential and its presence of local adaptations (Leidenberger 2013). With regard to *Fucus* it was mentioned by Wahl et al. (2011) that ‘moderate warming may not affect *Fucus* directly, but could have a large indirect impact via a synergistic interaction involving (i) a slight increase in the metabolic rate of consumers (= increased grazing pressure); (ii) a slight decrease in the defence strength of *Fucus* leading to; (iii) slightly higher fouling pressure and, in turn leading to; (iv) a slight decrease in available solar energy, further reducing; (v) defence strength and (vi) overall fitness’.

Until now, there is little Information available on resistance to isopod grazing in juvenile fucoid stages. The present study focuses on the effects of sequential stressors (temperature stress and grazing pressure) on feeding resistance of juvenile *F. vesiculosus* plants. According to this (1) the effect of high temperature on survival of fuvenile fucoids was tested. Additionally, we asked whether (2) juvenile fucoids which are exposed to feeding pressure by *I. baltica* induce anti-herbivore defence and if (3) this induction is influenced by previous temperature stress.

4 Materials and methods

Mature 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 2012 (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).

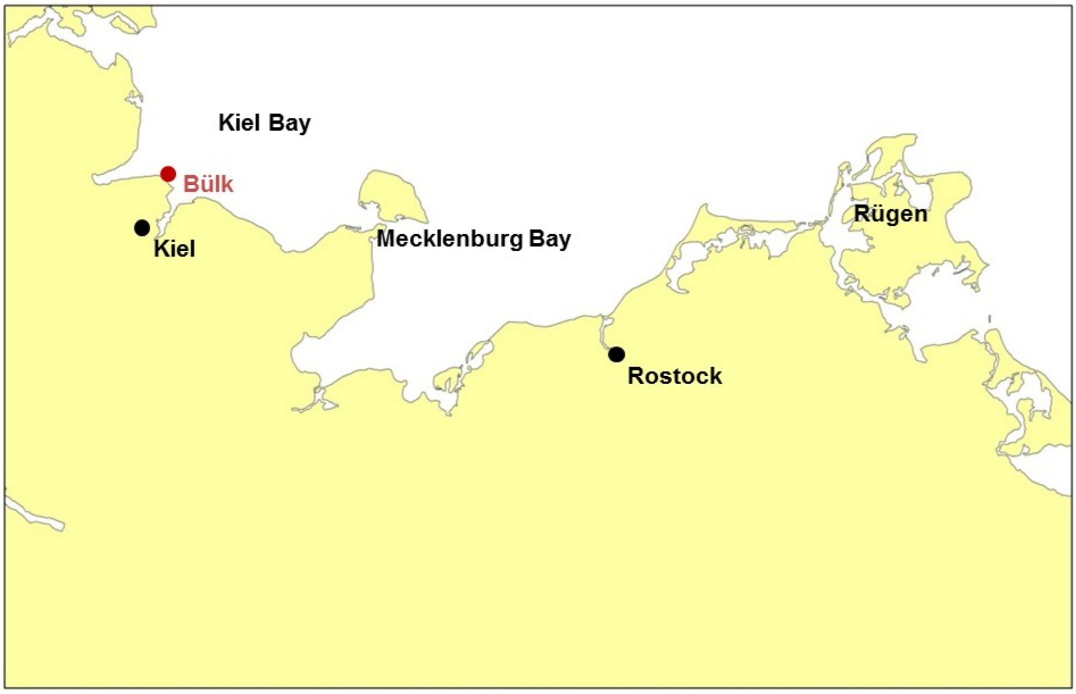

Fig. 1. Mature tips of *Fucus vesiculosus* were collected at the location Bülk.

To warrant genetic diversity in each experimental population, we used random mixtures of fucoid zygotes from different set of parents. For this purpose receptacles from 176 different *F. vesiculosus* individuals (5 receptacles per *F. vesiculosus* individuals) were collected in the field. Because *F. vesiculosus* gametes disperse 0.5-2 m from the adult plants, a distance of 2 meters between the different fertile *F. vesiculosus* individuals was kept.

I. baltica was collected in autumn from the Kiel Fjord and kept in a tank with seawater flow through at 15°C and fed with *F. vesiculosus*.

4.1 Production of *F. vesiculosus* 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 2008/ 2009).

The gamete release was induced separately for every *F. vesiculosus* individual 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 five 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 five hours. The time of exposure to light required for gamete release decreases with the maturity of the receptacles, and gametes only survive a few hours after release (Serrão et al. 1999). Consequently, receptacles were continuously monitored not to miss their gamete release, and fertilization was initiated as soon as possible after gamete release. All in all 17 males and 35 females released gametes. Gamete suspensions of all individuals were pooled. After fertilization, fucoid zygotes were collected with a glass pipette and stored in a beaker. 320 ml of the homogenous fucoid zygote suspension from the beaker was equally distributed on 160 (2 cm^3) sand stone cubes using a 10 ml glass pipette. The cubes then were fixed on PVC plates.

4.2 Incubation of juvenile *F. vesiculosus* and experimental setup

A schematic overview of incubation of juvenile *F. vesiculosus* (simply called juveniles hereafter) and experimental setup for temperature treatment and pellet assay is given in Figure 6.

Fucoid zygotes were placed first for seven days at 200 µmol $m^{-2}s^{-1}$ (16:8 hours) in a constant temperature chamber (15°C) and secondly for 108 days (June-October 2012) into the Kiel Fjord (54°22.483 N; 10°9.558 E), exposed to a water depth of 0.5 m. To prevent sedimentation of juveniles, PVC plates were slightly tilted. Further in a continuous rhythm of four weeks filamentous algae were removed by snorkelling. In October juveniles were harvested. On overall 159 sand stone cubes, juveniles in different sizes developed (Fig. 2).

Fig. 2. Juvenile *F. vesiculosus* algae on a sand stone cube in different sizes (0.3-3 cm).

4.3 Temperature treatment and defence induction

On every sand stone cube juveniles were counted and the length of every individual was measured, using a stereo microscope (6.4 x). Since juveniles varied in size (0.3-3 cm total length), they were grouped into different size groups:

< 1 cm 1-2 cm 2.1-3 cm

Sand stone cubes were mainly covered with juvenile fucoids from size group < 1 cm (Table 1).

Table 1. Total number of juvenile *F. vesiculosus* algae growing on sand stone cubes and total biomass (dry weight) of juveniles.

Size classes	**< 1 cm**	**1-2 cm**	**2.1-3 cm**
Number of juveniles	6288	180	19
Number of cubes	159	102	18
Dry weight (g)	3.3	0.5	0.1

Afterwards juveniles were transferred with their substrates (sand stone cubes) into 14 cm x 14 cm x 13 cm (length by width by height) plastic boxes containing 2.25 l filtered (0.2 µm) aerated seawater (renewed weekly) from the Kiel Fjord (54°19.800 N; 10°9.010 E), with salinity depending on the occurring salinity in the Kiel Fjord, which varied from 19 to 20 (measured by WTW Cond 315i) during experiment. Boxes were placed in constant temperature thermo bathes (precision: 0.1°C; Thermo Fisher Scientific; Fig. 3) of two different temperatures.

Fig. 3 Thermal treatment. *Fucus vesiculosus* germlings cultured in plastic boxes containing aerated seawater placed into water bathes).

In a previous study 15°C was detected as an optimal temperature for germination of *F. vesiculosus* zygotes whereas 25°C affected germination negatively (Maczassek 2008/ 2009). Thus, in the present study 15°C was supposed to be the optimal incubation temperature while 25°C represented temperature stress. Both treatments were replicated four times and during the experiment water was exchanged weekly. Cubes with juveniles were distributed to replicates so that in every replicate the same number and sizes of individuals was treated (17-22 cubes per replicate).

During temperature treatment juveniles were exposed to a light intensity of 100 µmol $m^{-2}s^{-1}$ (halogen-metal vapour lamps, 250 W; 10.000–12.000 K; light/dark period of 10/14 hours) and filamentous algae growing on juveniles were removed weekly. Survival of juveniles was controlled weekly by counting per replicate juveniles of three sand stone cubes (random samples). At larger size groups (1-3 cm) also physiological condition of juveniles was estimated weekly by measuring the maximal photochemical yield (Fv/Fm) of photosynthesis of juveniles with a Diving-PAM-fluorometer (Walz GmbH, Effeltrich, Germany). A detailed description of Fv/Fm measurement is given in Maczassek (2012), chapter ‘material and methods’.

Juveniles that were kept at 25°C were more fouled with filamentous algae vs. lower temperature. Furthermore during removal of filamentous algae as well as during Fv/Fm measurements stressed fucoids detached very easily from sand stone cubes and seemed to be less vital. After 21 days of temperature stress (25°C) number of juveniles from size group < 1 cm decreased (see results). Therefore we decided to start for ‘stressed’ juveniles the recovery period, i.e. a further incubation at 15°C for 14 days. According to this all in all ‘stressed’ juveniles were treated for 21 days with 25°C and afterwards for 14 days with 15°C and juveniles incubated at optimal temperature for 36 days with 15°C respectively.

After recovery period sensitivity of juveniles to feeding pressure with and without prior stress (i.e. 25°C and 15°C respectively) as well as with and without prior grazing of juveniles was investigated. For it after eight days of recovery period on every sand stone cube survived juveniles were counted. Afterwards number juveniles between different temperature treatment levels were standardised by removing surplus juveniles (15°C treatment) mechanically with a forceps.

For grazing treatment three individuals of *I. baltica* (2 x 1 cm, 1 x 1.5 cm total length) were allowed to feed on half of the juveniles per temperature treatment. To validate consumption by *I. baltica*, juveniles were checked daily for feeding traces (Fig. 4). Since no feeding traces could be found after two days, feeding pressure was increased by adding three more *I. baltica* individuals (1 x 1 cm, 1 x 1.5 cm, 1 x 2 cm total length). After two more days, only few feeding traces (Fig. 4) were observed. To ensure that juveniles induce anti-herbivore defence, feeding pressure was once again increased by adding three more individuals of *I. baltica* (2 x 1.5 cm, 1 x 2 cm total length) per replicate for two more days. Afterwards grazed and ungrazed algae from both temperature treatments were frozen at -20°C until food pellets were prepared.

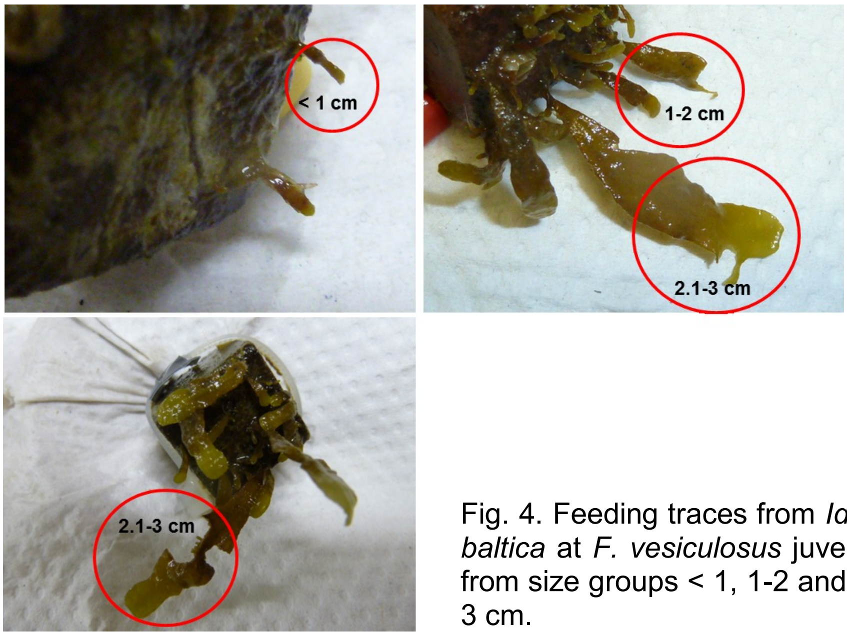

Fig. 4. Feeding traces from *Idotea baltica* at *F. vesiculosus* juveniles from size groups < 1, 1-2 and 2.1-3 cm.

4.4 Pellet assay

For preparing food pellets, frozen juveniles were freeze-dried (freeze dryer: Alpha 1-4 LSC; www.martinchrist.de) for 48 hours and subsequently crushed to algal powder. Afterwards algal powder was stored in airtight plastic tubes in a freezer at – 20°C until food pellets were prepared as follows:

58 mg of agar (Carl Roth) were mixed with 800 µl deionized water and heated to boiling in a microwave oven. The diluted agar was then poured into a mixture of 0.16 g germling powder and 640 µl deionized water, and after short stirring with a spatula, the mixture was poured on wax paper that was covered by mosquito gauze (mesh size: 1 x 1 mm). A second piece of wax paper was used as cover and the mixture was compressed with a panel until it gelled. After removal of the wax paper, the mixture of agar and juvenile powder had attached to the net, and squares of defined size (6 x 6 cells) were cut out.

For the pellet assay two pellets were placed into a Petri dish (9 cm) with 30 ml seawater. One of the two pellets contained powder from juveniles that have been treated with 25°C or 15°C (temperature treatment) and that were exposed or not exposed to *I. baltica* (grazing treatment) whereas the second pellet contained a control alga, i.e. adult *F. vesiculosus* that had not been treated with temperature and which was not exposed to *I. baltica*. Pellet containing the control alga was marked by removal of one corner (3 cells). Every temperature and grazing treatment was replicated four times and for each replicate three petri dishes were prepared in this way as pseudo-replicates to reduce grazer variability among *I. balitca* individuals, resulting in 48 Petri dishes. To each Petri dish one *I. baltica* individual (1.5 cm body length) was added (Fig. 5).

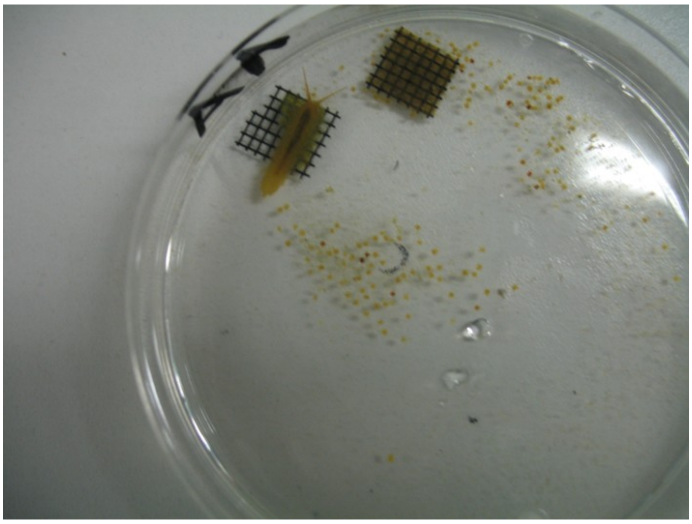

Fig. 5. *Idotea baltica* grazing on food pellets.

Afterwards petri dishes were placed in a constant temperature chamber (15°C). To avoid stress for the isopod incubation of petri dishes was at darkness. Incubation of a petri dish was stopped after approximately 12 hours when 50-100% of at least one of the two pellets had been eaten (Fig. 6).

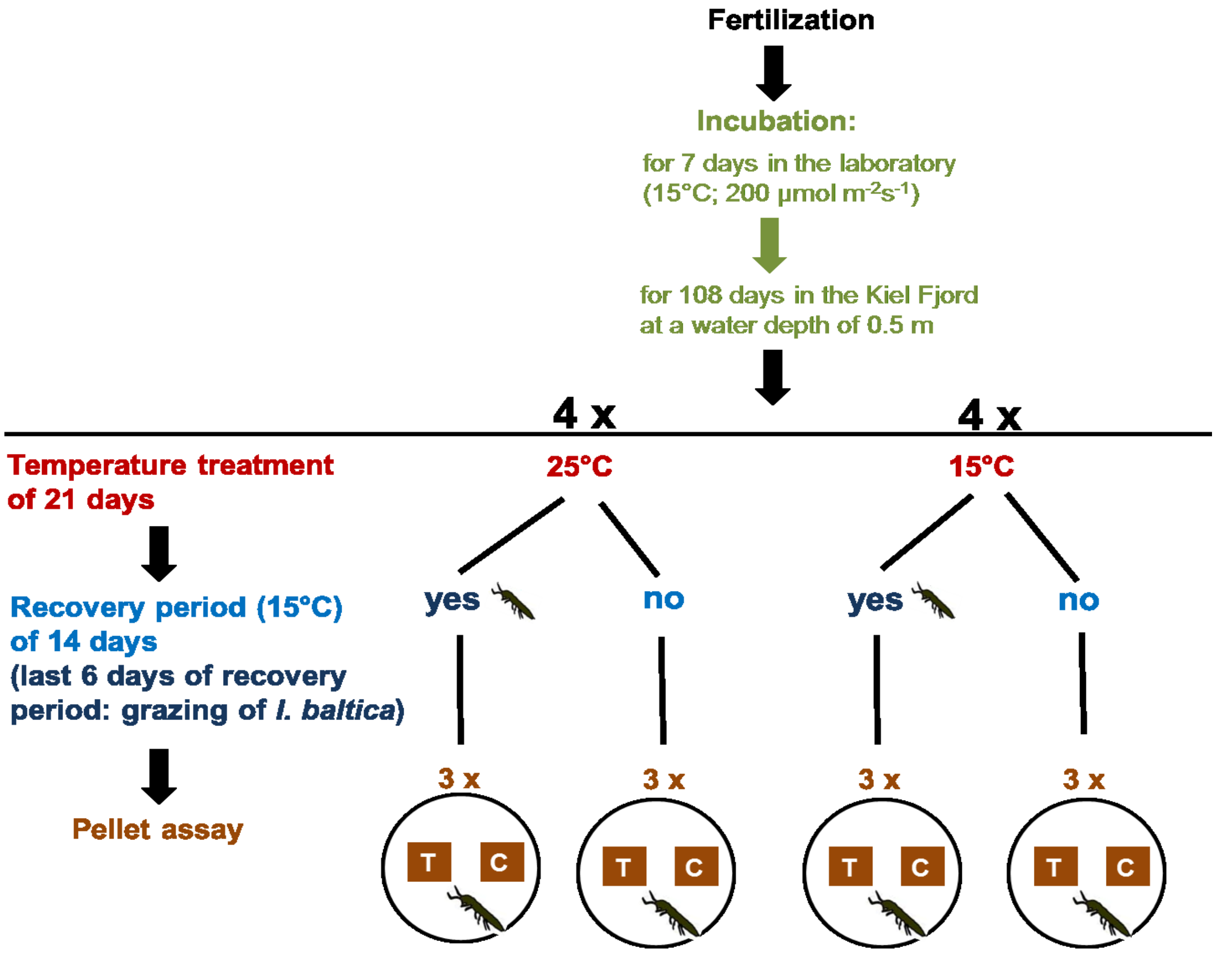

Fig. 6. Incubation of juvenile *F. vesiculosus* and experimental setup of the present study. T: pellet containing treated juvenile fucoids. C: pellet containing control/ adult alga.

5 Data analyses

5.1 Temperature treatment

Mortality of *F. vesiculosus* individuals (< 1 cm) at 25°C, compared to their mortality at 15°C (%, transformed with arcsine transformation) was analyzed with an One-way ANOVA (Statistica 8.0 software package; Statsoft, Hamburg). Homoscedasticity was found (Levine's test, $p < 0.05$). Since the transformed data (response variable: 'mortality') was not normally distributed (Shapiro-Wilks test, $p < 0.05$) the α-level was reduced to $p < 0.01$ to avoid a type 1 error (Underwood 1997) (Fig. 5, Table 2).

5.2 Pellet assay

Feeding preference of *I. balitca* for juveniles (Fig. 6) was calculated as an odds ratio

$$w = [(0.5+ t^{+})/(0.5+t^{-})]/[(0.5+c^{+})/(0.5+c^{-})]$$

(Fisher & van Belle 1993)

where w represents the effect size, which is the approximate relative risk of consumption of a given pellet; t represents numbers of cells of pellets containing juveniles that have been treated with 25°C or 15°C and that were exposed or not exposed to *I. baltica* for anti-herbivore induction; c represents the same for pellets containing a control alga, i.e. adult *F. vesiculosus* that had not been treated with temperature and which was not exposed to *I. baltica* for anti-herbivore induction; + and – indicate cells that were eaten or not eaten, respectively. Log (w) indicate a preference of *I. baltica* for juveniles of *F. vesiculosus* when it is > 0, while effect sizes < 0 indicate a preference of *I. baltica* for the control alga**.**

6 Results

6.1 Temperature stress

Mortality of juveniles from size group '< 1 cm' increased significantly with temperature (Fig. 7, Table 1). After three weeks the mean mortality was 59% (25°C) compared to 5% mortality (15°C).

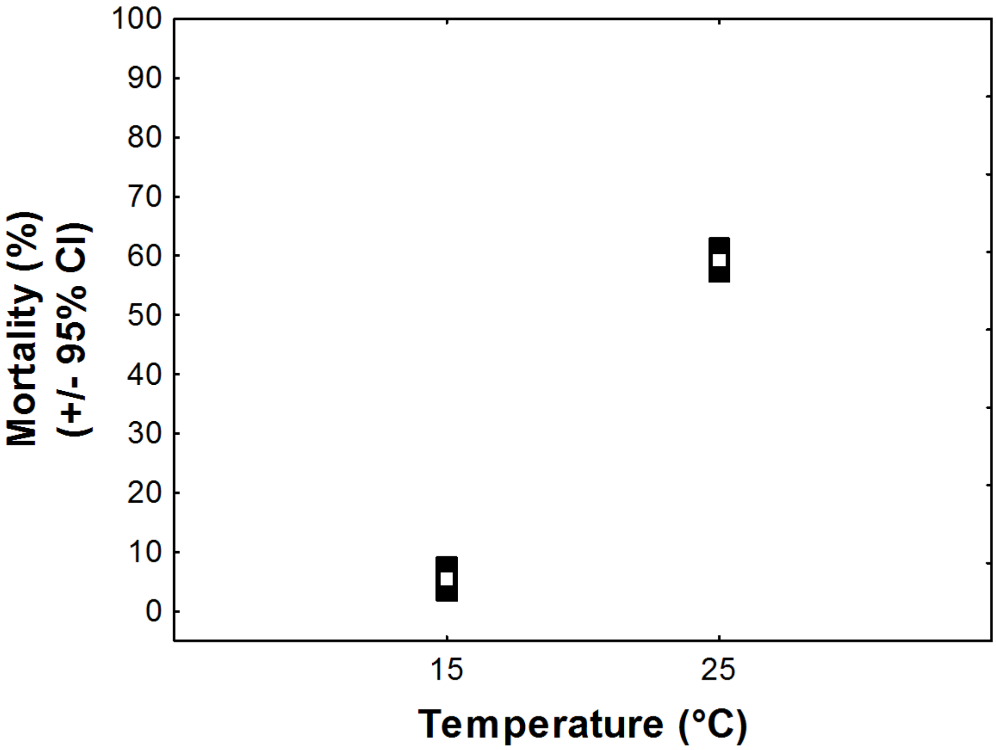

Fig. 7. Mortality of four months old *F. vesiculosus* individuals, < 1 cm (%, mean ± 95% CI, n = 6) exposed to two different temperatures (15 °C, 25 °C).

Table 2. One-way ANOVA for the effect of temperature on the mortality of *F. vesiculosus*.

	df	MS	F	p
Temperature	**1**	**0.0912585**	**95.1150**	**0.000067**
Error	6	0.009595		

In juveniles from size group 1-2 and 2.1-3 cm no mortality could be detected. Fv/Fm values were not different between the two temperature treatments (25 and 15°C) and varied between 0.72-0.75.

6.2 Feeding preference

Juveniles that have been treated at 25°C were slightly more consumed than those treated at 15°C. At 15°C palatability of previously grazed juveniles tends to be higher than of ungrazed juveniles. Whereas at 25°C a reversed effect with higher palatability of ungrazed juveniles was found. However, *I. balitca* preferred pellets containing adult *F. vesiculosus* over pellets containing juveniles of *F. vesiculosus* (Fig. 8).

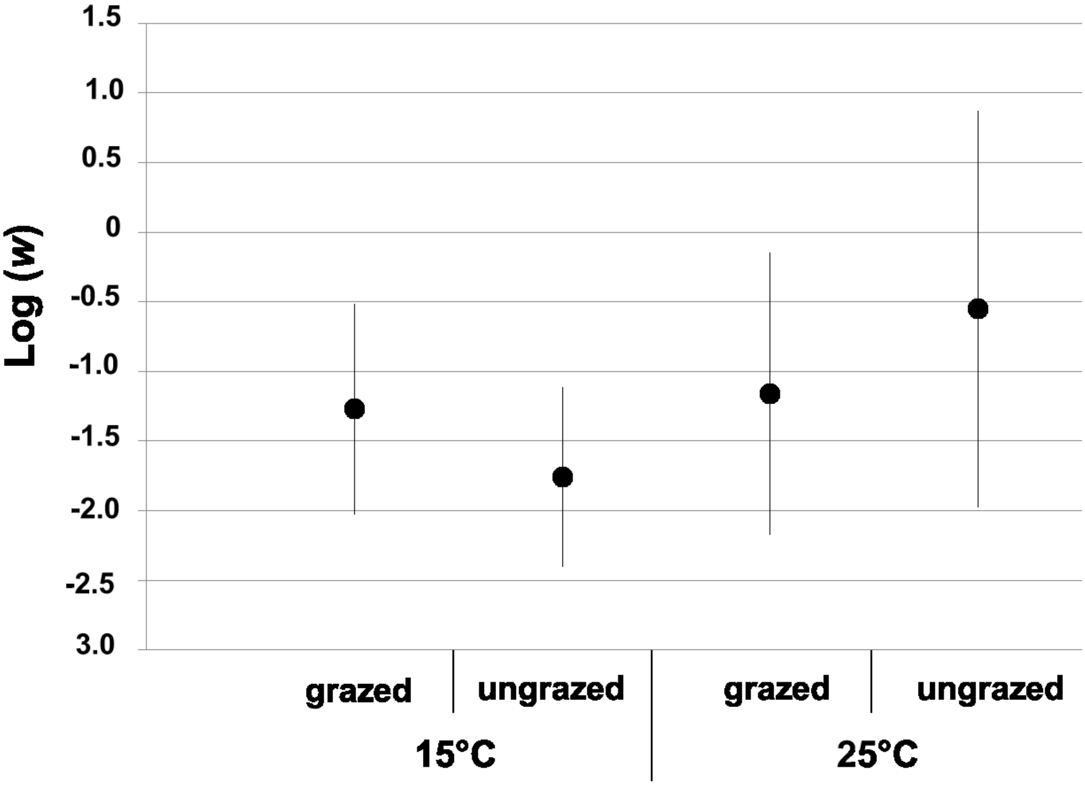

Fig. 8. Relative feeding preference (effect size log (*w*) ± 95% CI) of *Idotea baltica* for food pellets containing juveniles of *F. vesiculosus* that were treated at 15 and 25°C and afterwards exposed or unexposed to *I. baltica* and food pellets containing control/ adult *F. vesiculosus*. Effect sizes > 0 indicate a preference of *I. baltica* for germlings and effect sizes < 0 indicate a higher palatability of control alga for *I. baltica*.

7 Discussion

Mortality of four month old juvenile fucoids from size group < 1 cm was almost ten times higher at 25°C than at 15°C (Fig. 7). The high temperature applied was not unnatural since during summer we repeatedly measured temperatures up to 25°C (single measurements) in water depth *Fucus* individuals occur. Previous experiments also identified negative effects on germination success of fucoid zygotes due to thermal stress (Maczassek 2008/ 2009). Thus warm seasons may negatively affect summer recruitment of *F. vesivulosus*. In the coming decades an increase of intensity and frequency of heat waves due to climate change prolonged the periods of high temperatures in the Baltic Sea which may exacerbate unfavourable reproduction conditions during summer.

During incubation of fucoid offspring in the Kiel Fjord juvenile fucoids in different sizes developed (Fig. 2), probably due to intraspecific competition between juveniles (Steen & Scrosati 2004, Choi & Norton 2005). Only 40% of juveniles from size group < 1 cm survived at high temperature (Fig. 7) whereas juvenile fucoids larger than 1 cm (size groups 1-2 and 2.1-3 cm) were less impaired. Therefore sensibility of fucoids against temperature stress may not only be related to their age but also to their size. Wahl et al. (2011) mentioned that ‘severe high-temperature stress begins when the rate of protein denaturation cannot be neutralized by mechanisms such as increased production of chaperons (heat-shock proteins) or acceleration of protein biosynthesis (Csikasz-Nagy & Soyer 2008)’. Heat-shock protein synthesis is energy-intensive (Li & Brawley 2004) and smaller plants may have lower capacity for heat-shock protein synthesis.

Moreover very high fouling by diatoms on juveniles from size group < 1cm was observed (Fig. 9) which possibly caused additional stress, may affecting palatability and nutrient value.

Fig 9. Four months old *F. vesiculosus* germling (< 1 cm), covered with diatoms. Photographed by Inken Kruse & Carola Buchner, Olympus Germany

I. baltica preferred adult *Fucus* to juvenile fucoids independent of previous grazing pressure (Fig. 8). Although 25°C-treated individuals with prior grazing tend to be more consumed than without prior grazing, no evidence was found that grazing induced chemical defence in juvenile fucoids. Furthermore juvenile *F. vesiculosus* appeared a priori well protected against Idotea-grazing. Adult brown algae produce phlorotaninnes as feeding-deterrent response (Hay & Fenical 1988) and Denton et al. (1990) assumed a high susceptibility of juvenile *F. vesiculosus* to grazing, because small plants (length: 1.8 cm) contain significantly less concentrations of phlorotannins than large plants (length: 32.5 cm). It is known that grazing of *I. baltica* induces anti-herbivore defence in adult *F. vesiculosus* (Rohde et al. 2004) but to our knowledge no example is known juvenile fucoids are protected constitutively against feeding. This contradicts the commonly held assumptions that juvenile *F. vesiculosus* is generally more susceptible to herbivore grazing compareted to adult *F. vesiculosus* (Lubchenco 1983, Baker & Chapman 1990, Denton et al. 1990, Vadas et al. 1992, Lotze et al. 2001). Perhaps high temperature even inhibits not only induced defence in adult (Weinberger et al. 2011) but also constitutive defence in early *Fucus* development stages. Brown algae produce phlorotaninnes as feeding-deterrent response (Hay & Fenical 1988). Even the sole presence of *I. baltica* alone induce phlorotannin production in *F. vesiculosus* (Haavisto et al. 2010).

But Jormalainen et al. (2001) found that I. balitca is not deterred by phlorotannins and (Hemmi et al. 2005) showed that total phlorotannin concentration correlates poorly with resistance to herbivory in F. vesiculosus. Our results confirm the assumption that phlorotannins alone do not explain the resistance against I. baltica feeding (Haavisto et al. 2010). Defence of juvenile fucoids might be triggered by other anti-herbivore compounds than phlorotannin. For example galactolipids are reported as effective herbivore deterrents in F. vesiculosus (Deal et al. 2003) and may be responsible for the reduced palatability of the pellets containing juvenile F. vesiculosus. But results about phlorotannin production as response to feeding pressure are contrary. As mentioned by Leidenberber et al. (2012) ‘have previous studies shown that I. balitca prefers algae with low levels of phlorotannins or non-grazed parts (Wikström et al. 2006, Yun et al. 2010), while other studies have found no response or even attraction to phlorotanninrich parts (Jormalainen et al. 2001, Jormalainen et al. 2005) and thus further studies are necessary to investigate the relationship between Idotea spp. grazing and phlorotannin production in Baltic Sea Fucus spp.’ Those studies should consider a possible constitutive defence also in juvenile fucoid offspring and its possible drivers have to be determined in more detail.

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