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# **How climate change translates into ecological change:**

Impacts of warming and desalination on prey properties and  
predator-prey interactions in the Baltic Sea

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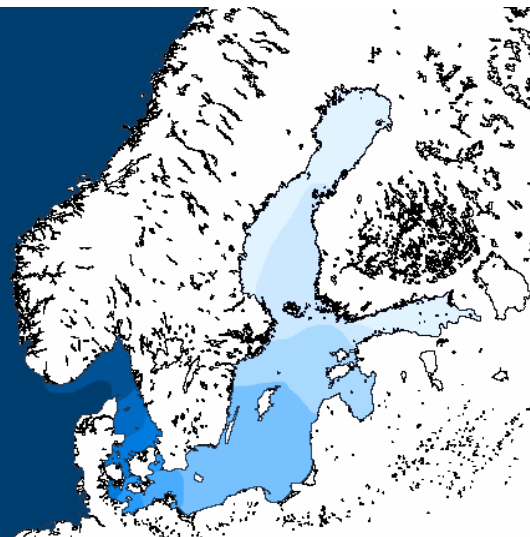
## **Dissertation**

zur Erlangung des Doktorgrades  
der Mathematisch-Naturwissenschaftlichen Fakultät  
der Christian-Albrechts-Universität zu Kiel

vorgelegt von

Ute Kossak

Kiel, 2006



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Referent/in: Prof. Dr. Martin Wahl

Korreferent/in: PD Dr. Martin Zimmer

Tag der mündlichen Prüfung: 15.12.2006

Zum Druck genehmigt: Kiel, 15.12.2006

gez. Prof. Dr. J. Grotemeyer

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Für meine Großeltern Armin und Gerda Busse  
die dies leider nicht mehr mit mir teilen können  
obwohl es ihnen sehr viel bedeutet hätte

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## Zusammenfassung

Die benthischen Artengemeinschaften in küstennahen Gewässern zählen zu den sowohl ökologisch als auch ökonomisch wichtigsten Systemen der Meere. Sie bestehen aus einem dichten Geflecht von Interaktionen der in ihnen lebenden Arten. Durch die Komplexität der Verknüpfungen, die häufig nicht nur zwei, sondern wesentlich mehr Organismen miteinander verbinden, ist es schwierig, diese isoliert zu untersuchen. Dennoch sind gerade solche Studien wichtig, denn die Forschung der letzten Jahre belegt, daß häufig geringe Abweichungen in Umweltparametern, wie zum Beispiel der Temperatur, Auslöser für weitreichende Veränderungen sein können. Die Folgen einer einzigen beeinflussten Interaktion können sich dabei kaskadenartig durch die gesamte Gemeinschaft fortsetzen. Aufgrund der globalen Klimaerwärmung wird es in Nordeuropa und der Ostsee in den nächsten Jahrzehnten nicht nur zu einer Erhöhung der Luft- und Wassertemperatur kommen, sondern auch zu Änderungen von Windstärke, Niederschlag, Strömungen, Salzgehalten und vielem mehr. Um die Folgen solcher Änderungen abschätzen zu können ist es wichtig, die Mechanismen ihrer Wirkung auf Artengemeinschaften zu kennen.

In der Ostsee werden benthische Gemeinschaften häufig von Miesmuscheln (*Mytilus edulis*) dominiert. Eine wichtige Interaktion in diesem Zusammenhang ist die Räuber-Beute-Beziehung der Muscheln mit einem ihrer Hauptfraßfeinde, der Strandkrabbe *Carcinus maenas*. Die Krabse kontrollieren die Abundanz der Muscheln. Fällt diese Kontrolle weg, kann *M. edulis* in kürzester Zeit fast alle anderen Arten verdrängen. Ist hingegen der Fraßdruck zu hoch und werden die Miesmuscheln zu stark dezimiert, geht dem System ein wichtiges Mitglied verloren, denn *M. edulis* stellt Siedlungssubstrat und Lückenhabitats für andere Organismen zur Verfügung und trägt in erheblichem Maße zur Nahrungsgrundlage vieler anderer Arten bei.

In dieser Arbeit habe ich mich besonders auf die Auswirkungen konzentriert, die die für die Ostsee prognostizierten Klimaveränderungen auf die Interaktion von Miesmuscheln und Krebsen haben können. Es wurde vermutet, daß sich die vorhergesagte Verminderung des Salzgehaltes negativ auf die Stabilität der Muschelschalen auswirken könnte. Da die Schalen der einzige Prädationsschutz dieser sessilen Organismen sind, würde eine geringere Stabilität den Räubern ihre Beute sehr viel leichter zugänglich machen und eine Verschiebung des Beutespektrums der Krabse wäre wahrscheinlich. Die ebenfalls vorausgesagte Temperaturerhöhung wird sich wahrscheinlich positiv auf die Wachstumsraten der Muscheln auswirken. Mit einer multifaktoriellen Versuchsanordnung konnte gezeigt werden, daß eine geringere Salinität sich tatsächlich in reduzierter Schalenstabilität niederschlägt. Zusätzlich wurde eine signifikante Interaktion zwischen den Faktoren Temperatur und Salzgehalt gefunden: bei niedriger Temperatur hatte der

Salzgehalt einen wesentlich geringeren Einfluß auf die Stabilität der Schalen als bei hoher. Für die Wachstumsraten war die Interaktion zwischen Salzgehalt und Temperatur von keiner Bedeutung, die positive Wirkung von erhöhter Temperatur wurde allerdings von dem wachstumshemmenden Effekt der verringerten Salinität ausgeglichen (vgl. Kapitel I). Der folgende Feldversuch, in dem die Wachstumsraten und Stabilität von Muschelschalen an verschiedenen Standorten in der Ostsee (d.h. unterschiedlichen Salinitäten) untersucht wurden, zeigte allerdings, daß die im Freiland sehr starken Unterschiede in Schalenstabilität nicht ausschließlich auf den Salzgehalt zurückzuführen sein können, da die Kontrollen im Labor keine solchen signifikanten Differenzen aufwiesen (vgl. Kapitel II). In einer abschließenden Untersuchung sollte geklärt werden, inwieweit sich die Änderungen der Schalenstabilität, die durch eine Reduzierung des Salzgehaltes um ca. 5 psu hervorgerufen werden, tatsächlich auf die Räuber-Beute Beziehung auswirken (Kapitel III). Die Ergebnisse von Fraßpräferenzversuchen mit zwei Krebsarten, *Carcinus maenas* und *Rhithropanopeus harrisi tridentatus*, machen deutlich, daß sich das Beutespektrum der Räuber tatsächlich verändert: beide Arten bevorzugten bei abnehmendem Salzgehalt größere Beute. Als Folge von reduziertem Wachstum und gleichzeitig erhöhtem Fraßdruck ist eine geringere Abundanz von Muscheln in der östlichen Ostsee wahrscheinlich, wohingegen für *M. edulis* in der westlichen Ostsee eine Verbesserung der Lebensbedingungen zu erwarten ist.



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## Summary

Benthic communities in coastal waters are among the ecologically and economically most important marine systems. Their species are densely linked by various interactions. The complexity of the interactions, which often connect not only two, but many organisms, makes it very difficult to study the isolated interactions. Such studies, however, are essential since recent research revealed that already small changes of ecological parameters, e.g. temperature, may have far reaching consequences. The effects of a single affected interaction can be carried forward to the entire community.

Due to the global climate warming, Northern Europe and the Baltic Sea will not only experience an increase in air and water temperatures within the next decades, but also changes in wind speed, precipitation, ocean currents, salinity and much more. To be able to estimate the consequences of such changes it is essential to know their impacts on benthic communities.

In the Baltic Sea, benthic communities are often dominated by blue mussels (*Mytilus edulis*). A key interaction in this context is the predator-prey interaction of mussels and their main predator, the shore crab *Carcinus maenas*. These crabs control the abundance of blue mussels: if this control disappears, *M. edulis* will rapidly rule out most other species in the habitat; if the predation pressure is too high, the mussel stock will be heavily depleted, and the community will lose an important species, since *M. edulis* provides numerous interstitial habitats and settlement substrates for other organisms. The mussels furthermore are the food basis of many species, such as fish, birds, crabs or sea stars.

In the present work, I concentrated mainly on the impacts of the predicted climate change scenario in the Baltic Sea on the interactions of blue mussels and shore crabs. It has been suggested that a decrease of salinity will have negative impacts on the mussel's shell stability. Since for this sessile species the shell is its only protection against predation, lowered shell stability would favour crab predation, leading to a shift in the crabs' prey spectrum. The predicted increase in water temperature, however, would possibly favour mussel growth.

In the course of a multifactorial experiment I could show that desalination is indeed reflected in diminished mussel shell stability. There were also significant interactions between the main factors temperature and salinity: the influence of salinity on shell stability was reduced at lower temperature. With regard to growth rates, on the contrary, the interaction between temperature and salinity was of no importance. The enhancing effect of increased temperature on growth rates, though, was compensated by the inhibiting impact of lowered salinity (Chapter I). Growth rates and shell stability of mussels from populations along the Baltic salinity gradient were investigated in a reciprocal transplant

experiment in the field. While there was a strong signal of diminished shell stability generated by reduced salinity in the field, no such significant differences were detected in the laboratory (Chapter II). To complete this study, I investigated the influence of reduced mussel shell stability – evoked by a salinity reduction in the range of 5 psu – on the interaction with predators. The results of prey selection experiments with two crab species, *Carcinus maenas* and *Rhithropanopeus harrisi tridentatus*, reveal an important shift in the predators' prey preference: both species selected larger prey when exposed to lower salinity (Chapter III). In consequence of reduced growth rates and simultaneously increased predation pressure, a decrease in mussel abundance is likely for the Eastern Baltic. For Western *M. edulis* populations, on the contrary, the predicted climatic changes will probably result in an improvement of living conditions.

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# Introduction

## Baltic benthic communities

Benthic communities are among the ecologically and economically most important ecosystems in the world (Costanza et al. 1997). In the Baltic Sea, benthic communities are commonly dominated by the blue mussel *Mytilus edulis* (Suchanek 1985, Reusch & Chapman 1997, Wahl 2001, Enderlein & Wahl 2004). Sometimes more than 90 % of the total biomass of shallow water communities consists of blue mussels (Kautsky & van der Maarel 1990, Reusch & Chapman 1997). Crab predation is one of the major factors in structuring benthic marine communities (Virnstein 1977, Leber 1985, Raffaelli et al. 1989), and the shore crab *Carcinus maenas* is known to counteract mussel dominance (Ropes 1968, Boulding 1984, Frandsen & Dolmer 2002). Therefore, the predator-prey interaction of these two species is of high importance for the Baltic ecosystem.

Due to its specific hydrographical and ecological conditions, the Baltic Sea is one of the most fragile ecosystems in Europe. Small shifts in the environmental conditions may have far reaching consequences for species' performance, local abundance and regional distribution (Arndt 1996, Lozán et al. 1996) because in this physiological demanding brackish habitat many species exist at the edge of their distributional range (Schlieper & Remane 1971, Westerbom et al. 2002, Bonsdorff 2006). The changes predicted by current climate models can be expected to have major impacts on at least two levels: mussel performance and mussel-crab interactions.

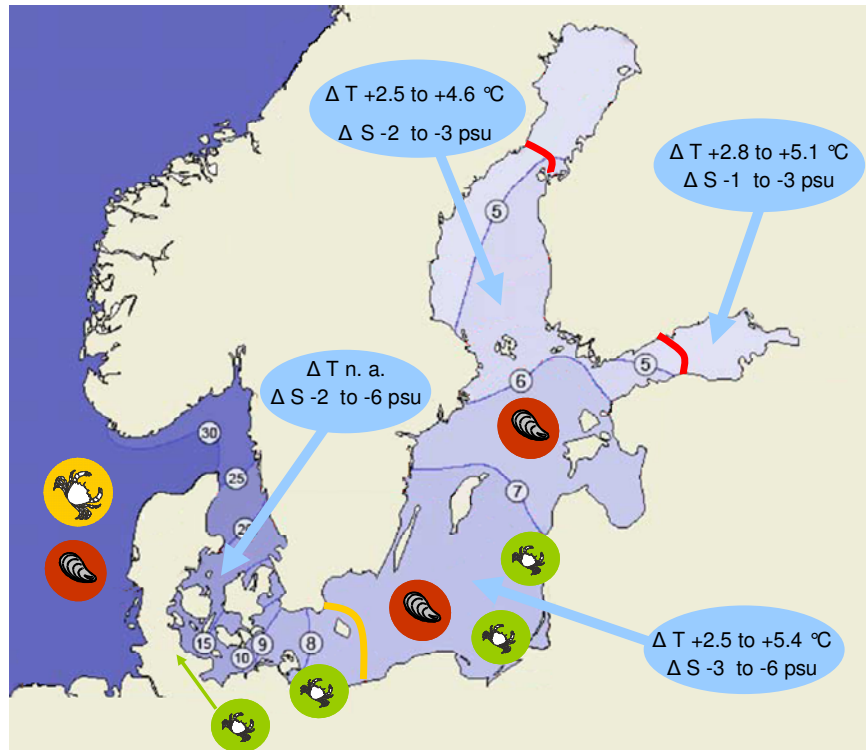
## Climate change in the Baltic region

Recent climate models predict drastic changes in many parameters for Northern Europe and the Baltic Sea. For the Western Baltic region (and a 'business-as-usual scenario' (HadCM3) relative to a reference period between 1960 and 1990), shifts in many environmental parameters such as temperature, CO<sub>2</sub> content, precipitation, salinity, wind speed, and ice cover have been observed or are predicted (Hupfer & Tinz 1996, Omsted et al. 2000, IPCC 2001a,b, Babarro & de Zwaan 2002, Lehmann et al. 2002, Walther et al. 2002, Meier 2006, BACC 2006). Of major importance for most organisms are presumably changes in temperature and salinity.

In the Baltic Sea yearly average temperature increased in the last century by 0.7°C which is faster than the average global warming (0.5°C, BACC 2006). Global climate model (GCM) simulations imply that regional warming over the Baltic Sea could be twice as high as the mean global temperature increase (BACC 2006). The extrapolation of climatic

change over the last 20 to 100 years predicts a rise of water temperature by up to 5°C in summer and up to 10°C in winter.

Salinity in the Baltic surface water is expected to decrease in a range of 3 to 5 psu because of increased yearly precipitation (plus 70-150 mm/y), along with an intensification of summer stratification (Hupfer & Tinz 1996, IPCC 2001, Graham 2004, Meier 2006). As surface salinity is mainly influenced by river runoff and precipitation over the Baltic (Meier 2006), the reduction in salinity should be more pronounced in summer than in winter time.



**Figure 1:** Salinity gradients and distribution ranges of species in the Baltic Sea.

Small crabs (green) = *R. harrisi*, for distribution see Kinne 1952, Jazdzewski & Konopacka 1993, Nehring 2000). Large crab (yellow) = *C. maenas*, mussel (red) = *M. edulis*, modified after Bonsdorff (2006). Salinity in psu, ΔT, ΔS = predicted changes in temperature and salinity (see Graham 2004 and Meier 2006).

Another parameter that is influenced by river runoff is eutrophication. The BACC report (2006) gives evidence that there might be an increase in nutrient transport to the Baltic Basin. Consequently, phytoplankton concentrations could rise, resulting in higher food availability for plankton feeders. Predictions of the various models do not only vary with season, but also with location (Figure 1).

Present climate models provide predictions regarding most physical parameters, but do not supply any information on the influence of such changes at the ecosystem level. Mussel responses to various single (and sometimes combined) factors such as temperature, pollution, hypoxia and salinity have been investigated (e.g. Böhle 1972, Cotter et al. 1982, Almada-Villela 1984, Björk et al. 2000), but there is a lack of knowledge concerning these interactions and ecosystem responses (Harley et al. 2006). Recent studies have shown the

dramatic impact of global change on interactions in various ecosystems. Small changes in, for instance, temperature, have strong effects: food webs can be destabilized (Emmerson et al. 2005), the equilibrium of species' abundance, supported by a key stone predator, can be shifted (Sanford 1999) and a mismatch between phyto- and zooplankton phenology can affect the food chain (Sommer 2005). Therefore, studies with the focus on the direct and indirect ecological effects of climate change on the Baltic communities and organisms are essential to fully understand the consequences of a changing climate.

## **Predator-prey interactions in the Baltic**

In the Western Baltic, mussels co-occur with a high density of predators, and Reusch and Chapman (1997) showed that highly abundant sea stars *Asterias rubens* were not able to completely control the enormous growth and recruitment potential of *Mytilus edulis*. They concluded that the mussels, without predatory control, could easily extend their dominant abundance to a 100 % cover of the substrate within one year. Laudien and Wahl (1999) observed this effect on substrata without direct contact to the bottom and consequently restricted access for predators, such as buoys and pontoons. Thus, biodiversity in these systems is highly dependent on mussel predation. Major predators differ between the Western and Eastern Baltic: In the Western part *A. rubens* and the shore crab *Carcinus maenas* feed on all sizes of mussels, but prefer prey smaller than 30 mm (Reusch & Chapman 1997, Leonard et al. 1999) while the periwinkle *Littorina littorea* forages on juvenile, freshly settled mussels (Wahl & Hoppe 2002). For the Eastern Baltic, losses to waterfowl and fishes (cyprinids and flounders) are reported by Kautsky (1981) and Westerboom et al. (2002).

*C. maenas* is restricted to the Western Baltic Sea (Bonsdorff 2006), but the presence of another brachyuran crab, the brackish mud crab *Rhithropanopeus harrisii tridentatus*, in the Baltic proper (Kinzelbach 1998) suggests similar crab predation pressure on Eastern *Mytilus* populations. Hence, *M. edulis* in the Baltic Sea is subject to crab predation along the entire salinity gradient from 5 to 33 psu.

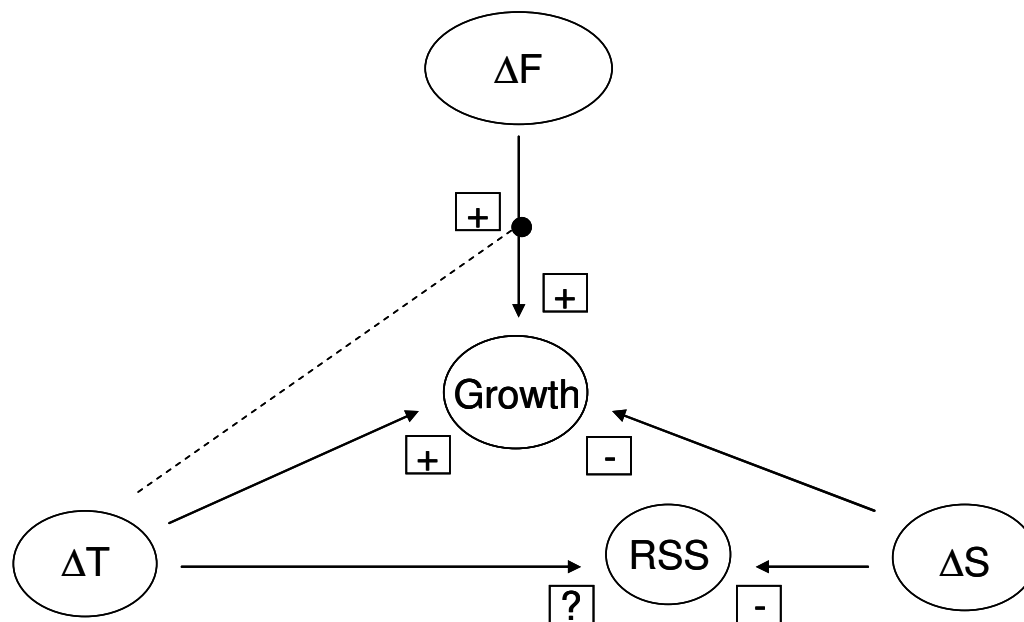
## Study organisms

### Prey - the mussel *Mytilus edulis*

Due to wide ecological tolerance, fast growth and high reproduction rates, *Mytilus edulis* is often highly abundant in the Baltic (Kautsky 1981, Wahl 2001). In the course of succession, mussels frequently outcompete other species and thus significantly reduce diversity, but simultaneously they act as ecosystem engineers by providing substratum and shelter for many associated species (Tsuchiya & Nishihira 1986, Kautsky & Evans 1987, Lohse 1993, Seed 1996, Commito et al. 2005) and by stabilizing soft bottom sediments (Lozán et al. 1996). As highly efficient filter feeders they functionally link phytoplankton and benthos and contribute to water purification (Kautsky 1981, Kautsky & Evans 1987, Lozán et al. 1996). Additionally, they are major components of the diets of starfish, crabs, fishes and sea birds (Kautsky 1981, Reusch & Chapman 1997, Westerbom et al. 2002). Hence, keeping in mind the enormous biomass of mussels, they represent a considerable part of the Baltic food source. Therefore, any change in the relative abundance of *M. edulis* in the Baltic shallow water will have far reaching consequences on community stability and dynamics, diversity, trophic interactions, and pelago-benthic processes and water quality.

Mussel features that most probably are affected by the predicted environmental changes are growth rates, shell stability and maximum size. In Baltic mussels, these characteristics seem to be affected by both salinity and temperature (Schlieper & Remane 1971, Kautsky 1982a, Tedengren & Kautsky 1986). Rising temperature and increased food availability are probably enhancing growth rates. Faster growth may reduce relative shell stability (Riisgard, pers. comm.). Salinity (i.e. concentration of minerals) is supposed to be positively correlated with shell stability (Schlieper & Remane 1971, Almada-Villela 1984, Kautsky et al. 1990), thus, along with salinity reduction we propose to find a decrease in shell stability (Figure 2).

Growth rates are important for competitiveness and reproduction (Kautsky 1982b) and both size and shell stability determine mussel susceptibility to many predators (Elner 1978, Hughes 1980). The mussels can escape predation by fast growth, either in body size or in shell thickness. Faster growth will lead to an earlier escape from predation by most consumer species (Elner & Hughes 1978, Enderlein & Wahl 2004) because larger mussels are less manageable and have thicker shells. On the other hand, changes in shell stability will affect only the consumption rate by those predators that crack the shell, such as crabs (Elner 1978) and birds (Nagarajan 2006). Fast growth will also improve competition for space, filtration rates and reproductive output (Riisgard & Randloev 1981, Kautsky 1982b, Riisgard et al. 2003).



**Figure 2:** Expected effects of altered temperature  $\Delta T$  ( $\pm 5^\circ\text{C}$ ), salinity  $\Delta S$  ( $\pm 5$  psu) and food availability  $\Delta F$  (doubled concentration) on growth rates and relative shell stability RSS of *M. edulis*. + positive effect, - negative effect, circle = interaction modulation, ? = unknown effect

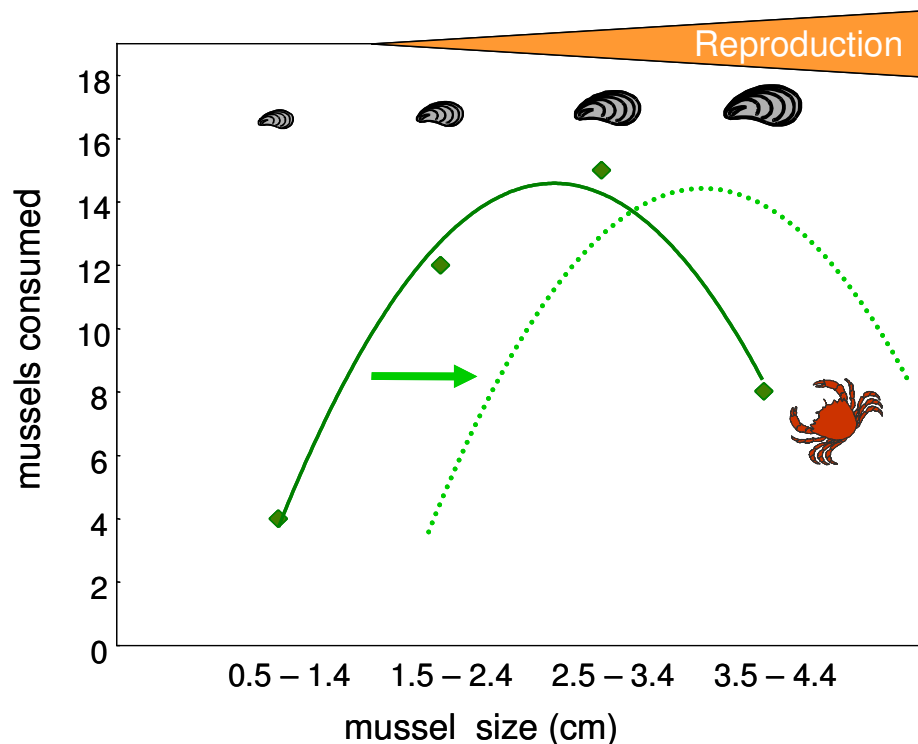
### **Predators – *Carcinus maenas* & *Rhithropanopeus harrisii tridentatus***

Crabs, and in particular the shore crab *Carcinus maenas*, are known to exhibit optimal foraging (Elner & Hughes 1978, Hughes 1980). This behaviour results in maximum energy uptake per unit energy spent by searching and prey handling. *C. maenas* uses various techniques to open its mussel prey and exhibits a high learning capacity for predatory skills (Ropes 1968, Elner 1978, Elner & Hughes 1978, Cunningham & Hughes 1984). According to Palmer (1981) and Boulding (1984), mussels can attain a size refuge beyond the critical size because many crab predators prefer small sized shell prey, which are not likely to damage claws (Juanes 1992). In the Kiel Bight, threshold sizes for *M. edulis* range between 33 mm shell length (sea stars) and 48 mm (crabs) (Reusch & Chapman 1997, Enderlein et al. 2003). However, the preferred size classes of *C. maenas* for mussel prey are much smaller, ranging from ca. 10 mm to 30 mm (Elner & Hughes 1978, Ameyaw-Akumfi & Hughes 1987, Enderlein et al. 2003). Shell thickness and shell stability are, besides prey shape and volume, important features on which *C. maenas* bases its foraging decisions (Boulding 1984, Mascaro & Seed 2001, Beadman et al. 2003).

*C. maenas* is abundant only in those Baltic Sea regions where salinity exceeds 10 psu (Arndt 1996), therefore this species' distribution will shrink at a decrease in salinity. However, in the same degree the area of distribution of another presumptive mussel predator, the mud crab *Rhithropanopeus harrisii*, will increase. This small brachyuran crab has been introduced from the Northwest Atlantic to Europe in the 19th century (Turoboyski 1973, Kinzelbach 1998, Nehring 2000 and references therein) and is now abundant in the Polish Baltic and adjacent estuaries (Turoboyski 1973, Jazdzewski & Konopacka 1993). It

also occurs along the German coast where salinity does not exceed 12 psu (e.g. in the Salzhaff near Wismar, Nehring 2000) and in the low-salinity Kiel Canal (Kinne & Rotthauwe 1952). *R. harrisii* feeds on small snails, algae and detritus, but mussel prey as *Dreissena polymorpha* and *Mytilus edulis* is also a principal food source (Kinne & Rotthauwe 1952, Tuboroyski 1973).

Assuming that temperature and food availability have a high impact on mussel growth (Kautsky 1982a) and that shell stability is related to salinity (Kautsky et al. 1990) we expect substantial changes in these mussel features (Figure 2). If the mussels' shell stability decreases in the course of salinity desalination, the crabs' preferred size classes could be shifted towards larger mussels (Figure 3). Mussels that have reached the refuge size are large enough to contribute to a high amount to the population's reproduction (Kautsky 1982b). With an upward shift of the predators' preferred prey size they would be under prolonged predation pressure, which, along with low growth rates, could diminish the reproductive success. Thus, a reduction in salinity could affect mussel abundance both directly (physiological stress) and indirectly (increased predation pressure, decreased competitiveness), resulting in fundamental shifts in Baltic benthic communities.



**Figure 3:** Optimal foraging in *Carcinus maenas*. Mussels consumed in 24 h. If mussel shell stability decreases, the optimal prey size could be shifted towards larger, reproductively more important mussels. Modified after Enderlein et al. (2003).



## Objectives

This study investigates how the predation-relevant features of the blue mussel *Mytilus edulis* are affected by the predicted climatic changes for temperature, salinity and food availability and if these possible changes are of relevance for the crab-mussel interaction. It does not account for the possible impacts on the physiology of the crabs and the resulting consequences for the predator-prey system. We also need to take into consideration that different *Mytilus* populations could be genetically adapted to local salinity conditions. Recently, many studies have been conducted on Baltic neighboring populations (see Riginos & Cunningham 2005 for review, a more detailed presentation of their results can be found in chapter II). Such genetic differences in salinity adaptation would follow the geographical shift in ambient salinity via larval dispersal, resulting in translocation of the respective *Mytilus* populations but not in local shifts in terms of growth rates or shell stability. Hence, in the case of genetic differences between populations concerning their adaptation to salinity, drastic changes at community level are improbable. By transplanting the mussels in a short period of time over sometimes large distances in the salinity gradient, we also simulated the species introduction process as it is frequently caused by ship hull fouling (Gollasch 1992). Thus, the results of this experiment do not only elucidate how Baltic mussel populations will react to climatic changes, but additionally give valuable evidence on the invasiveness of the species *M. edulis*.

In chapter I, the results of a first, basic experiment which was aiming at the understanding of the effects of the environmental parameters temperature, salinity and food availability on mussel growth rates and shell stability are presented and discussed. On the basis of the Kiel *Mytilus* population I tested the impact of each single environmental factor as well as the interactions between factors. In a multifactorial laboratory experiment, treatments reflected the predicted rise in temperature (+ 5°C), enhanced food availability (doubled concentration compared to natural conditions) and salinity changes in both directions (a range from 5 to 33 psu).

The study scope was then extended to mussel populations from all over the Baltic, looking specifically at the effects of changing salinity. Chapter II illustrates how a multilocal transplant experiment simulated the predicted reduction in salinity and how growth rates and shell stability of the different *Mytilus* populations were affected by the new environmental conditions. In order to verify the field experiment results, which reflect most probably not only salinity but any other environmental parameter such as temperature, food quality and quantity, currents, or light, the same experiment was run under controlled laboratory conditions.

The next challenge was to investigate whether presumable changes in mussel growth rates and shell stability are significantly affecting the crab-mussel interaction. In chapter III was

explored whether crabs can detect differences in mussel shell stability due to different ambient salinity, if they will select mussels with low shell stability and if the optimal prey size will change with changing ambient salinity. To test these hypotheses, mussels were cultivated in different salinity regimes for 4 to 12 months, and crabs were adapted to the experimental salinity for several weeks. Since the shore crab *C. maenas* is distributed in the Western Baltic Sea while the mud crab *R. harrisii* is gradually spreading from the Polish region, both species were considered major mussel predators and therefore included in the experiments.



## Chapter I

# Mussels Facing New Challenges: The Effects of Climatic Changes on a Baltic Key Organism

## Abstract

For the Baltic Sea, current global change models predict a warming of water temperature and an increase in precipitation rate. The latter is expected to reduce salinity and enhance eutrophication. Changes of these parameters, singly or in combination, may directly affect growth rates, shell morphology and shell stability, and indirectly the competitiveness and susceptibility to predation of one of the regional key species, the mussel *Mytilus edulis*. In a multifactorial experiment we showed that mussel growth rates increase with phytoplankton concentration only at higher temperature. Shell stability increases with temperature and salinity and was independent of food supply. There was substantial interaction among the three global change parameters. Expected effects of climatic changes are site-specific because extant regional conditions differ and predicted changes may shift them toward or away from the species' optimum. In the Western Baltic, we predict only small increases in shell stability but a stronger rise in shell growth. In the Baltic Proper populations, we do not expect any changes neither in shell stability nor in growth rates since the growth-enhancing effect of warming and the opposite effect of desalination will neutralize each other. For Eastern Baltic populations we expect a decrease in shell growth as well as in shell stability. Since mussels provide important ecosystem services (e. g. sediment stabilization, deceleration of water movements, water purification and habitat engineering), the predicted shifts in mussel abundance may have system-wide consequences. These results underline the importance of considering the interactions of several environmental parameters when studying the ecological impact of climate change.

## Introduction

Global climate change and its consequences have become one of the most urgent issues in the last decades. An increase in global average surface temperature by 0.6°C in the 20<sup>th</sup> century (IPCC 2001a) is only one of the alarming signals attributable to human activities (Santer et al. 1996, Tett et al. 1999, IPCC 2001a,b).

For the western Baltic region (and a 'business-as-usual scenario' (HadCM3) relative to a reference period between 1960 and 1990, the extrapolation of climatic change over the last 20 to 100 years and its modeling for the coming 50 to 100 years), Hupfer and Tinz (1996),

IPCC (2001a), Lehmann et al. (2002) and Walther et al. (2002) predict a rise of water temperature by up to 5°C in summer and up to 10°C in winter, a consequent reduction of ice cover by 30%, an intensification of summerly stratification, an increase in yearly precipitation (plus 70-150 mm/y) leading to a decrease of Baltic salinity of up to 5 psu (Omsted et al. 2000, Meier 2006). Predictions do not only vary with season, but also with location (Table 1).

**Table 1:** Climate Change. Predictions for the Baltic regions. After Graham (2004) and Meier (2006). Modeling followed the scenarios A2 and B2 as stated in the IPCC report (2001a, change of atmospheric CO<sub>2</sub> level from 353 ppm to 1143 and 822 ppm, respectively).

	Bothnian Bay	Bothnian Sea	Gulf of Finland	Baltic Proper	Belt Sea	Total Baltic
Temperature change [°C]	2.8 to 4.5	2.5 to 4.6	2.8 to 5.1	2.5 to 5.4	n.a.	2.6 to 5.0
Precipitation change [%]	13 to 23	11 to 24	12 to 22	6 to 15	n.a.	10 to 19
River runoff change [%]	11 to 40	6 to 28	- 1 to + 25	- 6 to - 30	n.a.	- 3 to + 16
Salinity change [psu]	- 1 to - 3	- 2 to - 3	- 1 to - 5	- 3 to - 6	- 2 to - 6	1.6 to - 4.2

As surface salinity is mainly influenced by river runoff and precipitation over the Baltic (Meier 2006), the reduction in salinity should be less pronounced in summer than in winter time. On the other hand, in the eastern and northern parts of the Baltic region winterly precipitation over land will reach the sea only after thawing in spring, and summerly desalination of surface waters may be enhanced by a more stable and longer stratification due to warming.

Models are not explicit about trends in eutrophication. They agree in that increased precipitation over Northern Europe will lead to enhanced river runoff into the Baltic (Hulme et al. 1999, Graham 2004). Since nutrient input into the Baltic is mainly through river runoff (Nehring & Aertebjerg 1996), eutrophication should also increase. Many efforts are made to reduce nutrient loads to the Baltic, for instance via environmental regulations. These efforts have led to a decrease in phosphate load. Though, we expect an increase in the use of artificial fertilizer due to the modernization of the agriculture in the Eastern European countries. Higher precipitation enhances the effect of nutrient washing out. Thus, an increase of nutrient loads via river runoff to the Baltic Sea is not improbable. With higher nutrient loads into the Baltic, we might expect higher phytoplankton concentration. This trend may be enhanced seasonally by a mismatch between phyto- and zooplankton phenology (Sommer 2005). Spatial heterogeneity is expected since nutrient loads will be highest in the vicinity of estuaries. Independently of nutrient load, primary production is increasing in the last decades as an indirect result of higher water turbulence (Lindahl 2003) and an extended growth period (Jones & Briffa 1995).

For shallow-water benthic organisms of the western Baltic, which are the main target of this study, warming and desalination may have the widest impact. Salinity may represent an additional stress for the species of predominantly marine provenience. Winterly warming may increase metabolic rates at times when plankton is scarce due to light limitation. Different species-specific reactions to these changes will have repercussions at higher organisational levels.

There is already evidence that global warming can lead to a re-distribution of species (Barry et al. 1995, Parmesan et al. 1999, Harley 2003). More indirectly, the physiological reaction to desalination of species with a wide temperature and salinity tolerance range, such as *M. edulis*, may not result in the species' disappearance but to a change in its competitiveness or susceptibility to consumption due to decreases in growth rates or shell stability, respectively. Such disruptions of interspecific interactions in food webs can have consequences for the stability of these systems (Emmerson et al. 2005).

Changes in salinity may have a particularly strong impact in the brackish Baltic, where the distribution of numerous species is determined by their osmotic tolerance (Schlieper 1955b, Schlieper & Remane 1971). The regional abundance of some species, such as crabs (*Carcinus maenas*), sea stars (*Asterias rubens*) or gastropods (*Littorina littorea*), may shift substantially even when the reduction in salinity appears small (Arndt 1996). Additionally, salinity seems to be one main factor affecting shell growth and maximum size of *M. edulis* in the Baltic (Kautsky 1982a, Tedengren & Kautsky 1986). Westerbom et al. (2002) showed that a difference of only 1.5 psu in mean salinity was sufficient to produce differences in growth rates of two *Mytilus* populations in a field study. Shell stability may also be influenced by environmental factors. It is a general yet unproven assumption that lowered salinity reduces shell thickness, and that fast-growing mussels produce thinner and more fragile shells.

In the past, isolated effects of many environmental factors like temperature, salinity, toxins or food availability on mussels have been studied (e.g. Schlieper & Remane 1971, Boehle 1972, Almada-Villela et al. 1982, Almada-Villela 1984, Bjoerk et al. 2000). However, most environmental factors do not operate in isolation, but interact with others.

Looking at environmental factors in isolation bears the risk of misjudging their ecological effects. Interactions among environmental variables can be extremely complex and the sum effect may be inflated by synergistic or reduced by antagonistic interactions. Moreover, the complex results of experiments with multiple stressors cannot be predicted from examining the environmental variables in isolation (Maslin 2004, Przeslawski et al. 2005). To add a further level of ecological complexity, we also need to consider that changes in morphology, behavior or life history of a species may be amplified by a resulting modulation of interspecific interactions such as competitiveness or susceptibility to

predation. Thus, there is an urgent need for information on the interactions both on the factor as on the response side.

The blue mussel *Mytilus edulis* Linnaeus (1758) is one of the most important benthic species in the Baltic Sea, creating habitats for a large number of associated species and providing food for invertebrates, fishes and sea birds (Kautsky 1981, Tsuchiya & Nishihira 1986, Seed 1996).

Mussel beds stabilize soft sediments, decelerate water movements, and, by their high filtration activity, contribute to the purification of the water body (Lozan et al. 1996). Any climate-driven change in mussel abundance will be amplified on the community level by the importance of these ecosystem services. In many marine shallow water habitats, mussels are competitively dominant due to high reproduction rates, fast growth and wide ecological tolerance when insufficiently controlled by predators (Kautsky 1981, Dobretsov & Wahl 2001, and refs therein). Thus, the blue mussel is one of the key players in the Baltic ecosystem, and any change in its life history, its ecological performance and the interaction with its predators may have far-reaching consequences for the whole ecosystem. Mussel features that most probably are affected by the predicted environmental changes are growth rates and shell stability. Growth rates are important for competitiveness and reproduction and both growth rate and shell stability determine mussel susceptibility to many predators. Thus, the vulnerability of *M. edulis* with regard to one of its major consumers, the shore crab *Carcinus maenas*, mainly depends on size and stability of the shell. The mussel can escape predation by fast growth, either in body size or in shell thickness. Blue mussels in the Baltic Sea are small compared to the mussels in oceanic conditions (Schlieper & Remane 1971, Kautsky 1982a, Bulnheim & Gosling 1988, Kautsky et al. 1990). This is believed to be due mainly to osmotic stress at low salinities (Tedengren & Kautsky 1986, Tedengren et al. 1990). Additionally, Baltic mussels have thinner shells than their conspecifics in the North Sea (pers. observation). The reason for this remains unclear. Faster growth will lead to an earlier escape from predation by most consumer species (Elnor & Hughes 1978, Enderlein & Wahl 2004) whereas changes in shell stability will affect only the consumption rate by those predators which crack the shell, such as crabs. Fast growth will also improve competition for space, filtration rates and reproductive output (Riisgard & Randloeve 1981, Kautsky 1982b, Riisgard et al. 2003).

In a multifactorial laboratory experiment, seven different levels of salinity were fully crossed with present and future temperature, and ambient or doubled phytoplankton concentration. Treatment levels simulated present and future conditions at different sites in the Western Baltic according to generally accepted climate models (Beniston et al. 1998, IPCC 2001 a,b, Omsted et al. 2000, Meier 2006). The objective of this study was to evaluate how these key traits, growth rate and shell stability in the blue mussel *M. edulis*, are affected by predicted climate change. Based on the observed responses of growth rates and shell

stability to the simulated climate changes we would be able to predict the reaction of mussels to future climate conditions. Many other shell building organisms, in particular other bivalves, but also species like barnacles or serpulids, should face similar physiological challenges. Since mussel beds with all their ecological interactions to other species are widespread not only in the Baltic, but also worldwide in many marine and brackish systems, we consider them a model system for many highly productive ecosystems. The Baltic Sea being a high productive coastal ecosystem belongs to the ecologically and socio-economically most important ecosystems of the world (Harley et al. 2006) and is among the first to be threatened by global changes due to anthropogenic influences (IPCC 2001a). Environmental conditions in the Baltic are comparable with conditions in many other estuarine systems. Therefore the understanding of the interactive mechanisms of different variables on a Baltic model organism will provide information how shifts in environmental factors may influence the functioning of brackish ecosystems.



## Materials and methods

### Study organism

Juvenile blue mussels *Mytilus edulis* Linnaeus (1758), with an initial shell length of 5 to 9 mm, were collected from settlement panels deployed in the Kiel Fjord 5 months earlier (August 2003). The mussels were kept in filtered sea water (ca. 17 psu) in the lab at 12°C for two months before the start of the experiment and were daily provided with natural plankton (20-100µm) in natural concentration from the Baltic Sea.

In a 3-factorial indoor-mesocosm experiment, juvenile blue mussels were grown under different salinity, temperature and food regimes in an attempt to simulate predicted future environmental conditions.

### Environmental parameters

#### Salinity (S)

Initial salinity was 17 psu. Experimental salinities were 5, 12, 17, 20, 24, 29, and 34 psu, a range which covers the whole salinity gradient where *M. edulis* naturally occurs. Prior to the experiment, test mussels were gradually (5 psu per week) adapted to the experimental salinities. Salinities higher than 17 psu were obtained by adding marine salt to natural Baltic Sea water. Salinities lower than 17 psu were obtained by diluting Baltic Sea water with fresh water. Salinity was measured with digital a conductimeter (Cond 330I, Tetracon 325, WTW Germany) to the nearest 0.1 psu.

#### Temperature (T)

Temperatures were (i) T1 = ambient Kiel Fjord water temperature (February till May, 20 - year - average for a given calendar week, or (ii) T2 = T1 plus 5°C to simulate conditions 50 years into the future. T1 and T2 ranged from 6°C to 12°C and from 11°C to 17°C, respectively. Temperature was kept constant in two separated climate chambers.

#### Food concentration (F)

There are no precise predictions concerning future phytoplankton concentration, though there is evidence that primary production increases due to climate change (Lindahl 2003). We therefore arbitrarily used typical present day values for phytoplankton concentration and a doubling of that for possible future conditions in high productivity areas like estuaries. Food consisted of cultured algae (*Dunaliella* sp. and *Rhodomonas* sp.) in (i) typical ambient food concentration during experimental time (F1,  $3 \times 10^3$  cells/ml, Clausen & Riisgard 1996) and (ii) increased food concentration (F2,  $6 \times 10^3$  cells/ml). Fresh food (adjusted to experimental salinity) was dripped (20 ml/min) into the experimental units for 2h each day. Air bubbling kept the algae in suspension.

### Setup and processing

At each of the seven salinities, four treatment combinations were applied (low temperature + low food concentration = T1F1, low temperature + doubled food concentration = T1F2, high temperature + low food concentration = T2F1, high temperature + doubled food concentration = T2F2). The number of replicates was five (salinities 12 and 17) or two (salinities 5, 20, 24, 29, 34). Light period was 10 hours/day, with an intensity of 1000-1500  $\mu\text{mol}/\text{m}^2/\text{sec}$ . The experiment was conducted from February 2004 to May 2004. This time period was chosen as in the Baltic mussel growth rates are normally highest in early spring and summer (Kautsky 1982b).

Each experimental unit consisted of a 2 l aquarium. Each aquarium contained 20 mussels, 10 of them individually tagged with 2 mm diameter opalith discs, glued to the mussel shell after removing the periostracum with sand paper. Growth was measured in shell length (from umbo to shell edge, longest distance). Individual growth of the tagged mussels was measured with a digital caliper to the nearest 0.1 mm and growth rates per week were calculated. Growth of all ten mussels was averaged. This provided one growth value per replicate (aquarium) with dampened variability in growth (Kautsky 1982a) among genotypes. The remaining ten untagged mussels were used to measure shell stability. For this purpose, at the end of the growth experiment, mussels were deep frozen ( $-18^\circ\text{C}$ ) for one week before processing. The soft body was removed from the shell. Shell stability was measured as shell breaking resistance.



**Figure 4:** "Shell cracker", device for assessment of shell stability.

For this purpose, the left shell was laid flat on its opening and weight gradually added to a central  $\text{mm}^2$  at the highest point of the shell until it broke (Figure 4). Breakage pressure (= shell stability) was calculated and is given as  $\text{g}/\text{mm}^2$ . Shell stability measurements were done with 5 specimens from each experimental unit and subsequently averaged. Because shell stability increases with mussel size, shell stability was standardized for unit mussel size by dividing by shell length. This yielded the relative shell stability (RSS).

## **Data analysis**

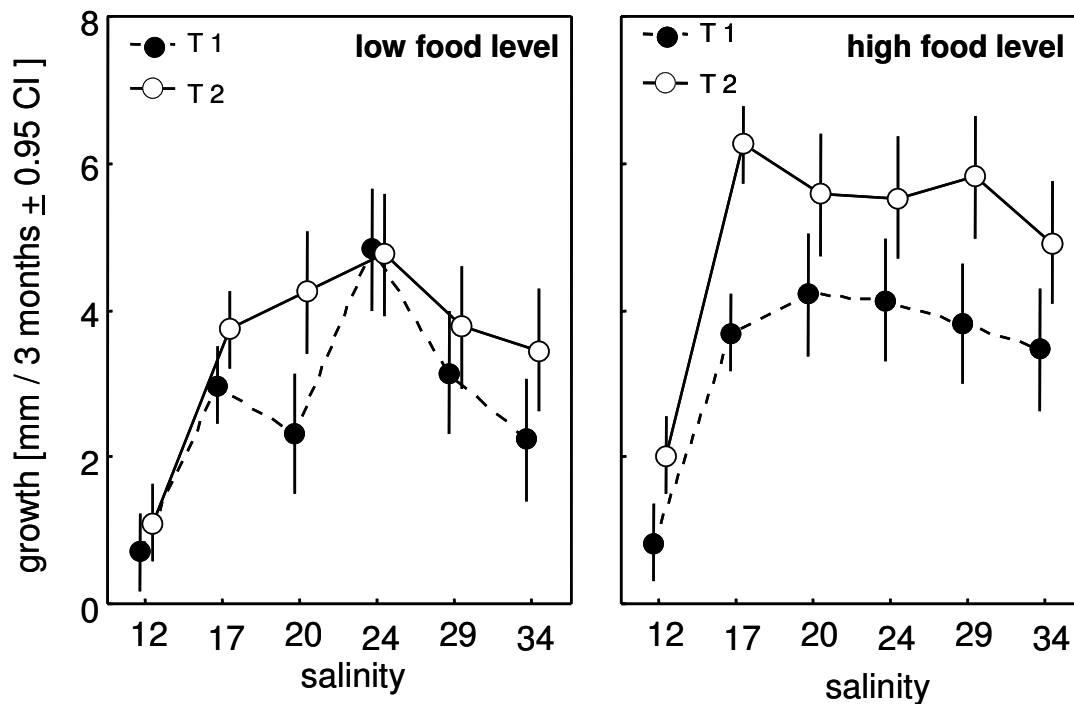
Differences in the effects among factor levels and interactions between main factors (salinity, temperature, food) were analyzed by a 3-factorial ANOVA after testing for normality of distribution and homogeneity of variances. The significance level was 0.05. The effects of climatic change were analyzed using log effect ratios of growth rates and shell stability (mussel property under predicted conditions divided by mussel property under present conditions). Data for meta-analysis were pooled over both food levels, when food concentration had no effect on a variable, which was the case for stability but not for growth.

## Results

The experiment lasted for 12 weeks. All mussels kept at 5 psu died within the first 8 weeks. For this reason, the following results are restricted to the salinities 12 to 34 psu.

### Growth rates

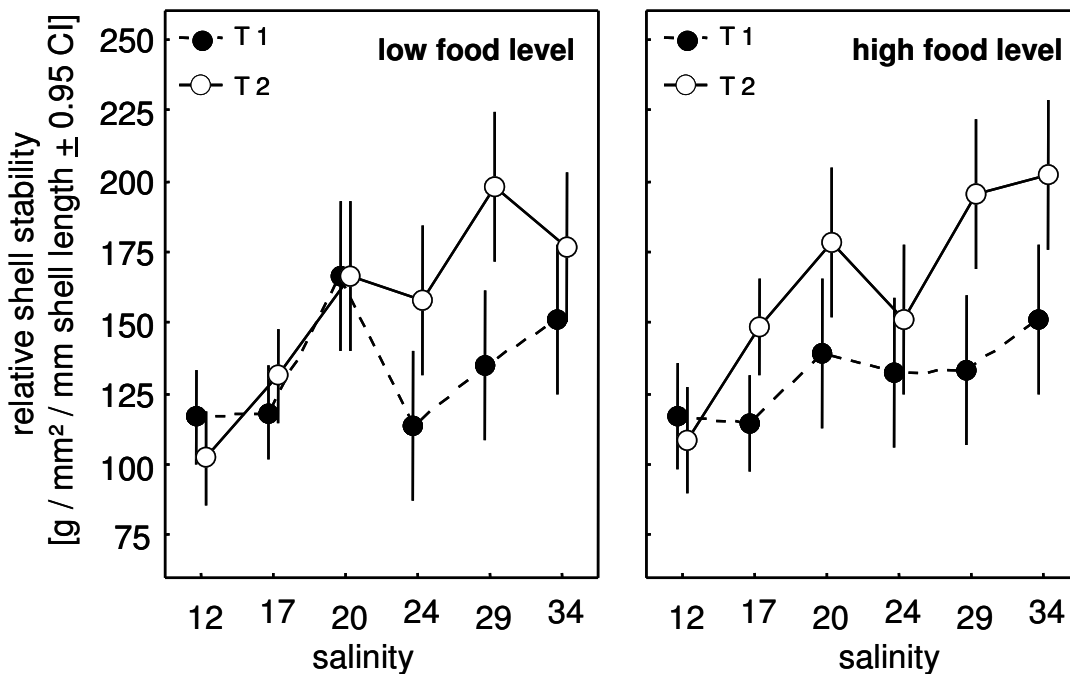
Growth rates were significantly influenced by salinity S, temperature T, and food concentration F (Table 2). Interactions were found between the main factors S - F and T - F, but not between T - S, (Table 2). Warmer temperature led to faster growth, this effect being enhanced by higher food concentration F<sub>2</sub> (Figure 5). More food produced more growth only when temperature was higher. Growth rates significantly decreased when salinity was shifted from 17 to 12 psu, and tended to be lower at salinities higher than 24 (Figure 5). The shape of this relationship seemed quite stable under different food – temperature regimes.



**Figure 5:** *Mytilus edulis* – growth rates [mm shell length / 3 months] ± 0.95 confidence interval. Open circles: T1 = ambient water temperature, filled circles: T2 = ambient water temperature +5°C. Low food level = 3x10<sup>3</sup> cells/ml, High food level = 6x10<sup>3</sup> cells/ml.

### Shell stability

Shell stability was significantly influenced by S and T but not by F (Figure 6). There was a significant interaction between the main factors S and T (Figure 6). At lower temperature T1, salinity had no effect on shell stability. At higher temperature T2, on the other hand, stability was directly related to salinity. Stability was significantly greater at the two highest compared to the two lowest salinities. A positive linear correlation between growth rates and shell stability was found for T2 ( $r^2 = 0.41$ ,  $p < 0.05$ ), but not for T1. Thus, enhanced growth due to increased temperature and eutrophication had a positive effect on the shell stability of Baltic mussels.



**Figure 6:** *Mytilus edulis* – relative shell stability [kg/mm<sup>2</sup>/mm shell length] ± 0.95 confidence interval. T1 = ambient water temperature, T2 = ambient water temperature +5°C. Low food level = 3x10<sup>3</sup> cells/ml, high food level = 6x10<sup>3</sup> cells/ml.

### Effects of predicted climate change

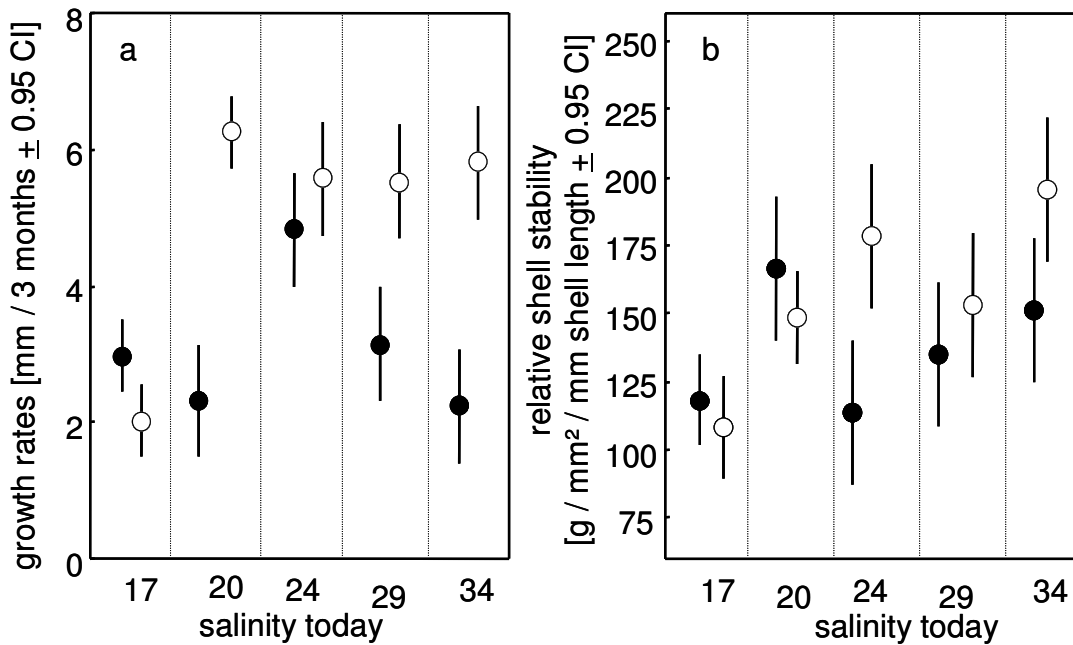
Climate change simulation (5°C warmer and less saline) lead to significant changes in growth rates and shell stability (Figure 7). The meta-analysis (Figure 8 and Figure 9) of log effect ratios (effect of future conditions divided by the effect of present conditions) shows that for mussels in low saline conditions the predicted shifts will lead to significantly reduced growth rates and shell stability. Mussels in higher ambient saline conditions, on the contrary, show significantly enhanced growth rates and shell stability.

**Table 2:** *Mytilus edulis*. Statistical results of a 3-factorial ANOVA for growth rates (a) and relative shell stability (b). S = salinity, T = temperature, F = food concentration.

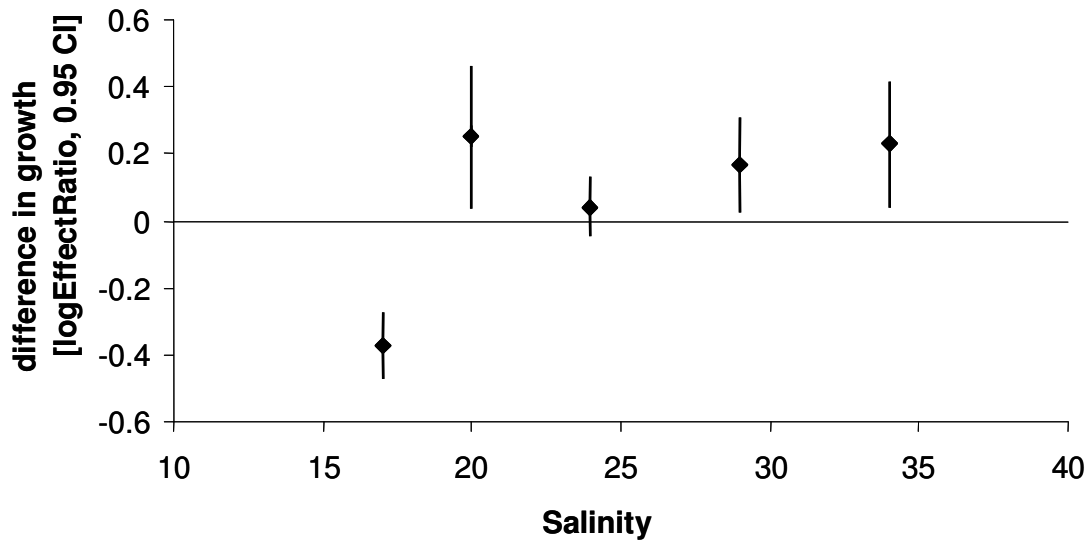
a) growth	SS	df	MS	F	p
S	135.36	5	27.07	79.00	p < 0.01
T	22.95	1	22.95	66.96	p < 0.01
F	17.55	1	17.55	51.21	p < 0.01
S + T	2.94	5	0.59	1.72	0.148
S + F	6.00	5	1.2	3.50	p < 0.01
T + F	2.71	1	2.71	7.91	p < 0.01
S + T + F	2.53	5	0.51	1.48	0.216
error	16.45	48	0.34		

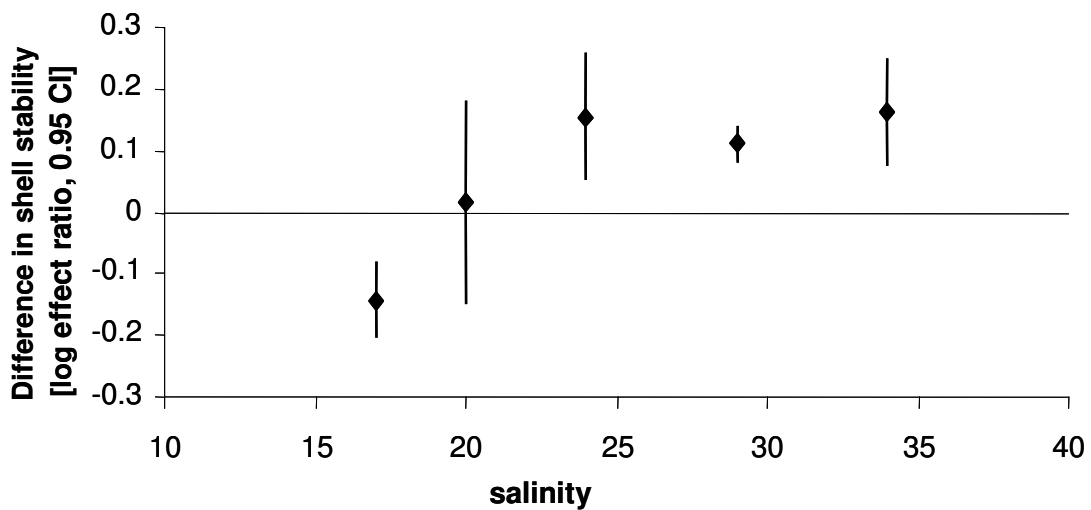
b) shell stability	SS	df	MS	F	p
S	34154	5	6831	19.87	p < 0.01
T	11064	1	11064	32.18	p < 0.01
F	134	1	134	0.39	0.535
S + T	8988	5	1798	5.23	p < 0.01
S + F	550	5	110	0.32	0.898
T + F	441	1	441	1.28	0.263
S + T + F	1386	5	277	0.81	0.551
error	15815	46	344		



**Figure 7:** *Mytilus edulis*. Growth and relative shell stability under today's conditions in comparison with those under predicted conditions. Predicted = temperature elevated by 5°C, salinity lowered by 3 – 5 psu, food availability doubled. Filled circles – today ambient conditions, open circles - predicted conditions. Vertical bars show 0.95 CI.



**Figure 8:** Log effect ratio of growth rates (predicted/present conditions). Means  $\pm$  0.95 CI are shown. Negative values indicate a decrease in growth rates, positive values indicate enhanced growth.



**Figure 9:** Log effect ratio of shell stability (predicted/present conditions). Means  $\pm$  0.95 CI are shown. Negative values indicate a decrease in shell stability; positive values indicate enhanced shell stability.

## Discussion

Growth rates of the blue mussel *Mytilus edulis* were significantly influenced by salinity (S), temperature (T), and food supply (F), whereas shell stability was significantly influenced by S and T, but not by F. In both cases there were strong interactions between the different factors, which underscores the importance of testing climate change parameters in combination.

### Influence on shell growth

Salinities lower than 17 psu proved detrimental for the blue mussels: at 12 psu, growth rates decreased significantly, while at 5 psu all mussels died within 8 weeks. During the experiments of Qiu et al. (2002), specimens kept at 5 psu died after only 6 days. This underlines the fact that not all mussel populations are able to adapt to conditions corresponding to the extremes of the species' distributional range.

Salinities higher than 20 psu, however, did not lead to a further increase in growth rates (except for some of the 'low food' treatments). In contrast, there was a trend of decreasing growth from 24 psu to fully marine conditions (34 psu). This is consistent with the findings of several other authors (Boehle 1972, Kautsky 1982a, Seed 1996, Westerbom et al. 2002). Almada-Villela (1984) found that growth of mussels at 22.4 psu was significantly higher than growth rates at 16, 12.8 or 6.4 psu, but also slightly higher than that of mussels at 32 psu.

Almada-Villela (1984) suggests that the lower threshold for any shell growth is close to 12.8 psu. Malone & Dodd (1967) state that the calcification process in mussels that are not adapted to a reduced salinity is depressed at 14.7 psu. However, *M. edulis* can tolerate salinities much lower than 12 psu and penetrate far into the inner Baltic (Kautsky 1981, Tedengren & Kautsky 1986). Among the limited number of species that have managed to adapt to the conditions of extremely reduced salinity in the Baltic Sea, blue mussels are one of the most tolerant. They are able to exist and to reproduce in ambient salinities as low as 4-5 psu (Schlieper & Remane 1971, Davenport 1979, Almada-Villela 1984, Westerbom et al. 2002). But beside survival, low salinity levels can also reduce life span and efficiency of reproduction and recruitment in *M. edulis* (Kautsky 1982b, Kautsky et al. 1990).

In nature, salinity interacts with other parameters. The observation that brackish waters may appear suitable for high mussel growth rates (Belding 1931 in Almada-Villela 1984, Pratt & Campbell 1965 in Almada-Villela 1984), may rather be due to better feeding conditions in these particular environments, i. e. lagoons and estuaries (Seed 1976 in Almada-Villela 1984). In our experiment, food concentration was controlled and it is apparent that salinity in the meso- to oligohaline range per se reduced growth rates.



Temperature had a significant influence on growth rates; however, it was not the strongest determining factor. Our results underline the findings of Kautsky (1982a) that salinity seems to be the main factor controlling mussel growth in the Baltic, interacting with temperature, food supply, light, population structure and other factors. Almada-Villela et al. (1982) found a broad temperature range (5 to 20 °C) in which *M. edulis* growth occurred. Temperatures above 20 °C lead to a sharp decrease in growth rates. At temperatures below 5 °C, growth rates were constant but low, combined with a reduction in faeces production. However, temperatures applied in this study ranged from 6 to 17 °C and should therefore perfectly fit in the range where growth occurs. Beyond 12 psu, warmer conditions ( $\Delta$  5 °C) accelerated growth by 25% to 50%, especially so under enhanced food conditions.

### **Influence on shell stability**

Our assumption of reduced shell stability of mussels growing in less saline water was confirmed by the results. Again, this effect was temperature dependent being significant in the warmer regime, while at the lower temperature only a trend towards reduced shell stability could be seen. Malone & Dodd (1967) reported that calcification in *M. edulis* occurs from 5 to 23 °C and in a salinity range of 20 to 37 psu. In our experiment, shell formation occurred at a much lower salinity level (12 psu), but at a far reduced rate compared to higher salinities. The effects of a disturbed shell building process are reflected by the reduced shell stability at low salinity levels.

Our study is the first to look at effects of S and T on the shell stability. It is known that Baltic mussels are small and thinner shelled compared to the mussels in oceanic conditions (Schlieper & Remane 1971, Kautsky 1982a, Bulnheim & Gosling 1988, Kautsky et al. 1990); this is believed to be due to osmotic stress at low salinities (Tedengren and Kautsky 1986, Tedengren et al. 1990). However, mussels reach peak performance in this regard at 25 psu and not under fully marine conditions. Climate driven changes in shell stability and growth, positive or negative, may have severe consequences for the mussels, as for this sessile, non-toxic organism the shell is its major protection against predation.

Blue mussel populations in the Baltic Proper are limited by food and space availability and by predators like the shore crab *C. maenas* or the sea star *Asterias rubens*. In some places, however, predation plays a key role in distribution (div. authors in Westerborn et al. 2002). The threat by predators like crabs, gulls or fish may be counteracted by increased shell thickness (Smith & Jennings 2003). For most predators, size and energy content (e.g. the growth rates) of the mussel are of highest importance. For shell cracking predators like crabs, fish, eiders and sea gulls, the mussels' performance in terms of shell stability is just as important as its growth. Predation pressure on a single blue mussel specimen by *Carcinus maenas*, for instance, is affected by the mussel's shell length and shell thickness (Enderlein 2000). Thus, mussels can escape predation in at least two different ways: either

they escape by growth, or they protect themselves by the development of a thick and resistant shell. An early escape from a predator's prey spectrum will favor individual survival, successful reproduction and ultimately population growth.

Since both parameters (growth rate and shell stability) are strongly influenced by environmental factors, climate change will presumably not only directly affect the mussels' fitness in terms of reproductive success but also its susceptibility to predation. Other biotic factors such as mechanical stress by epibiotic organisms, interspecific competition for food and space as well as intraspecific competition also impact the mussel's performance. But an enhanced susceptibility to predation can overrule other effects.

The strong interactions between main factors illustrate that the effects of multifactorial changes as happen in the course of climate change or introduction of species into new habitats can not be extrapolated by the isolated effects of single factors. Some authors report similar results for other response variables: Cotter et al. (1982) found an interaction of salinity and temperature with respect to the vulnerability of exposure to zinc. Environmental stress was shown to lead to higher susceptibility of mussels towards lack of oxygen (Babarro & de Zwaan 2002) or to infection (Lenihan et al. 1999). In general, however, the multiple stressor approach is the exception (Vinebrooke et al. 2004). Our results show clearly that climate change effects may depend on the starting conditions, e.g. salinity. At a salinity of 17 or below climate change as simulated here produces different results than at medium and full marine salinities. Therefore, effects will be discussed separately.

### **Effects of predicted changes on mussels living in the E Baltic (17 psu & below)**

In the scenario of a steady warming, a reduction in salinity and an increase in food availability in the Baltic Area as predicted by several models (Hulme et al. 1999, Omsted et al. 2000, Graham 2004, Meier 2006), mussels in the eastern Baltic will experience a reduction in growth rates as well as in shell stability (Figure 8). The desalination-induced decrease in growth rates is only partially compensated by warmer temperature in combination with higher food availability (Figure 5). If salinity decreases without a rise in temperature, a loss in shell stability ensues (Figure 6). More food allows higher growth rates when temperature is high, but not at lower temperature. However, it is not very likely that the prediction of warming will not come true. Food has no effect at all on shell stability. Consequently, for the eastern *Mytilus* populations we predict several ecological consequences of the predicted shifts in their environment. First, a reduction in shell stability is likely to increase the mussels' vulnerability towards their shell-cracking predators, e.g. the crabs. Additionally, when growing slowly, the mussels stay under predation pressure by all consumers for a longer time. Griffith and Hockey (1987) suggest that mussels of about 10 to 60 mm pass through a "window of vulnerability" to predators because most of them

are able to feed on small mussels. If mussels grow more slowly, intraspecific competition may decrease but the window is 'wider', thus increasing the relative importance of predation. Simultaneously, the interspecific competition increases, and the mussels' abundance might become reduced in places where they are dominant in the present. Since in mussels reproductive output is related to size, this effect could be enhanced by a reduced reproductive success.

Finally, a shift in salinity will lead to changes in the distribution of *M. edulis*. In the Gulf of Finland, *M. edulis* lives at the edge of its salinity tolerance at 4.5 psu (Seegerstrale 1944 in Westerstrom et al. 2002). A further decrease in salinity is not tolerable for this species and will shift its distribution southwards and westwards. In regions where *Mytilus* lives in the deeper water to avoid the low saline surface water, the mussels could be forced to move even deeper, where feeding conditions may be not sufficient, and the risk of hypoxia is higher.

#### **Effects of predicted changes on mussels living in the W Baltic (20 psu & higher)**

Mussels of the western part of the Baltic will experience quite different effects. In populations presently living at salinities above 24, a reduction in salinity does not decrease but may even increase growth rates. At all higher salinity levels, an increase in temperature as well as a rise in food availability increases growth rates (Figure 5). In the case of no change in temperature and food, but a decrease in salinity, shell stability slightly decreases, while food alone has no effect on shell stability and a rise in temperature enhances shell stability (Figure 6). Thus, for the predicted conditions, we expect both enhanced growth rates and increased shell stability for western *Mytilus* populations (Figure 7 - Figure 9).

These changes in the mussels' performance are likely to favor their resistance to predators. Their faster growth allows them to outgrow the "window of vulnerability" (Griffith & Hockey 1987) at an earlier life stage – under the assumption that consumers are not affected by climate change. Fast growing mussels intensify intraspecific competition for space and food, but may perform better in the interspecific competition – if competing species are not similarly affected by climate change. Besides the shift in the predator-prey interaction we therefore expect a higher abundance and enhanced dominance of the blue mussels in the western Baltic.

#### **Consequences for the ecosystem**

Mussel beds combine the capacity of a sediment trap with the ability to actively filter the water and thus contribute in two different ways to the water purification. In the long run they can help restoring macrophyte communities (Reusch et al. 1994). A decrease in mussel abundance as we predict it for the Eastern Baltic would most probably lead to a reduction

in water clearing by mussels. This may entail increased stress for macrophytes. Mainly due to eutrophication, in many parts of the Baltic the former macrophyte dominated communities retreat from deeper water layers and even tend to switch to benthic ephemerals or phytoplankton dominated communities. Even if nutrient loads decrease, macrophytes often do not restore, probably due to water turbidity (Munkes 2005). Rooted macrophytes, which can act as particle traps, could decrease the water turbidity. It is likely that other filtering organisms will benefit from the reduction in mussel abundance and will occupy this ecological niche, but none of them matches the blue mussel in the efficiency of filter feeding and sediment trapping. Also the habitat engineering function of mussels is not performed by other regional species in a comparable way.

The predicted climate change is unequally distributed among the seasons. Thus, warming and enhanced precipitation will mainly take place in the winter months. But even moderate warming in summer should not be favourable for the mussels in most cases, as even present day summer temperatures are already at the mussel's upper tolerance limit in many areas and further warming could be detrimental. While rainfall is predicted to be reduced in summer, the high winter precipitation stays immobilized as ice or snow in most eastern and northern Baltic regions until the spring thaw. Thus, the main freshwater and nutrient input can be expected in spring and early summer, the season of plankton blooms and maximum mussel growth. Because water stratification is more stable in future warmer summers, surface layers may be quite desalinated despite presumably reduced summer precipitation.

Higher temperatures in winter time, on the other hand, represent a different threat to *M. edulis*. Honkoop & Beukema 1997 found that mussels regularly lose body mass in winter time, mainly due to a lack in food availability, and this effect was even higher in mild winters. Since phytoplankton in winter is limited by light not temperature, higher metabolic activity of mussels in warmer winters will lead to enhanced loss of soft body mass. The simultaneous decrease in salinity could strengthen this effect, leading not only to thinner shells but also to a decrease in growth rates.

Based on the knowledge of the interactive effects of salinity, temperature and eutrophication (e.g. food availability) we may speculate about the performance of the highly invasive species *M. edulis* in new regions. With their high tolerance to physiologically demanding conditions, rapid growth in a wide range of ecological niches and a high reproductive potential, mussels possess a high invasive potential. At least in areas where salinity exceeds 24 psu and where water temperature is not substantially higher than 20°C, the mussel's invasiveness should be high and even increase during predicted climate change.

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## Conclusion

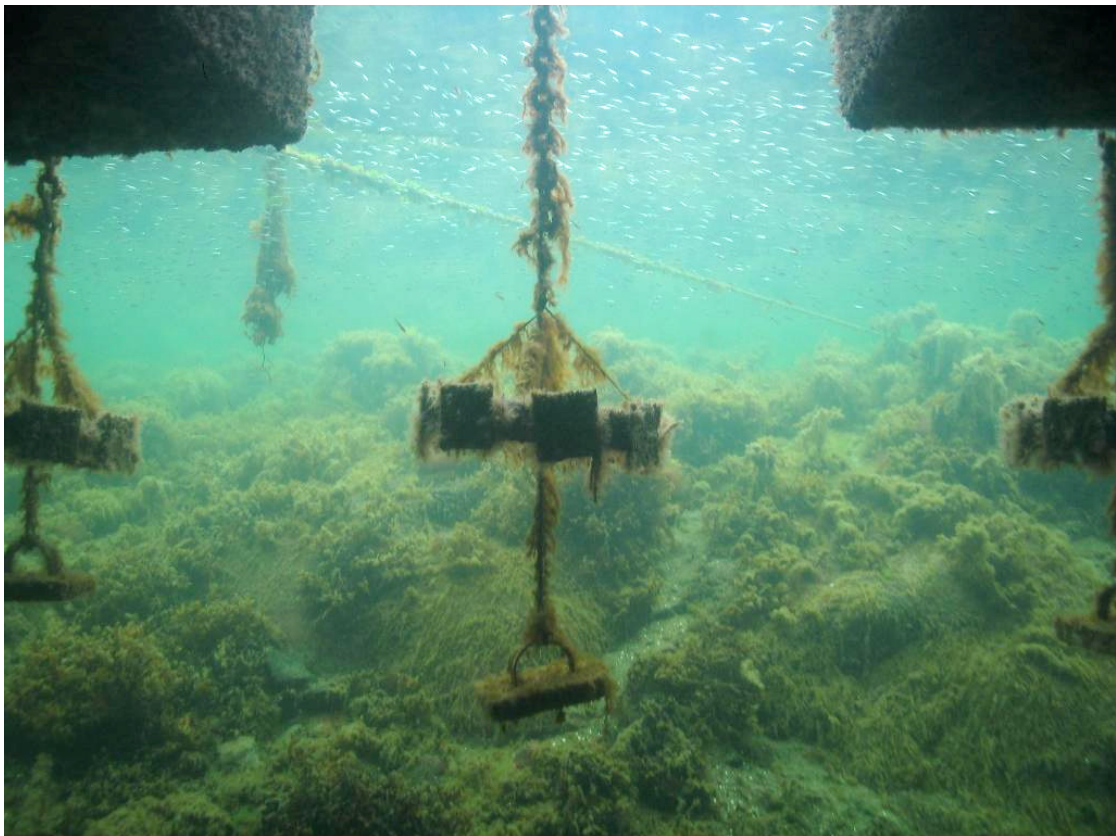
We conclude that the expected effects of climate change on the Baltic Blue mussel *M. edulis* could lead to a shift in the species' regional distribution and local abundance. Eastern populations living at the edge of their salinity tolerance at 4.5 psu will disappear in consequence of a further reduction in salinity. Populations at low salinities (17 - 10 psu) will experience higher predation pressure due to reduced shell stability with simultaneously increasing interspecific competition because of decreased growth rates. Both effects could lead to a reduction in abundance.

For Western Baltic blue mussels we expect both enhanced growth rates and increased shell stability. This might intensify intraspecific competition but should also increase interspecific competitiveness. Vulnerability towards shell cracking predators could decrease if the predators' performance is not simultaneously enhanced by the climatic changes. A higher abundance is therefore probable for *M. edulis* at medium and high salinities (20 – 34 psu).

Generally, invasiveness of *M. edulis* should be highest in environments where salinity conditions are not fully marine (70 – 80% saltwater). In most temperate regions, environmental changes as predicted by the models (reduction in salinity, warming, enhanced food availability) should favour the performance of the blue mussels.



## Chapter II



# **Mussels in a changing world: The Effects of Climatic Changes on a Baltic Key Organism**

## **Abstract**

The Baltic Sea is one of the most sensitive ecosystems in Europe. Because of its brackish character, many of its inhabiting species are living at the edge of their distributional range. For such marginal populations, changes in salinity as predicted by recent climate models, may have far reaching consequences with regard to distribution, reproduction and abundance. In this study we attempted to determine the consequences of such future salinity shifts on one of the major Baltic species, the mussel *Mytilus* spp. We transplanted juvenile mussels reciprocally between sites featuring salinities in the range from 6 to 33 psu. Transplantation from one site to the adjacent station in eastward direction simulated the predicted reduction in salinity of 4 to 6 psu. Since field experiments always comprise many uncontrollable factors (e.g. temperature, food availability, pH, currents, light regime etc.) the same experiment was repeated in the laboratory under controlled conditions. Growth rates and shell stability were used to compare the performance of the mussels at different sites and salinities. In most cases, field and lab results matched surprisingly well. Mussels from all populations seemed to grow best at intermediate salinity (20 to 29 psu), and increasing salinity generated increasing shell stability. We found three main clusters of mussel populations that showed the same properties with regard to maximum growth rates, shell stability and phenotypic plasticity.

## **Introduction**

### **Climate Change**

Northern Europe, as all other regions at mid and high latitude, has been experiencing a general warming of terrestrial and aquatic habitats for several decades (BACC 2006). Additionally, shifts in many other environmental parameters such as precipitation, wind speed, ice cover, and salinity, have been observed or predicted (Hupfer & Tinz 1996, Omsted et al. 2000, IPCC 2001a,b, Babarro & de Zwaan 2002, Lehmann et al. 2002, Walther et al. 2002, Meier 2006). Faced with this complex change organisms may be confronted with the simultaneous appearance of multiple stressors. If they do not migrate with shifting climate zones they may be affected in two ways: directly, at the physiological



scale (performance change), and indirectly as their interactions with other organisms are altered.

The Baltic Sea, due to its specific hydrographical and ecological conditions, is one of the most fragile ecosystems in Europe. Because of its brackish water, many marine and limnic species exist at the edge of their distributional range. Even small shifts in environmental conditions may have far reaching consequences with regard to a species' distribution, reproduction and abundance (Arndt 1996, Lozán et al. 1996). Present climate models provide predictions regarding most physical parameters, but do not supply any information on the influence of such changes at the ecosystem level because responses of organisms and their reactions to (or interactions with) multiple physical changes are not known. Therefore, studies that focus on both direct and indirect ecological effects of climate change on the Baltic communities and organisms are essential to fully understand the consequences of a changing climate.

In the Baltic, yearly average temperature increased in the last century by 0.7°C, which is faster than the average global warming of 0.5°C (BACC 2006). GCM (Global Climate Model) simulations imply that regional warming over the Baltic Sea could be twice as high as the mean global temperature increase (BACC 2006). The extrapolation of climatic change over the last 20 to 100 years and its modeling for the coming 50 to 100 years (and a 'business-as-usual scenario' (HadCM3) relative to a reference period between 1960 and 1990) predicts a rise of seawater temperature by up to 5°C in summer and up to 10°C in winter. In the wake of this warming, other changes will occur, such as reduced thickness, extent and duration of winterly ice cover, increased winter runoff and a longer growing season. An increase in yearly precipitation (plus 70-150 mm/y) will lead to a decrease of Baltic salinity of up to 5 psu and an intensification of summer stratification (Hupfer & Tinz 1996, IPCC 2001a,b, Graham 2004, Meier 2006). Because migration of sessile organisms is restricted to larval dispersal, their capacity to migrate to more favorable regions is limited. Thus, adult mussels may be more impacted by climate change than motile life forms. For sessile benthic species of the Baltic, warming and desalination may represent the most immediate challenge. Enhanced metabolism due to warming may increase growth and reproduction when food is abundant but can lead to severe energy balance problems in the winter months when food (e.g. light-controlled phytoplankton) is scarce (Honkoop & Beukema 1997). Changes in salinity may have even stronger impacts in the brackish Baltic where the distribution range of many species is determined by their osmotic tolerance (Schlieper & Remane 1971). Often, very small changes in salinity prove to be sufficient to evoke reduced growth and reproduction (Westerbom et al. 2002) or shifts in regional abundance (Arndt 1996). Responses of particular species become impossible to predict when several physical parameters interact with regard to their physiological impact. A further level of complexity is reached when we consider the modification of interactions by

shifting environmental parameters. When climate change impacts interacting species with unequal intensity or direction, species' interactions (competition, predation, etc.) will change quantitatively and/or qualitatively. Thus, the impact of climate change on a given species may be amplified or buffered (Wahl, *subm.*).

### **The mussel *Mytilus***

In the Baltic Sea, the mussel *Mytilus spp.* is among the most important species. Due to their wide ecological tolerance, fast growth and high reproduction they are often competitively dominant in Baltic communities (Kautsky 1981, Dobretsov & Wahl 2001, and references therein). In their ecological role as ecosystem engineers (*sensu* Jones et al. 1994), mussels provide substratum and shelter for many associated species (Tsuchiya & Nishihira 1986, Kautsky & Evans 1987, Seed 1996, Commito et al. 2005). Mussel beds contribute to water purification and current deceleration and can contribute to soft sediment stabilization (Lozán et al. 1996). As highly efficient filter feeders they functionally link phytoplankton and benthos (Kautsky 1981, Kautsky & Evans 1987). Additionally, they are major components of the diets of sea stars, crabs, fishes and sea birds (Kautsky 1981, Westerbom 2002, Reusch & Chapman 1997). Therefore, any change in mussel performance and/or abundance will have far-reaching consequences on community structure and functioning. In Baltic mussels, maximum size, shell growth, and shell stability seem to be affected by both salinity and temperature (see also chapter I, Schlieper & Remane 1971, Kautsky 1982a, Tedengren & Kautsky 1986).

In this study we investigated the effects of salinity shifts on the blue mussel *Mytilus* with regard to its growth, shell performance and the resulting consequences for predator-prey interactions. Since the regionally most important mussel predators, the shore crab *Carcinus maenas* and the sea star *Asterias rubens*, select their prey by size (both species) and shell strength (crabs only) (Elner 1978, Jubb et al. 1983, Sommer 1999), we ask how these two features of the mussels are affected by changing environmental conditions. When food is abundant, increasing temperatures up to a critical threshold may be expected to favour growth and thus lead to a faster escape from predation. On the other hand, accelerated growth may go along with decreased shell stability (Riisgaard, *pers. comm.*), especially when warming coincides with desalination, i.e. reduced availability of minerals. The mussels' susceptibility to predation thus seems to be controlled by two contrasting responses to climate change: on the one hand, faster escape from predation by higher growth rates, on the other hand, increased vulnerability to predation due to lowered shell stability.

### **Introduction to new habitats**

Climatic changes are not the only environmental shifts that mussels are facing in the course of global change. Unintentional introductions of species into new habitats via ship hull fouling, ballast water and tank sediment (Gollasch 2002) may cause the establishment of non-native species. Such invasions may or may not have severe economical and ecological consequences for the affected region (Carlton & Geller 1993, Gollasch & Mecke 1996). During the last two centuries, mussels have been introduced to many coasts of both hemispheres and they successfully established at many places (Carlton 1999, McDonald & Koehn 1988, Griffith et al. 1992, Branch & Steffani 2004). Such a transfer of mussels between habitats may represent a change of physical parameters (temperature, salinity, etc.) similar in range to but much faster than climate change in a given location. For the invasive success of mussels its responses to key parameters such as temperature and salinity are crucial.

### **The genetic background**

The Baltic Sea is inhabited by *M. edulis*, *M. trossulus*, and their hybrids (Bulnheim & Gosling 1992, Gardner & Thompson 2001, Riginos & Cunningham 2005). According to Riginos & Cunningham (2005), mussels from the North Sea and the Skagerrak are morphologically indistinguishable from other *M. edulis* populations, whereas Baltic mussels have comparatively thinner shells and smaller sizes at maturity. In the Baltic, *M. trossulus* seems to have a greater tolerance of low salinity than *M. edulis* (Johannesson et al. 1990, Väinölä & Hvilsum 1991). Interestingly, Gardner and Thompson (2001) report the contrary for the hybrid zone in North East America.

The Belt Sea is the region with the highest rate of hybridization, with the *M. edulis* type entering from the North Sea and the *M. trossulus* type from the inner Baltic; additionally there seems to be a high rate of introgression of *M. edulis* genes into the Baltic (Väinölä & Hvilsum 1991, Riginos & Cunningham 2005, Kijewski et al. 2006). However, the majority of mussels in the Baltic are hybrids and Riginos and Cunningham (2005) even describe the Baltic mussel populations as a “hybrid swarm”. Moreover, the taxa *M. edulis* and *M. trossulus* can also be considered subspecies, depending on what definition of species boundaries is used (Riginos & Cunningham 2005). Therefore, in the following we will refer to the mussels of different populations as *Mytilus* spp., without the attempt to differentiate between the several taxa.

### **Adaptation to a brackish environment**

Life in brackish environments has physiological consequences for *Mytilus*: O<sub>2</sub> consumption is increased, heart rates are reduced (Schlieper 1955a), NH<sub>4</sub>-N excretions are higher, while O : N ratios for Baltic mussels are lower compared to North Sea mussels (Tedengren &

Kautsky 1986). All this indicates that Baltic mussels are suffering from osmotic stress, resulting in lower growth rates, reduced maximum attainable size, earlier sexual maturity and shortened life span (Schlieper & Remane 1971, Bulnheim & Gosling 1988, Tedengren et al. 1990). The lower salinity of brackish water has consequences for *M. edulis* shell quality: the activity of the shell producing tissue, the shell calcium content and organic substance levels are compromised, resulting in lighter shells (Schlieper 1955b).

Mussels show high plasticity in growth and maximal size, depending on many biotic and abiotic factors such as temperature, salinity, food availability or wave exposure (Seed & Suchanek 1992). Transplant experiments with Baltic mussels confirm this: after transfer to higher saline conditions, the animals reached normal size. However, they still showed very thin shells and physiological differences that are favorable in low salinities as for example higher rates of nitrogen excretion and a negative energy balance (Kautsky et al. 1990, Tedengren et al. 1990)

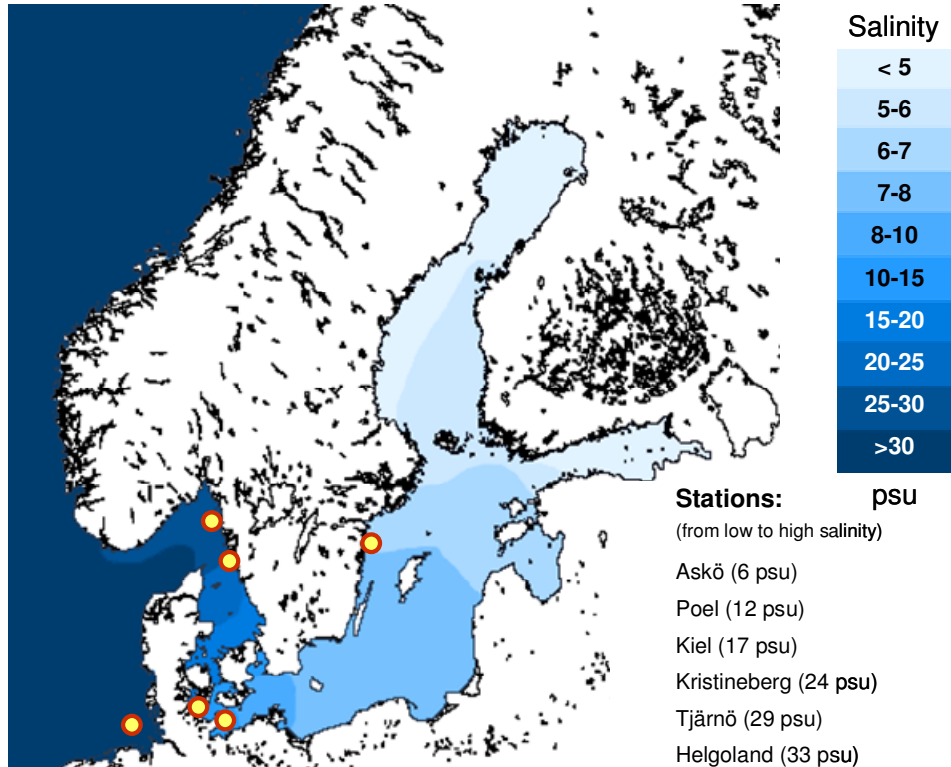
### **Objectives**

In this study we assessed how salinity differences, by simulated climate change, affect the growth rate and shell stability of mussels. In addition, we determined differences in the capability of salinity adaptation between mussel populations. We combined field and lab experiments to compare information obtained under natural, but uncontrolled, and less natural, but tightly controlled, conditions. We did not restrict our treatments to the predicted reduction in salinity because by ship hull, mussels are transported over large distances and confronted with new environmental conditions (Gollasch 2002). These shifts, following human trade, are bidirectional: from low saline water to higher salinity or vice versa. Whether this global change phenomenon results in successful establishment of *Mytilus* spp. in new habitats depends to a high degree on the species' ability to adapt to altered salinity regimes.

## Materials and methods

### Study organisms & sites

Juvenile blue mussels *Mytilus edulis* Linnaeus (1758), with an initial shell length of 10 to 25 mm, were collected at six sites with different salinities: Helgoland (54°11'N 7°53'E, 33psu), Kiel (54°19'N 10°8'E, 17 psu) and Poel (53°60'N 11°23'E, 12 psu) in Germany, and at Tjärnö (58°53'N 11°9'E, 29 psu), Kristineberg (58°15'N 11°28'E, 25 psu) and Askö (58°49'N 17°38'E, 6 psu) in Sweden (Figure 10). Animals were transported to Kiel in climatized, running and aerated seawater, where they were kept at 15°C for 15 days for adaptation. Mussels were kept in filtered flowing seawater adjusted to the salinity of their provenance, and were fed with *Rhodomonas*- and *Dunaniella*- phytoplankton cultures.

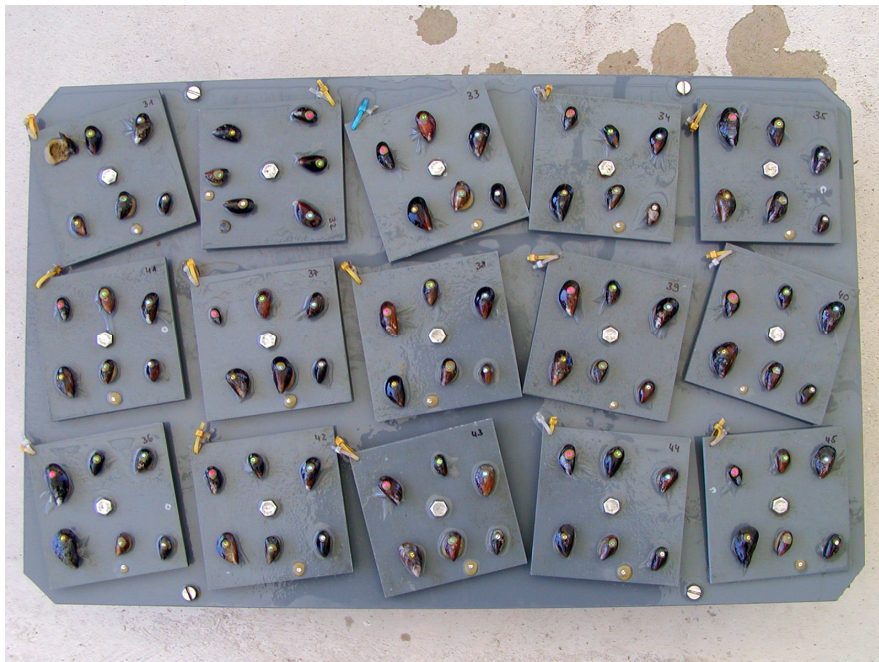


**Figure 10:** Field stations in the Baltic salinity gradient.

### Field transplant experiment

Mussels were individually tagged with 2 mm diameter opalith discs, glued to the mussel shell after removing the periostracum with sand paper. Animals from each provenance had the same color but different numbers, so that each individual could be recognized. Shell length of the mussels was measured with a digital caliper before they were glued to the experimental units consisting of 10x10 cm PVC-panels. Six mussels, one from each station, were blocked on one panel (Figure 11). Prior to the start of the experiment,

mussels were gradually (max.  $\pm 5$  psu per 3 days) adapted to their future experimental salinities. Experimental salinities were 5, 12, 17, 20, 25, 29, and 33 psu, a range that covers the whole salinity gradient where *M. edulis* naturally occurs. Salinities higher than 17 psu were obtained by adding marine salt (Tropic Marine, Dr. Biener) to natural Baltic Sea water. Salinities lower than 17 psu were obtained by diluting Baltic Sea water with fresh water. Experimental units were then transferred by car in climatized plastic containers with aerated sea water to the six stations and fixed on 4 PVC carriers in a way that the mussels were placed 1m below water surface. The experiment lasted from June to September 2004. From wild local populations, samples of ca 50 specimens (10 to 50 mm) were collected to measure shell stability. Temperature at the sites was logged during the experiment (StowAway TidbiT onset loggers).



**Figure 11:** Field experiment setup. Mussels from all station are individually tagged and then glued to a PVC panel. For transportation, panels were fixed as shown and placed in boxes with aerated sea water.

### **Laboratory experiment – manipulated salinity changes**

Mussels were labeled and shell length was measured as above. Ten mussels of each provenance were placed in a 3 l tank. These pseudoreplicates provided the mean values for the true replicates (each aquarium) and minimized the risk of sample loss by natural mortality. Individual growth was measured and averaged. Untagged mussels were used to measure shell stability. The experimental setup resulted in blocks of 6 aquaria containing mussels from Askö, Poel, Kiel, Kristineberg, Tjärnö and Helgoland, respectively. Each block was run with one of the experimental salinities which were the same as in the field (6, 12, 17, 25, 29, 33 with an additional intermediate salinity (20 psu)), and each salinity was replicated 3 times. One experimental unit consisted of 6 small water tanks and two 30 l reservoirs. A pump placed in the lower reservoir filled the upper reservoir, allowing the

water to flow through the small water tanks (2 l aquaria) back into the lower reservoir. This resulted in a total water volume of ca 75 l for each water cycle. Weekly, the water was completely exchanged (see above for details). The mussels were fed daily (except for Sundays) with phytoplankton cultures (*Rhodomonas* sp., *Dunaniella* sp. grown at 20 psu, 1 l for each water cycle). Salinity was controlled daily after feeding and kept within a range of  $\pm 0.5$  psu. The experiment was conducted from February 2004 to May 2004 at 15°C, 12 h light/dark.

### Sample processing

At the end of the experiment, mussels were deep frozen (-18°C) for one week before processing. Freezing does not affect shell stability (t-test for independent samples,  $T_{52} = 1.026$ ,  $p = 0.309$ ). The soft body was completely removed from the shell and dried to a constant weight. Shell length was measured with a digital caliper to the nearest 0.1 mm.

Shell stability was measured as shell breaking resistance. For this purpose, one of the shell valves was laid flat on its opening and weight gradually added to a central mm<sup>2</sup> at the highest point of the shell until it broke. Breakage pressure (= shell stability) was calculated (g/mm<sup>2</sup>). Shell stability measurements were done with 5 specimens from each replicate and subsequently averaged. Shell stability increases with mussel size (Kautsky et al. 1990). To obtain a size-independent measure for shell stability it was standardized for unit mussel size by dividing breakage pressure by shell length. This yielded the *relative* shell stability (RSS).

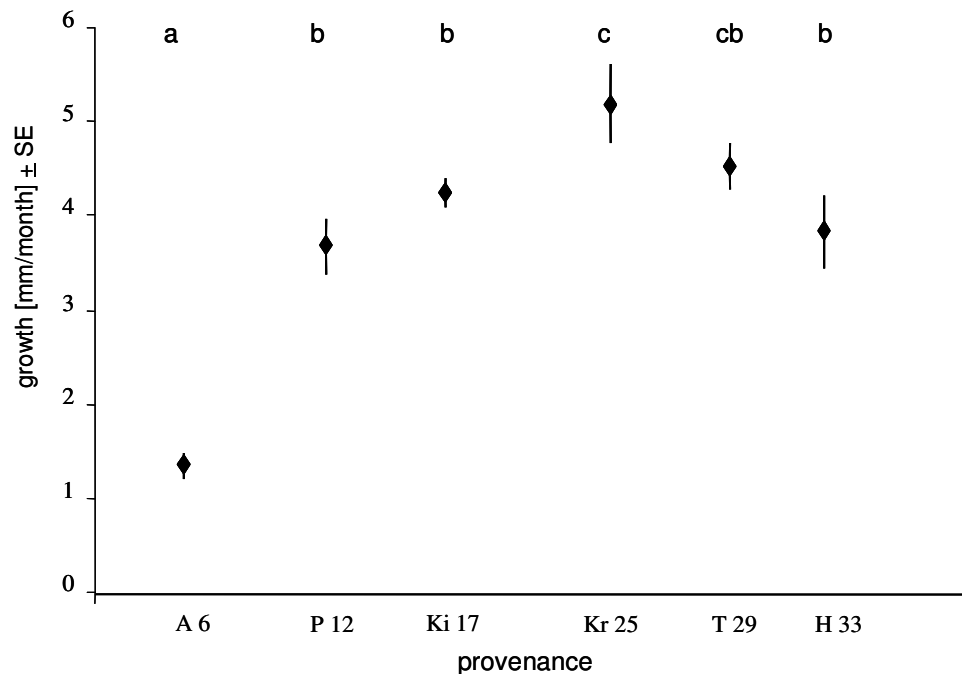
For better comparison of laboratory and field results we standardized growth rates relative to maximum monthly growth values: for each population the highest observed value at any salinity was equated to 100 %. Then, growth under different treatments was expressed as percent of the population's maximal growth.

Effects of and interactions between main factors (provenance, salinity or recipient site, respectively) were analyzed with a 2-factorial ANOVA after testing for normality of distribution and homogeneity of variances (and log-transforming of data, if necessary). A posthoc multiple comparison test (Tukey's HSD) was used to check differences between treatments. Effects of the predicted reduction in salinity were tested by an unpaired t-test. Correlation between shell stability and growth rate was calculated using Pearson's product-moment-correlation. A probability level of  $< 0.05$  was accepted as statistically significant.

## Results

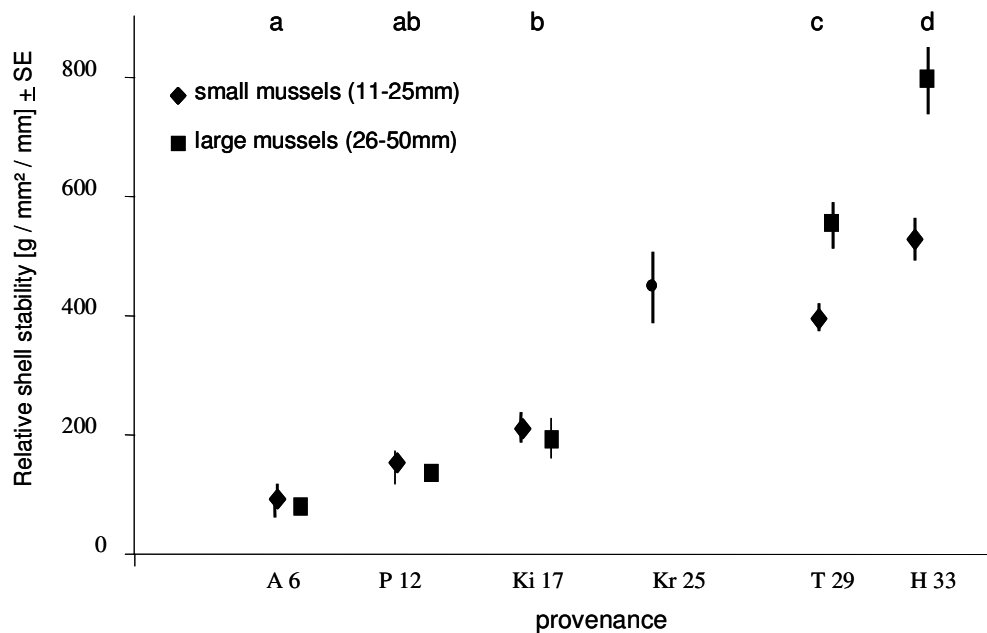
### Autochthonous populations

Growth rates and shell stability for the local populations of all stations differed significantly (1-factorial ANOVA,  $F_5 = 17.11$ ,  $p < 0.001$ ) and are shown in Figure 12 and Figure 13, respectively. Kristineberg (25 psu) population showed the highest growth rate ( $5.24 \pm 0.42$  mm/month SE). Growth rates of all other populations, except for Tjärnö (29 psu), were significantly lower (posthoc Tukey's LSD,  $p < 0.05$ , see Figure 12). Growth rate of the Askö population (6 psu) was significantly lower than of all other mussel populations ( $1.39 \pm 0.13$  mm/month). Relative shell stability (RSS) significantly increased with increasing salinity (1-factorial ANOVA,  $F_4 = 64.24$ ,  $p < 0.001$ ; Figure 13). RSS was highest at Helgoland ( $528 \pm 35$  g/mm<sup>2</sup>/mm), second highest in Tjärnö ( $395 \pm 22$  g/mm<sup>2</sup>/mm) and similarly low in Kiel, Poel and Askö (212, 149 and 91 g/mm<sup>2</sup>/mm, respectively). For mussels from Helgoland and Tjärnö, RSS was significantly higher in large ( $> 25$ mm) than in small ( $\leq 25$ mm) mussels. No such difference could be found in the other populations. Samples from Kristineberg were lost unfortunately and are replaced in Figure 13 by means of Kristineberg mussels transplanted to Kristineberg during the experiment.



**Figure 12:** Growth rates of the autochthonous *Mytilus* populations at the investigated stations. Growths per month  $\pm$  SE. Arabic numerals show the salinity at the field station. A = Askö, P = Poel, Ki = Kiel, Kr = Kristineberg, T = Tjärnö, H = Helgoland.





**Figure 13:** relative shell stability (RSS) of the autochthonous *Mytilus* populations at the investigated stations. RSS in g / mm<sup>2</sup> / mm ± SE. Arabic numerals show the salinity at the field station. A = Askö, P = Poel, Ki = Kiel, Kr = Kristineberg, T = Tjämnö, H = Helgoland. Squares = large mussels (26-50mm), rhombi = small mussels (11-25mm), circle = the value for Kristineberg results from data of the transplant experiment, not from separate data collection.

### Growth rates

Predation, wave action and other impacts caused the loss of some material, but none of our experimental blocks was lost during the experiment. From 144 mussels transplanted to each site we were able to recover 98 live specimens in Helgoland, 75 in Tjämnö, 58 in Kristineberg, 104 in Kiel, 110 in Poel and 83 in Askö.

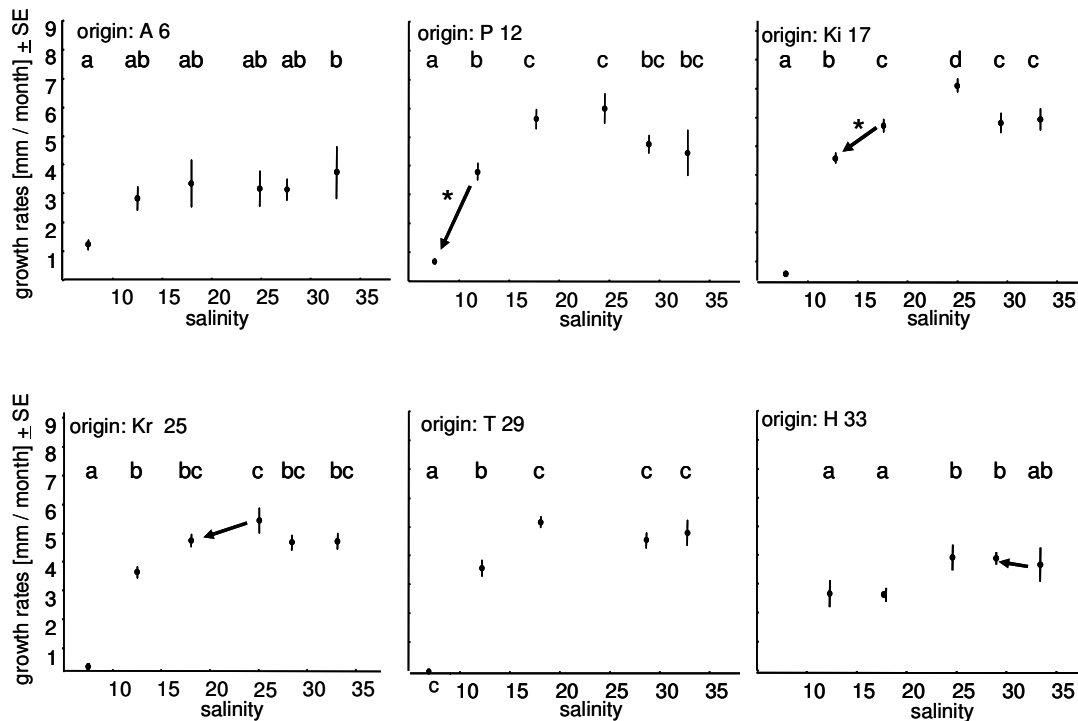
Growth rates in the field ranged from 0.08 ( $\pm$  0.02 SE) mm/month (Tjämnö mussels in Askö) to 6.71 ( $\pm$  0.22) mm/month for Kiel mussels in Kristineberg (Figure 14). They were significantly influenced both by the mussels' provenance (2-factorial ANOVA,  $F_3 = 17.25$ ,  $p < 0.001$ ) and by transplantation site (presumably due to salinity changes at their new or recipient site, 2-factorial ANOVA,  $F_3 = 13.99$ ,  $p < 0.001$ ). There was a significant interaction between provenance and destiny as well (2-factorial ANOVA,  $F_{23} = 2.887$ ,  $p < 0.001$ ). At Tjämnö and Kristineberg there was also a detectable significant experimental block effect (2-factorial ANOVA,  $F_2 = 5.30$ ,  $p < 0.01$  and  $F_2 = 6.46$ ,  $p < 0.05$ , respectively).

Growth rates in the laboratory were in the range from 0.01 mm/month ( $\pm$  0.01 SE) for Askö mussels kept at 6 psu to 2.19 mm/month ( $\pm$  0.34 SE) for Tjämnö mussels kept at 29 psu. They were significantly influenced by provenance (2-factorial ANOVA,  $F_4 = 17.01$ ,  $p < 0.01$ ) and salinity ( $F_5 = 15.88$ ,  $p < 0.01$ ) and the interaction between provenance and salinity was significant ( $F_{29} = 1.66$ ,  $p < 0.05$ ).

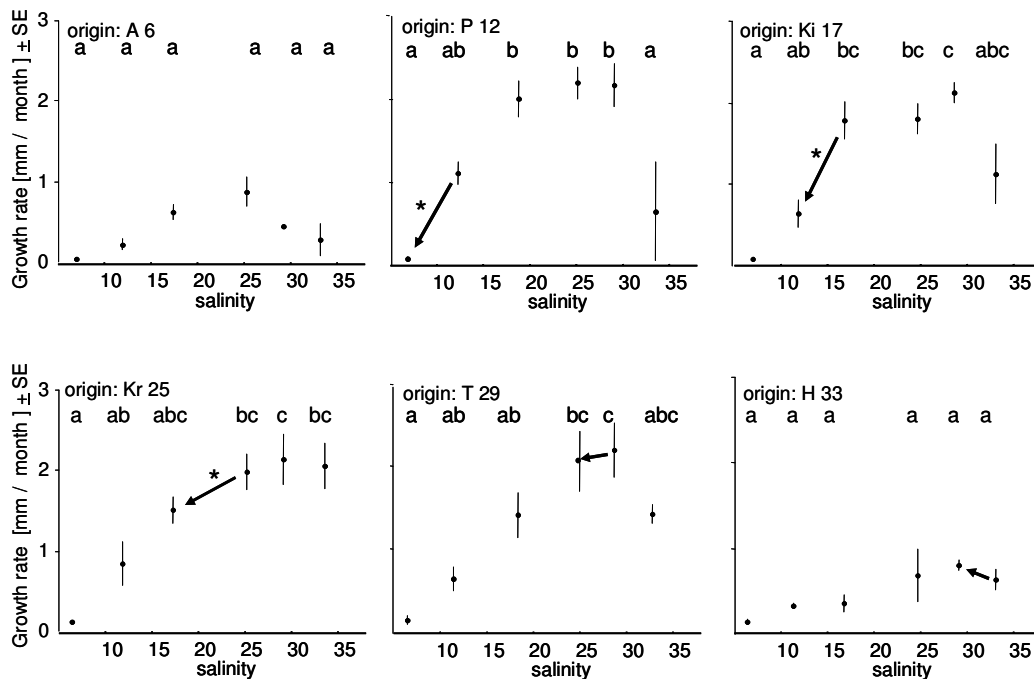
In the field, the populations from Kiel and Poel displayed a significant decrease in growth rates at the climate relevant salinity reduction from 12 to 6 and from 17 to 12 psu,

respectively (Figure 14) (T-test for independent samples,  $T_{39} = 8.99$ ,  $p < 0.001$  and  $T_{40} = 4.08$ ,  $p < 0.001$ ). For the Kristineberg population, this decrease was not significant. The Helgoland population did show a (non significant) converse tendency with slightly increasing growth rates with decreasing salinity. No tests could be done for Askö population (a further reduction in salinity was not possible) and for Tjärnö (no mussels were transplanted to Kristineberg). Results in the lab emphasize these findings (Figure 15): a salinity reduction in the climate relevant range leads to significant decreases in growth rates for mussels from Poel, Kiel and Kristineberg. The decrease is visible but not significant for Tjärnö mussels, and again we find a slight increase in growth rates for mussels from Helgoland.

Growth rates in the lab and in the field followed a very similar model with high values at intermediate salinities and low growth at the extremes (6 and 33 psu, respectively). This pattern was more pronounced in the lab than in the field. Mussels from Askö and Helgoland showed very low growth rates (< 1mm/month) over the whole range of salinities in the laboratory, and no significant differences between salinity treatments could be detected. However, growth rates followed the same pattern as in the other populations with highest values at medium salinities. In Figure 18, the high degree of congruence between the two regressions can be seen.



**Figure 14:** Growth of transplanted mussels. Growth [mm/month] ± SE. Arabic numerals show the salinity at the field station. Arrows indicate climate change simulation. Asterisks indicates significance between treatments (t-test,  $p < 0.05$ ). A = Askö, P = Poel, Ki = Ki el, Kr = Kristineberg, T = Tjärnö, H = Helgoland.



**Figure 15:** Growth of laboratory mussels. Growth [mm/month]  $\pm$  SE. Arabic numerals show the salinity at the field station. Arrows indicate climate change simulation. Asterisks indicates significance between treatments (t-test,  $p < 0.05$ ). A = Askö, P = Poel, Ki = Kiel, Kr = Kristineberg, T = Tjärnö, H = Helgoland.

### Relative shell stability

In the field, relative shell stability (RSS) varied between 92 g/mm<sup>2</sup>/mm (Askö mussels transplanted to Tjärnö) and 420 g/mm<sup>2</sup>/mm (mussels from Kristineberg at Kristineberg, 24 psu) and was significantly influenced by provenance (2-factorial ANOVA,  $F_3 = 39.43$ ,  $p < 0.001$ ) and destiny (presumably salinity) at all sites (2-factorial ANOVA,  $F_3 = 29.44$ ,  $p < 0.001$ ). There was a significant interaction between these factors as well ( $p = 0.003$ ,  $F = 2.075$ ,  $df = 23$ ). RSS tended to increase from low (6 psu) to medium (24 psu) salinity in all mussels except for those originating from Helgoland (Figure 16). There was an unexpected (and in most cases significant) drop off in RSS at 29 psu (Tjärnö) in all mussels. Shell stability was strongly correlated to growth rates (Pearson's product-moment-correlation, Fisher  $z_{474} = 0.1614$ ,  $r = 0.16$ ,  $p < 0.001$ ).

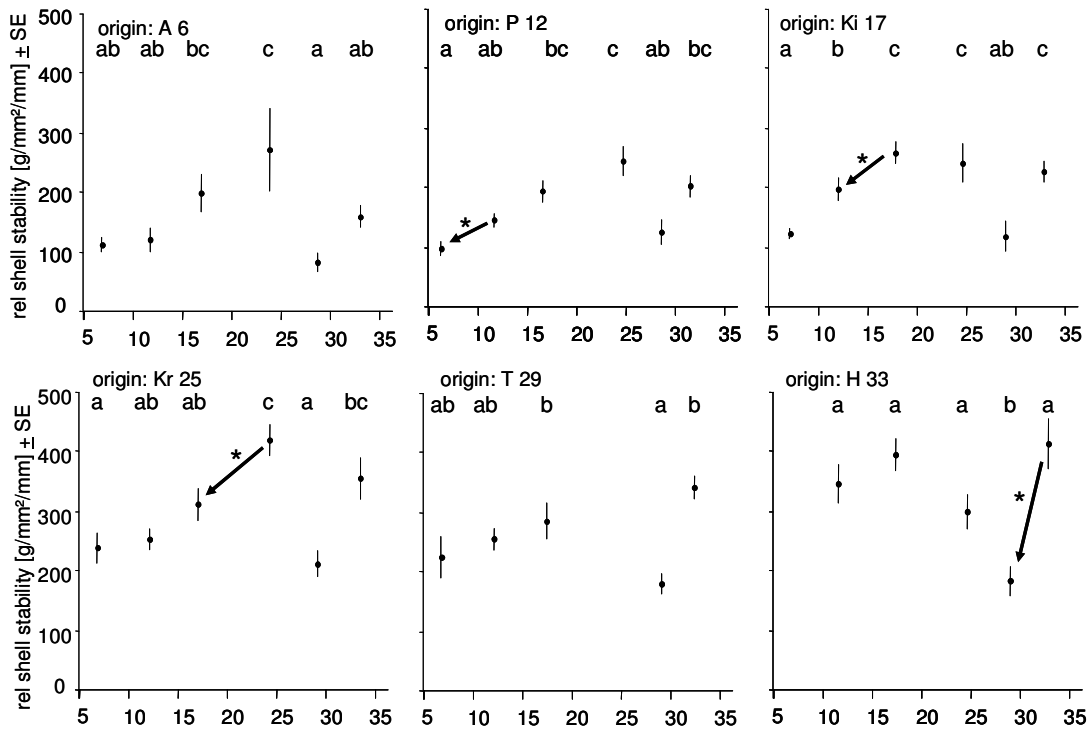
RSS in the lab was significantly influenced by provenance as well as by salinity (2-factorial ANOVA,  $F_3 = 20.01$ ,  $p < 0.01$  and  $F_5 = 2.56$ ,  $p < 0.05$ ); there was no significant interaction between the main factors, nor was there a correlation between shell stability and growth rates (Pearson's product-moment-correlation, Fisher  $z_{1124} = 0.0300$ ,  $r = 0.03$ ,  $p = 0.754$ ). In mussels originating from localities with low salinity (Askö, Poel, Kiel), there was no difference in RSS at different salinities, mostly the values for RSS varied between 100 and 200 g/mm<sup>2</sup>/mm. In Kristineberg and Tjärnö mussels (24 and 29 psu, respectively), RSS was between 200 and 300 g/mm<sup>2</sup>/mm, while for Helgoland mussels most values varied between 300 and 400 g/mm<sup>2</sup>/mm. Thus, the significant influence of provenance on RSS

shown by the ANOVA probably relates to the intrinsic differences between populations, not between treatments.

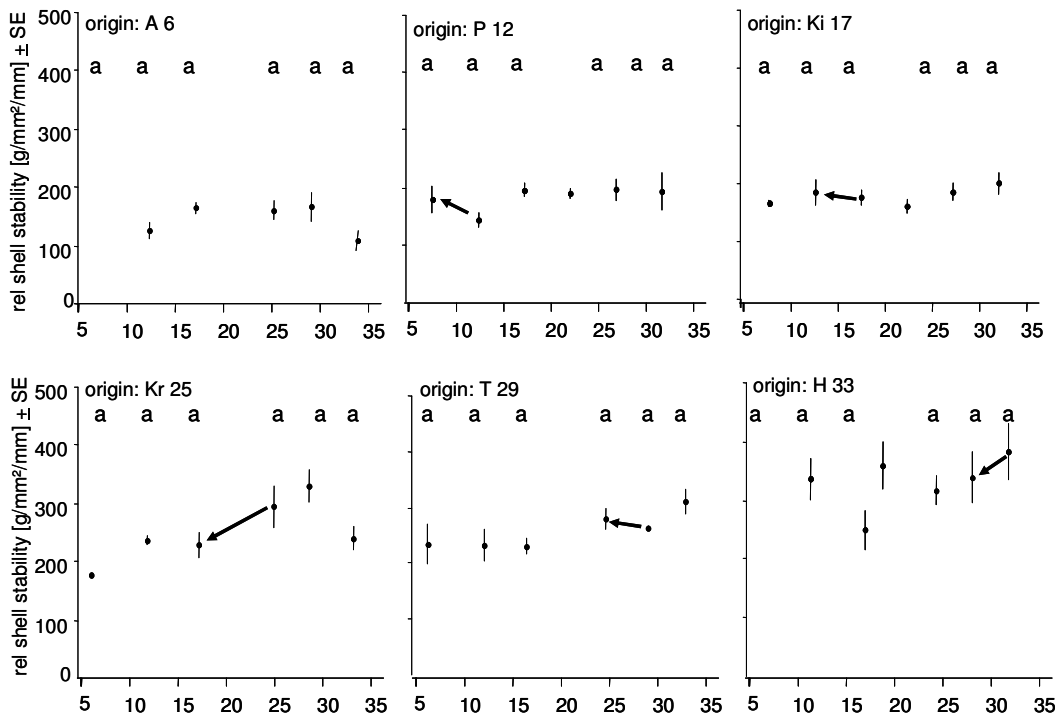
Again, laboratory and field data show a similar pattern of increasing RSS with increasing salinity. This time, the pattern is more distinct in the field than for the laboratory. While there is no significant change of RSS in the climate change relevant salinity range in the laboratory data (Figure 17), all of the reductions in the field (Figure 16) are significant (T-test for independent samples, Helgoland:  $T_{26} = 5.07$ ,  $p < 0.001$ , Kristineberg:  $T_{26} = 2.90$ ,  $p < 0.01$ , Kiel:  $T_{39} = 2.39$ ,  $p < 0.05$  and Poel:  $T_{38} = 2.76$ ,  $p < 0.01$ , Table 3). When comparing the %max RSS values (Figure 19) we see that the regression for laboratory results is highly analogous to that for the field data, even though RSS values are always higher in the lab than in the field.

**Table 3:** Results of t-test (independent samples) between local recent and predicted conditions. S = Salinity [psu], growth = growth per months, RSS = relative shell stability.

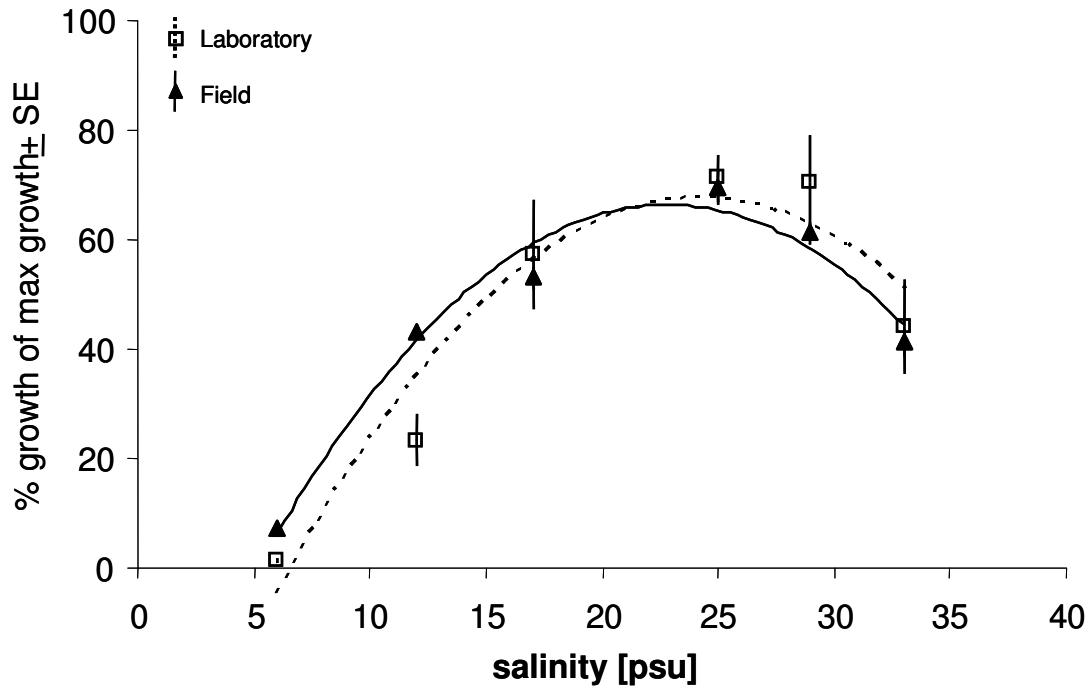
<b>Laboratory</b>		t-value	df	p
S 33-S29	growth	1,26	4	0,275
(Helgoland)	RSS	-0,68	4	0,534
S 29-S25	growth	-0,25	4	0,816
(Tjämnö)	RSS	0,81	4	0,463
S25-S20	growth	-2,80	4	* 0,049
(Kristineberg)	RSS	-1,69	4	0,167
S17-S12	growth	-4,55	4	** 0,010
(Kiel)	RSS	-1,69	4	0,167
S12-S6	growth	-7,47	4	** 0,002
(Askö)	RSS	1,51	3	0,229
<b>Field</b>		t-value	df	p
S 33-S29	growth	-0,32	30	0,753
(Helgoland)	RSS	5,07	26	*** 0,000
S25-S20	growth	1,45	29	0,159
(Kristineberg)	RSS	2,90	26	** 0,008
S17-S12	growth	4,08	40	*** 0,000
(Kiel)	RSS	2,39	39	* 0,022
S12-S6	growth	8,99	39	*** 0,000
(Askö)	RSS	2,76	38	** 0,009



**Figure 16:** RSS of transplanted mussels. RSS in [g / mm<sup>2</sup> / mm] ± SE. Arabic numerals show the salinity at the field station. Arrows indicate climate change simulation. Asteriks indicates significance between treatments (t-test, p < 0.05). A = Askö, P = Poel, Ki = Kiel, Kr = Kristineberg, T = Tjärnö, H = Helgoland.

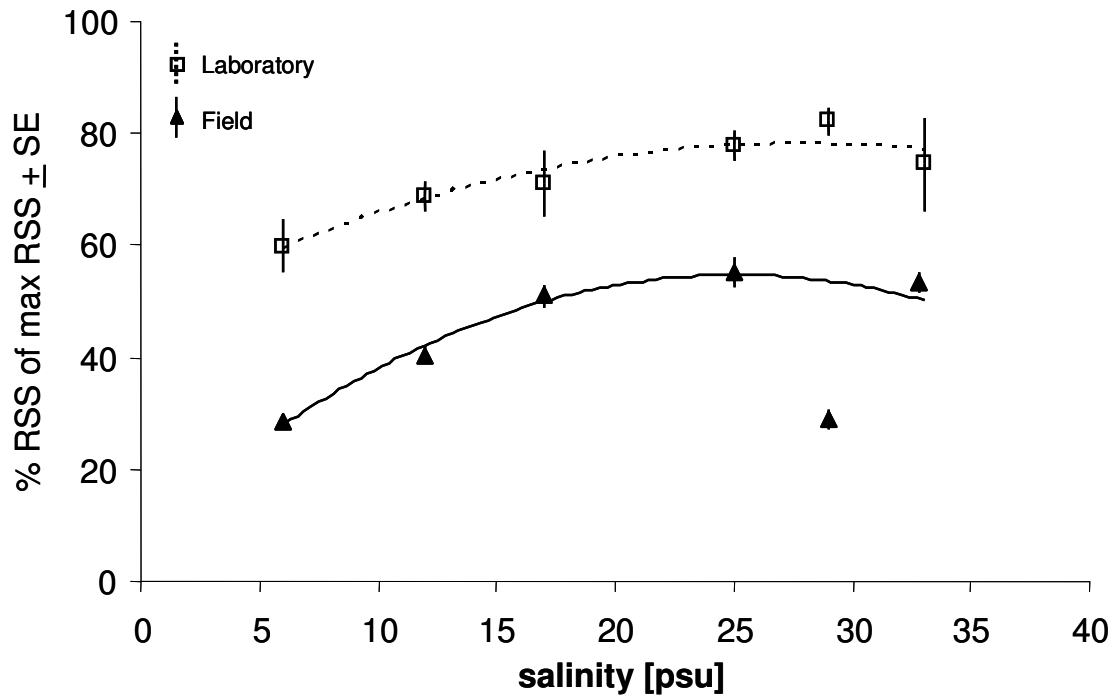


**Figure 17:** RSS of laboratory mussels. RSS in [g / mm<sup>2</sup> / mm] ± SE. Arabic numerals show the salinity at the field station. Arrows indicate climate change simulation. Asteriks indicates significance between treatments (t-test, p < 0.05). A = Askö, P = Poel, Ki = Kiel, Kr = Kristineberg, T = Tjärnö, H = Helgoland.



**Figure 18:** Comparison of growth in transplanted and laboratory mussels. For each population the highest observed value irrespective salinity was set 100%. Subsequently, % of max. growth values were pooled for all populations within salinities. Some of the standard errors SE are too small to be shown. Squares and dotted line: laboratory results. Triangles and full line: transplant results.

Lab:  $y = -0.2166x^2 + 10.515x - 60.001$ ,  $R^2 = 0.9215$ , Field:  $y = -0.2124x^2 + 9.6897x - 44.085$ ,  $R^2 = 0.9666$



**Figure 19:** Comparison of RSS in transplanted and laboratory mussels. For each population the highest observed value irrespective salinity was set 100%. Subsequently, % of max. RSS values were pooled for all populations within salinities. Some of the standard errors SE are too small to be shown. Squares and dotted line: laboratory results. Triangles and full line: transplant results. The field value 29 psu relates to Tjärnö where the high ascidien cover occurred and was therefore excluded from the regression calculation.

Lab:  $y = -0.0391x^2 + 2.1765x + 47.804$ ,  $R^2 = 0.8994$ , Field:  $y = -0.0735x^2 + 3.693x + 8.3992$ ,  $R^2 = 0.9922$

## Discussion

Using shifts in salinity as major component of climate change in the Baltic Sea, we found strong impacts on growth rates and relative shell stability (RSS) in *Mytilus* populations. We detected 3 clusters of populations that reacted in similar ways with regard to growth and RSS. Mussels of all populations investigated showed the capability to adapt to shifts in salinity. However, the range of their phenotypic plasticity differed enormously: while mussels from the middle part of the Baltic displayed good growth rates over a wide range of salinities, mussels from Helgoland and Askö seemed to be more restricted in their adaptational abilities.

### Autochthonous populations

Autochthonous populations at the stations differed markedly in terms of growth rates and shell stability (Figure 12, Figure 13). Growth rates were highest in the Kristineberg population. This might be due to better environmental conditions or to different genetic and/or phenotypical potential of this population. However, temperature was not significantly higher in Kristineberg than at the other stations (Table 3), and food availability (chlorophyll a concentration) was good but not higher than at Tjärnö or Helgoland (Lindahl 2004, Wiltshire & Manly 2004), which supports the assumption of population specific differences. In the laboratory experiment we showed that mussels of all provenances grew best at a salinity of 24 (Figure 15, Figure 18), which suggests that the high Kristineberg growth rates might also be the result of optimal salinity conditions. The extremely low growth rate of Askö mussels may be a consequence of very low salinity, since temperature and chlorophyll a concentrations did not differ significantly from the other stations. Littorin and Gilek (1999) also report a low yearly growth of 3.4 mm from *Mytilus* in the Askö region. Growth rates of autochthonous populations in Helgoland, Tjärnö, Kiel and Poel were very similar and ranged from ca. 3.5 to 4.5 mm/month. These four populations seem to be equally well adapted to their environmental conditions.

RSS was lowest in the Askö population but showed a positive relationship with ambient salinity. Stability was nearly eight times higher in the Helgoland population than in Askö mussels. Elner (1978) found that shell stability is highly dependent on habitat conditions in *Mytilus*. He demonstrated that mussels from exposed habitats had lower breaking resistance than mussels from sheltered environments. His study contrasts with our results, where the mussels from Helgoland (with high RSS) lived in a very exposed rocky habitat, while the Askö mussels (displaying low RSS) were taken from a calm, sheltered bay. Leonard et al. (1999) made the observation of a positive correlation between growth rates and shell thickness, and we similarly found a positive correlation between growth rates and shell stability. Since growth rates were low in Askö as well as in Helgoland mussels, other factors than exposure and growth played an important role in determining the RSS. Both

field transplantation and – more convincingly because all other parameters were kept constant – the lab salinity manipulations do not support our original hypothesis that the RSS gradient from E to W was mainly influenced by increasing salinity. Additional factors, e.g. genetics, exposure, growth rates, predation pressure, boring epibionts, may blur any salinity effect.

Our results have relevance for mussels introduced to new locations with different salinity. However, climate change associated salinity shifts happen over decades, which may allow populations to adapt physiologically or by microevolution to the new conditions. Over incremental time, mussels may eventually exhibit the RSS values shown by the autochthonous populations examined in this study.

### **Growth rates**

In the multi local transplant experiment, we found that growth rates of Baltic mussels were not only influenced by the site where they were growing, but to a large extent also by their provenance. These results were confirmed in the laboratory experiment. Growth rates increased with increasing salinity from 6 to 24 psu, but no further increase could be found at 29 or 33 psu. In the field, other site properties such as temperature or food could affect growth. However, at the site of fastest growth (Kristineberg, 24 psu) neither phytoplankton concentration nor mean temperature differed markedly from those found at the other stations (see Table 4 for temperature, and Lindahl 2004, Wiltshire & Manly 2004 for phytoplankton). Besides, the laboratory results unequivocally attribute this growth maximum to the salinity treatment. Almada-Villela (1984) found a very similar salinity-dependency of growth in *M. edulis*, with only small differences in the growth rates at salinities higher than 20 psu and a sharp decline from 19 to 12 psu. Our data show the same strong decline between 17 and 12 psu.

Many studies suggest that growth rates and overall performance in mussels have a positive correlation with increasing ambient salinity (Schlieper & Remane 1971, Böhle 1972, Almada-Villela 1984, Westerborn et al. 2002). On the other hand there are also indications for better mussel growth at lower salinities: Babarro & de Zwaan (2002) showed better *Mytilus* performance related to suboptimal conditions as anoxia or low salinity and explained this by a reduction in bacterial infection whose virulence was lowered by the physiological stress. Almada-Villela (1984) found higher *M. edulis* growth rates at 22.4 psu than at 32 psu, even if the difference was not significant. Growth rates of mussels transferred from fully marine water to 12.8 or 16 psu were reduced and 50 % of the mussels in 12.8 psu died. The rest of the animals recovered after a couple of weeks and reached normal growth values. In our study, however, no enhanced mussel mortality was observed at 12 psu for any mussel population. In contrast, mortality in mussels kept at 6 psu was high, and no normal growth rates were reached throughout the experiment.



These mussels clearly suffered from hyposalinity, expressed not only by constantly high mortality but also by low filtration activity and low byssus production (pers. observation). This underlines the fact that acclimatisation to low salinity takes place but still has an upper tolerance threshold that cannot be overcome during an adult lifetime.

**Table 4:** temperatures at field stations [in °C ± SD].

site	mean °C	SD
Helgoland	17,31	1,27
Tjärnö	17,02	3,12
Kristineberg	17,06	2,73
Kiel	15,67	2,78
Poel	16,44	3,55
Askö	14,99	4,02

Growth rates were generally higher in the field than in the lab (Figure 14, Figure 15). Kinne (1971) states that nearly all invertebrates show lower growth rates in the lab than in the field, even when kept at similar conditions (e.g. salinity). This is not surprising since even if many adverse

factors such as predators, unfavorable temperatures etc are precluded in the laboratory, it is very difficult to establish optimal conditions regarding food supply (quantity and, particularly, quality), water current or bacterial infection. We tried to provide 24h food supply in sufficient concentration ( $2-6 \times 10^3 \text{ ml}^{-1}$ , Riisgard 1991) in our experimental setup; however, occasional depletion in phytoplankton could not be avoided. Additionally, the monocultures provided less balanced nutrition than the mixed diet of many phyto- or zooplankton species in the open water. Some bacteria might be favored by laboratory conditions and by infection reduce growth rates of the mussels. Another factor influencing shell growth in *Mytilus* spp. is population density (Kautsky 1982a), but since density was the same for all treatments, such effects can be excluded for this study.

The high growth rates of mussels from all populations transplanted to Kristineberg (where salinity is oscillating around 25 psu) correspond to maximal laboratory growth rates at salinities between 20 and 29 psu. This confirms that *Mytilus* of all Baltic populations share the same salinity requirements with respect to growth, independently of parameters associated with 'provenance' (adaptation to home conditions, genetic identity). However, absolute growth rates of mussels from Askö and Helgoland populations were always lower than those of the other populations, even though they displayed the same pattern. Probably the two marginal populations show higher specialization to their stable habitat, where changes in salinity are small compared to the other sites where salinity can fluctuate in a range of more than 5 psu within some hours. The price for this adaptation could be reflected in generally reduced growth rates due to permanently enhanced energy costs for physiological compensation.

### Relative shell stability

The influence of salinity on relative shell stability (RSS) of the laboratory mussels differed strongly between populations. In the lab, salinity had no significant influence on RSS of mussels from Askö, Poel and Kiel. Mussels originating from higher salinities (Kristineberg,

Tjärnö and Helgoland) had higher mean RSS, but only in mussels from Kristineberg did salinity have a significant effect. In the field, on the contrary, the recipient site (e.g. salinity) proved to be an important factor in determining the RSS. In mussels from all populations, RSS increased with increasing salinity of the recipient site. However, when transplanted to a new site, the stability of the shell portion formed in the new environment did not always match that of the autochthonous population (fig. 5). Obviously, the provenance of the animals, i.e. genetic background, continued to affect RSS interacting with environmental parameters. This is consistent with the findings of Kautsky et al. (1990) that mussels from Askö, transplanted to Tjärnö, soon reached the size of the local mussels while their shells remained more fragile.

Highest growth rates occurred at intermediate salinities (in a range of 20 to 29 psu). Since shell stability relates to mussel size (Kautsky et al. 1990), this means that *absolute* shell stability increased as well along the salinity gradient. With increasing salinity, the risk of predation thus diminishes in two ways: by leaving the window of vulnerability earlier in life (Griffith & Hockey 1987) and by producing thicker and more resistant shells during the phase of vulnerability. At the highest salinity (33 psu), growth rates were slightly sub-maximal, however, these mussels were building a shell with particularly high RSS. The Helgoland population probably is subject to high predation pressure that may enforce a trade-off between fast shell growth and the production of a thick, resistant shell. Indeed, the presence of predators has been shown to provoke shell thickening and strengthening in *Mytilus* (Leonard et al. 1999). Mussels growing at low salinity (6-12 psu), in contrast, were slow growing *and* produced a thin and weak shell. They would be most vulnerable to crab predation, but no large decapod crustaceans are found below 12 psu (Lozán 1996). However, in the last decades the crab *Rhithropanopeus harrisi* has been introduced from the Atlantic Ocean into European brackish waters (Jazdzewski & Konopacka 1993) and is progressively colonizing the Baltic Sea. This brachyuran decapod actively feeds on mussels and may become an important predator for the eastern populations.

Like the effect on growth rates, salinity influence on RSS seems to be more prominent in the low salinity range of 6 to 20 psu. At the station Tjärnö (29 psu), however, RSS suddenly dropped for mussels from all provenances. This is rather unexpected, and was not observed in the lab. We therefore assume that this reduction in shell stability was not related to local salinity conditions but rather to a severe ascidian epibiosis of the mussels at Tjärnö. Ascidians covered the experimental plates in a thick layer (up to 15 cm) during August and September (personal observation). They were removed twice, but recolonized rapidly.

### Comparison with genetic background

This study is complementary to the recent genetic studies on the *Mytilus* spp. complex (see Riginos & Cunningham 2005 for review) and our results corroborate many of the genetic findings. According to Riginos & Cunningham (2005), “*M. edulis* alleles predominate among non-Baltic Sea populations, whereas *M. trossulus* alleles predominate among Baltic Sea populations”. Populations in-between showed intermediate properties and were therefore judged to be hybrids. The results of the present study support the conclusions of Riginos & Cunningham (2005) that there are three different clusters of *Mytilus* in the Baltic Sea. The geographical distribution of these groups, however, does not fully correspond to previous findings. In our study, the Helgoland population clearly differed from the rest of the involved populations in terms of growth rates and RSS. Since this was the only population located definitely outside the Baltic Sea, the most appropriate description would be “non baltic”. The second cluster detected in our study was the largest one, comprising all populations from Tjärnö to Poel. This region is considered the zone of highest hybridization in the Baltic (see Riginos & Cunningham 2005). The Askö population was different from this “middle cluster”, and could be considered the “baltic” type (Riginos & Cunningham 2005).

The experimental period of 3 months should have been sufficient for the mussels to adapt to a new salinity since adaptation processes in mussels occur within some weeks (Böhle 1972, Almada-Villela 1984). These are the time spans mussels would face in the course of translocation and invasion events. A translocation of mussels would probably result in successful invasion of animals from the highly adaptive group, and in the demise of mussels originating from the adaptively inferior populations. Parameter shifts driven by climate change occur slower and it is possible that populations react differently when they have a longer time period to adapt. But even over several decades mussels may not be able to overcome some physiological thresholds. During the last 5000 years in the brackish Baltic environment they were not able to push their salinity tolerance beyond 4-5 psu (Schlieper & Remane 1971, Westerbom et al. 2002, Kautsky 1982a). Hence, populations living at the edge of their range in the eastern (and northern) part of the Baltic will disappear upon further desalination. The action of additional stressors linked to global change (i.e. warming, pollution, anoxia) may aggravate the situation even for populations not at their physiological limit (Incze et al. 1980, Cotter et al. 1982).

Besides physiological restrictions, climate change may affect other interactions of mussels such as competition. If desalination, warming and the shift of other environmental parameters impact mussels more negatively than their competitors, mussel populations may shrink even well within their physiological range. Other filter feeders, e. g. freshwater bivalves, could invade the Baltic habitats, following further desalination. The invasive

species *Dreissena polymorpha* is spreading throughout Europe (Karatayev et al., 1997, Orlova & Panov 2004) and might easily outcompete physiologically stressed *Mytilus* spp.

The western Baltic *Mytilus* spp. populations will not escape consequences from predicted climatic changes. Honkoop and Beukema (1997) state that the timing of environmental events is of high importance for their consequences. They found that warming in a period of large food abundance leads to enhanced growth, while after mild winters they detected high body mass losses in mussels due to elevated metabolism during a period of low food availability. These effects are not surprising, even for the more stable environment of Helgoland. There is already evidence that global warming can lead to a re-distribution of species (Barry et al. 1995, Parmesan et al. 1999, Harley 2003). More indirectly, the physiological reaction to desalination of species with a wide temperature and salinity tolerance range, such as *M. edulis*, may not result in the species' disappearance but to a change in its competitiveness or susceptibility to consumption due to decreases in growth rates or shell stability, respectively. Such disruptions of interspecific interactions in food webs can have consequences for the stability of these systems (Emmerson et al. 2005).

Generally, the stress on the Baltic mussel will decrease from the innermost parts towards the North Sea with the highest impact on populations living at salinities between 6 and 12 psu. Some predicted events may even enhance mussel performance, such as moderate warming, growth period extension, and (for populations living at high salinities) a salinity reduction. We conclude that most Western Baltic *Mytilus* populations should be able to face the changes in their environment, as long as no additional stressors as pollution or introduced predators amplify the resulting physiological stress. For the Eastern populations, however, the struggle will be harder since they already live at the lower range of their salinity tolerance.

**Chapter III**



## The salt in the soup:

# Will desalination affect a Baltic key predator-prey interaction?

### Abstract

The effects of global change on ecosystems can be direct (on the organism) or indirect (on the interactions of the organism). In this study we investigated the impact of shifts in an environmental parameter, salinity, on a predator-prey interaction. In the Baltic Sea, the interaction between crabs (*Carcinus maenas*) and mussels (*Mytilus edulis*) is of high importance for the stability and composition of benthic communities. In the Eastern Baltic, the brachyuran crab species *Rhithropanopeus harrisi* has been introduced and was therefore included in the study. Mussel shell stability is related to ambient salinity. It is also an important feature in crab prey selection. Crabs and mussels were reared under different salinity conditions and prey preference was investigated at low, medium and high ambient salinity (12, 24 and 33 psu, respectively). For the predators, energy content of the prey was of higher importance than shell stability. In both crab species, *C. maenas* and *R. harrisi*, reduced ambient salinity resulted in increased preferred prey size.

### Introduction

In many Baltic communities, the mussel *Mytilus edulis* often is the dominating species on shallow hard bottom (e.g. Wahl 2001), and in some regions more than 90 % of the total biomass consists of blue mussels (Kautsky & van der Maarel 1990, Reusch & Chapman 1997). In the Western Baltic, mussels co-occur with a high density of predators, however, Reusch and Chapman (1997) could show that highly abundant *Asterias rubens* were not able to completely control the enormous growth and recruitment potential of *M. edulis*. They concluded that the mussels, without predatory control, could easily extend their dominant abundance to a 100% cover of large areas within one year. This effect can also be observed for substrata without direct contact to the bottom and, thus, without direct access for benthic predators, as buoys, pontoons and ropes (Laudien & Wahl 1999). Despite a substantial number of species associated with mussel beds (Tsuchiya & Nishihira 1986, Kautsky & Evans 1987, Commito et al. 2005), high mussel dominance leads to reduced benthic diversity (Reusch et al. 1994). Thus, biodiversity in the Baltic is highly dependent on the control of mussel dominance by predation.

Mussel predators differ between the Western and Eastern Baltic. In the Western part, periwinkles *Littorina littorea* feed on juvenile, freshly settled mussels (Wahl & Hoppe 2002)

as do juvenile starfish and crabs. The sea star *A. rubens* feeds on all sizes of mussels, depending on predator size, even though a refuge size of 33mm shell length is reported from Reusch and Chapman (1997). Eider ducks swallow mussels in whole complete with their shell (Hamilton et al. 1999), while gulls and crows drop them on stones (Garza 2005) and oystercatchers hammer a hole in the dorsal or ventral valves (Nagarajan et al. 2006). For the Eastern Baltic, major losses to waterfowl and fishes (cyprinids and flounders) are reported by Kautsky (1981) and Westerborn et al. (2002). Crab predation is one of the major factors in structuring benthic marine communities world wide (Virnstein 1977, Leber 1985, Raffaelli et al. 1989). While predation by birds is restricted to the surface water and sea star distribution is limited by salinity (Bonsdorff et al. 2006), *M. edulis* in the Baltic Sea is subject to crab predation along the entire salinity gradient from 5 to 33 psu: *C. maenas* is restricted to the Western Baltic, but the presence of another brachyuran crab, the mud crab *Rhithropanopeus harrisii tridentatus*, in the Eastern Baltic suggests similar crab predation pressure on Eastern *Mytilus* populations. *C. maenas* is known to counteract mussel dominance in Baltic benthic communities (Frandsen & Dolmer 2002), hence, the predator-prey interaction of these two species is of high importance for the Baltic ecosystem.

### Predators

*Carcinus maenas*, as many other crabs, exhibits optimal foraging behaviour (Elner & Hughes 1978). According to the optimal foraging theory by Hughes (1980) this results in the maximization of net energy uptake during the prey searching and handling process. *C. maenas* is wide spread in the Baltic Sea, but restricted to regions where salinity exceeds 10 psu (Arndt 1996,



Figure 20: *Carcinus maenas*.

Bonsdorff 2006). It readily feeds on *M. edulis* and uses various techniques to open its mussel prey (Ropes 1968, Elner 1978, Hughes & Elner 1979, Cunningham & Hughes 1984): in ca 80% of attacks, the crab will try to crush the umbonal or posterior end; however, these are attack methods which are not always successful. Prising apart the shell is used in 20 % of the attacks, but has proved to be successful in all cases (Cunningham & Hughes 1984). Additionally, the crabs exhibit a high learning capacity for predatory skills. Through practice on abundant prey, the crabs can improve the attack efficiency and thus the profitability of the prey. Cunningham & Hughes (1984) could show that the acquired skills lasted for at least 2 days but were lost after 4 days.

*Rhithropanopeus harrisii tridentatus*, the mud crab, is another presumptive mussel predator which has been introduced to Europe from the NE Atlantic in the last century (Turoboyski 1973, Nehring 2000). This invasive species is now abundant in the Polish Baltic and adjacent estuaries (Turoboyski 1973, Jadzewski et al. 1993) and has also spread along the



**Figure 21:** *Rhithropanopeus harrisii*.

German coast (e.g. in the Salzhaff near Wismar, Nehring 2000). Additional records are reported from the Kiel Canal (Kinne & Rotthauwe 1952) and the Schlei estuary (I. Bobsien, pers. comm.).

*R. harrisii* is euryhaline and has been found in salinities ranging from fresh water up to 25 psu (Turoboyski 1973 and references therein). Thus, this small brachyuran crab can be considered a complementary predator, foraging in Baltic regions where *C. maenas* does not occur. Feeding in *R. harrisii* seems to change with habitat. Small snails, algae, detritus but also *Dreissena polymorpha* and *M. edulis* are prominent food items (Kinne & Rotthauwe 1952, Tuboroyski 1973). Salinity changes as predicted from BACC (2006) could impact the physiology of the crabs (growth, respiration, moulting cycles), but also their distribution and their foraging habits.

### **Prey – *Mytilus***

Mussels in the Baltic Sea are occurring in all salinities from 4-5 to 33 psu (Lozán 1996, Schlieper & Remane 1971), but they are conspicuously affected by the low salinity. Maximum shell length decreases from more than 70 mm in the North Sea to 55 mm at 15 psu and 20mm at 5 psu. Shell thickness and longevity, too, relate directly to salinity (Lozán 1996). With their enormous biomass (up to 5000 individuals per square meter, Zander & Blessin 1996) they constitute a major food source for many other organisms (Kautsky 1981, Kautsky & Evans 1987).

Unlike in predation of sea stars where muscle strength or overall size are determining mussel vulnerability, crab predation relates to shell size and shell stability (Boulding 1984, Mascaro & Seed 2001, Beadman et al.2003). Consequently, if the predicted salinity decrease takes place, the expected decrease in mussel growth rates as well as in shell stability should enhance their vulnerability to predation.



### Predator – prey interaction

The shore crab *C. maenas* is a non visual forager and needs to handle its prey for a while to consider whether it is optimal or sub-optimal and needs to be rejected (Hughes & Elner 1979, Jubb et al. 1983, Ameyaw-Akumfi & Hughes 1987, Hughes & Seed 1995). Shell thickness and shell stability are, besides prey shape and volume, important features on which *C. maenas* bases its foraging decisions (Boulding 1984, Mascaro & Seed 2001, Beadman et al. 2003). *M. edulis* is able to increase shell thickness, byssus production and posterior adductor diameter when exposed to predators (or waterborne cues) (Côté 1995, Leonard et al. 1999, Frandsen & Dolmer 2002) in order to escape predation. According to Palmer (1981) and Boulding (1984), mussels can attain a size refuge beyond the critical size (= maximum size of vulnerability, Vermeij 1976) since many crab predators prefer small sized shell prey which are not likely to damage claws (Juanes 1992). In an experiment with *C. maenas* from the Irish Sea no mussels larger than 50 mm could be opened by crabs with a carapax width (CW) of 70 mm (Ameyaw-Akumfi & Hughes 1987). In the Kiel Bight, size refuges for *M. edulis* range from 33 mm shell length (sea stars) to 48 mm (crabs) (Reusch & Chapman 1997, Enderlein et al. 2003).

According to the optimal foraging theory (Hughes 1980), prey should be ranked by profitability. Profitability curves for crab species with different claw morphologies and foraging behaviour differ conspicuously. According to Seed & Hughes 1995, for *C. maenas* prey profitability follows a monomodal distribution, peaking at medium sized mussels, while for *Calappa acellata* profitability is independent of prey size, and increases monotonically with prey size in *Callinectes sapidus*. Thus, the time taken by *Carcinus* to break open mussels is approximately an exponential function of prey shell length with the result that mean profitability (yield/handling time) peaks at intermediate sizes of mussels (Elner & Hughes 1978). This has been experimentally confirmed (Leonard et al. 1999). Crabs prefer mussels smaller than 30 mm, because mussels of this size can be crushed instead of using other time consuming methods (Ameyaw-Akumfi & Hughes 1987).

In the last years, changes in many environmental parameters such as temperature, CO<sub>2</sub> content and ice cover have been observed in the Baltic region, and further shifts, e.g. in precipitation, salinity or wind speed are predicted (Lehmann et al. 2002, Walther et al. 2002, Meier 2006, BACC 2006). Baltic salinity is expected to decrease by up to 5 psu (BACC 2006). Since the distribution range for many species in the brackish Baltic Sea is determined by salinity (Schlieper & Remane 1971) and many organisms are already living at the edge of their salinity tolerance (Schlieper & Remane 1971, Westerborn et al. 2002) the local composition of benthic communities will be affected by any further salinity reduction. Such environmental shifts due to climatic change can impact the species in two different ways: **directly**, by influencing the organisms' physiology, morphology, recruitment and behaviour, or **indirectly** via the impact on any other species that is interacting with the

species as for instance prey, predator or competitor (Schiel et al. 2004, Harley et al. 2006). According to the authors, the combination of these impacts results in ecological responses at different scales, such as patterns (distribution, biodiversity) or physiological processes (e.g. productivity). At the physiological level, each species responds to climate change in its own characteristic manner (Schiel et al. 2004). If interacting species exhibit different sensitivity to climate change, the symmetry of their interaction is prone to shift. With changing species interactions, resulting shifts in community structure and dynamics are inevitable. If a key species of a community is severely affected, its functional replacement by another species is not always warranted because redundancy in marine systems is suggested to be low (Micheli & Halpern 2005). Crabs as well as mussels are functionally important species in Baltic benthic ecosystems

Griffith and Hockey (1987) suggest that mussels of about 10 to 60 mm pass through a “window of vulnerability” to predators because most of them are able to feed on small mussels. If, due to decreasing salinity, shell stability is reduced, it is likely that the mussels’ vulnerability towards their shell-cracking predators, e.g. the crabs, increases. In a previous study (Chapter II) we found that desalination by the predicted amount generally decreases growth rates and – to a lesser degree - shell stability. This should influence mussel-predator interactions: when mussels produce weaker shells, the crabs’ preferred prey size class could shift towards larger prey. This means that the mussels stay under predation pressure for a longer time and the reproductively highly important size classes larger than 35 mm will be affected. Since in mussels reproductive output is related to size (Kautsky 1982b), this effect could result in reduced reproductive success.

The objectives of this study were

- i.) to detect impacts of ambient salinity on the preferred mussel size of *Carcinus maenas* and *Rhithropanopeus harrisi tridentatus*
- ii.) to investigate whether changes in preferred mussel size are due to salinity impacts on the prey or on the predator
- iii.) to investigate the crabs’ capability to differentiate between mussels with differing shell stability and body mass index

## Materials and methods

### Study organisms

#### *Mytilus edulis*

Small juvenile mussels (< 5 mm) were collected from chains, ropes and algae at the IfM-Geomar Pier in Kiel. Steps of 5 psu twice a week were used to gradually adapt the animals to the experimental salinities of 5, 7, 9, 12, 17, 20, 24, 29 and 33 psu. Fortnightly, additional juvenile mussels were collected and added to the mussels in the lab yielding in different size classes of *Mytilus edulis* in the aquaria. In September 2006, when the experiments took place, mussel size varied between 7 and 42 mm. The first collection date was in May 2005, the last in May 2006. Mussels were kept at 15°C in tanks with flowing sea water of the adjusted salinity (70 l for each salinity). Water was exchanged weekly, and salinity was checked after feeding and corrected if necessary (in a range of  $\pm 0.5$  psu). Food consisted of monocultures of *Rhodomonas sp.* and *Dunaniella sp.* and was provided daily (except on Sundays). Water of the experimental salinities was obtained by either diluting filtered Kiel Fjord water with tap water, or by adding high saline water (Tropic Marine Salt, Dr. Biener GmbH). Kiel tap water is of high quality (< 0.02mg/l NH<sub>4</sub>, 114mg/l chloride, according to Kieler Stadtwerke). Artificial salt water was prepared two days in advance to permit complete dissolution. Salinity was measured with a conductimeter (WTW, Germany).

#### *Carcinus maenas*

Specimens of *Carcinus maenas* were collected from traps at the IfM-Geomar Pier in Kiel (17 psu) in June 2006. Crabs were fed with *M. edulis* (5 – 40 mm shell length) and kept at 15°C solitarily in plastic 20 l tanks with 12, 17, 20, 24, 29 and 33 psu aerated sea water. Water of the respective salinity was obtained in the way described above. Adaptation to the experimental salinity took place in several steps of up to 5 psu within one week. Stones and plastic shields served as refuges for the animals. We adapted 12 - 15 specimens with a CW of 40 - 50 mm for each salinity. For the experiments, only crabs with a CW of 45 - 55 mm were used. Animals that were molting in the week before the experiments or in the week following the experiments were excluded, since feeding of crabs is reduced while preparing ecdysis, as well as during the shell hardening process (Ropes 1968). No difference in crab sex was made, but ovigerous females were excluded. All animals were kept for 3 months in the lab for adaptation before the experiment.

### ***Rhithropanopeus harrisi tridentatus***

Specimens of the species *Rhithropanopeus harrisi* were collected in June 2006 by dredging in Flemhude Lake which is connected to the Nord-Ostsee-Kanal. Salinity at the sampling site was 7 psu; water depth was 2 - 3 m. Animals were separated into 4 groups which were adapted to 5, 7, 9 and 12 psu immediately. 7 crabs were kept together in a 20 l plastic tank with sand bottom and aerated water. Food consisted of small *M. edulis* (5 - 20 mm) and of the flesh of larger, pre-opened mussels. Water with the respective salinities was obtained as described above, and was renewed weekly. Only animals between 10 and 15 mm CW were used. No difference in crab sex was made, but ovigerous females were excluded from the study. Animals were kept for 3 months in the lab before the beginning of the experiment.

### **Experimental setup**

#### ***Carcinus maenas***

The day before the experiments, animals were transferred into 12 l plastic tanks, containing fresh water of the experimental salinity (12, 17, 20, 24, 29 or 33 psu, respectively), a refuge and aeration. They were starved 24h for standardizing the hunger level. We did choose this short starvation period since crabs with a high hunger level are likely to grasp the first prey they reach instead of selecting between different mussels (Jubb et al. 1983). The experiments took place at 15°C and dimmed light. Crabs were offered mussels (*M. edulis*) which differed by size and / or culture salinity and the first mussel selected and successfully opened was recorded. Care was taken that the animal indeed “selected” its prey and did not just grab any mussel. According to Jubb et al. (1983), crabs react to prey that is touched by the pereopods, even if another mussel is held in the chelae. The selection process was judged successful if several of the presented mussels had been touched before finally one prey was selected and successfully opened. The experiment was considered a failure when crabs had not chosen a prey after 5 hours.

#### ***Rhithropanopeus harrisi***

Single specimens of *Rhithropanopeus harrisi* were brought into the experimental tanks the day before the experiment for adaptation and were starved for 24h. Tanks contained salt water of the respective salinity treatment, and two or three small stones as refuge. Temperature was 15°C and the photoperiod was 12h dark : 12 h light. Experiments started in the evening and were stopped 14 h later in the morning because most animals did not feed during the day.

## Experiments

In the description of experiments I will refer to the following abbreviations:

N = number of crabs (replicates), lower ciphers = salinity treatment,  $N_p$  = number of experiments with each crab (pseudoreplicates).

### Experiment I (*C. maenas*):

*Does preferred prey size differ between crabs adapted to different salinities?*

Each crab (adapted to a salinity of 12, 17, 20, 24, 29 or 33 psu) was offered 7 mussels that were grown at 17 psu (Kiel Fjord salinity). Mussel sizes were 10, 15, 20, 25, 30, 35 and 40 mm ( $\pm 1$  mm) and they were adapted to the crab salinity two days before the experiment to avoid a physiological shock when transferring them to the experimental salinity.  $N_{12} = 3$ ,  $N_{12p} = 3$  to 4.  $N_{17} = 4$ ,  $N_{17p} = 2$  to 8.  $N_{20} = 4$ ,  $N_{20p} = 8$  to 9.  $N_{24} = 4$ ,  $N_{24p} = 3$  to 6.  $N_{29} = 4$ ,  $N_{29p} = 3$  to 7.  $N_{33} = 4$ ,  $N_{33p} = 2$  to 6.

### Experiment II (*C. maenas*):

*Is the preferred prey size dependent on the salinity where mussels were grown?*

Each crab (all adapted to 17 psu), was offered 6 mussels that were grown in different salinities (9, 12, 17, 20, 24, 29 and 33 psu) but had the same shell length (20 - 25 mm). We wanted the mussels to be in the upper range of the animals' prey size range, assuming that *C. maenas* would display more differentiated preference when confronted with challenging prey. Therefore we used crabs that were smaller than 45 mm in this experiment.  $N = 22$ . Body mass indices were taken from Kiel mussels (15 - 25 mm shell length) that were grown in the laboratory at 15° for 4 months and calculated as mg tissue dry weight \* shell length<sup>-2</sup>.

### Experiment III (*C. maenas* & *R. harrisi*):

*Does ambient salinity affect the prey selection?*

*C. maenas*, adapted to 12, 24 and 33 psu, were offered 5 mussels of different sizes (15, 20, 25, 30, 35 psu) which were grown in the same salinity as the crab. Treatments were restricted to a low, a medium and a high salinity (12, 24 and 33 psu, respectively) since a high number of replicates was considered to be more important than a high amount of treatment levels.  $N_{12} = 9$ ,  $N_{24} = 10$ ,  $N_{33} = 7$ ,  $N_p$  in all salinities = 1 - 4.

Specimens of *R. harrisi*, adapted to 5, 7, 9 and 12 psu, were offered over night six mussels (6, 7, 8, 9, 10 and 11mm shell length) that were grown in the same salinity. In the morning, the mussels that had been opened were recorded.  $N_5 = 3$ ,  $N_{p5} = 2 - 10$ ,  $N_7 = 5$ ,  $N_{p7} = 1 - 9$ ,  $N_9 = 6$ ,  $N_{p9} = 1 - 5$ ,  $N_{12} = 3$ ,  $N_{p12} = 7 - 10$ .

### Data analysis:

Data are reported in figures as means  $\pm$  standard error (SE) unless otherwise stated. A significance level of 0.05 was accepted as statistically significant.

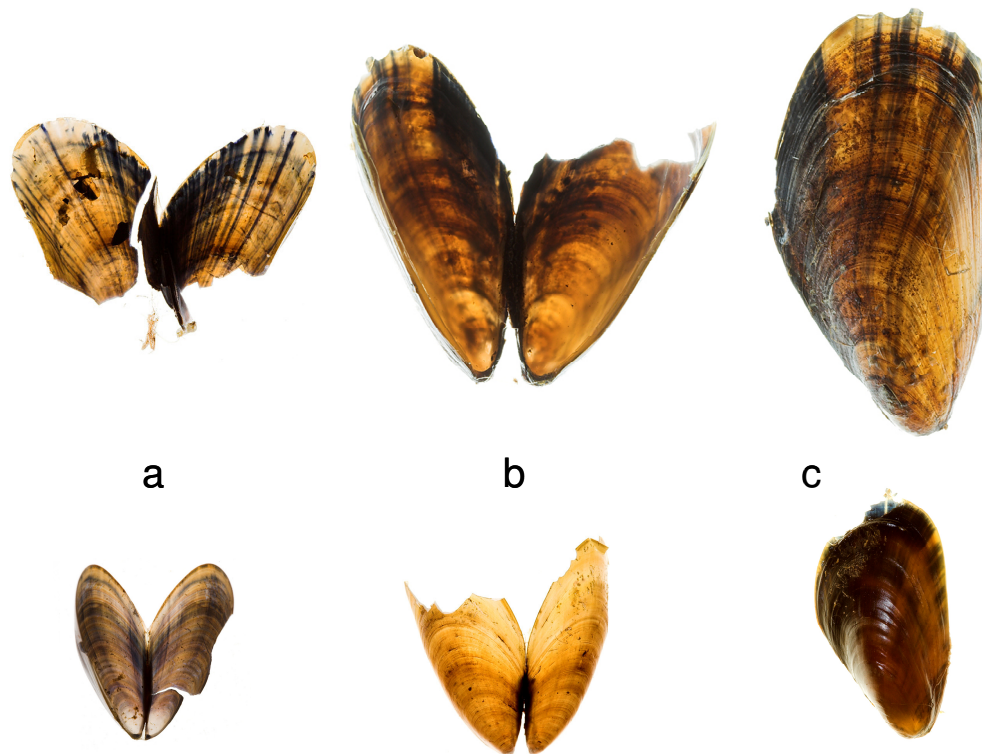
Experiment I: Differences between treatments were analyzed using a 2-factorial ANOVA (factors: salinity and mussel size) and Tukeys HSD (post hoc), after testing for normality of distribution and variance homogeneity.

Experiment II: Differences in body mass indices between salinity treatments were tested for normality of distribution and variance homogeneity and then analyzed by a 1-factorial ANOVA. Prey preference in *C. maenas* is given as percentage of all mussels consumed.

Experiment III: Since crab size was unequal between species, the preferred mussel size was expressed relative to consumer size. The largest mussel consumed by *C. maenas* or *R. harrisi*, respectively, was set as 100%. in order to account for different sizes of the species. Sizes of all other mussels are given as percentage of this maximum size, and were arcsin transformed before further analysis. Linear regression was analyzed with Statistika 6.

## Results

In the course of our study of the feeding preference of Baltic crabs *Carcinus maenas*, exhibited the opening techniques described in the literature. In general, the mussels offered to the crabs were too large to be crushed outright; in *C. maenas* this opening technique is normally used only for mussels below 10 mm shell length (Elner 1978). In our study, in most cases *C. maenas* was crushing the umbone or the posterior end of the prey which is the most common method for mussel prey between 10 and 30 mm (Elner 1978, Cunningham & Hughes 1984). With this technique, crabs successfully opened their mussel prey within some minutes. Crabs that selected mussels of the largest size classes (30 and 35 mm) often took much more time to open their prey and sometimes did not succeed during the experiment. Mussels that had been selected but were unsuccessfully rejected often had chipped edges in the posterior part of the shell. Since *Rhithropanopeus harrisii tridentatus* was feeding merely over night, except for one individual, we could not observe the opening methods. However, it seems probable that they used the same techniques as *C. maenas* since the patterns in shells leftover of opened mussels were similar in both species (Figure 22).



**Figure 22:** *M. edulis* opened by *C. maenas* (upper row) and *R. harrisii* (below). a- mussel crushed at the umbonal end, b- mussel crushed at the posterior end, c- mussel with chipped edge due to unsuccessful attack.

**Experiment I (*C. maenas*):**

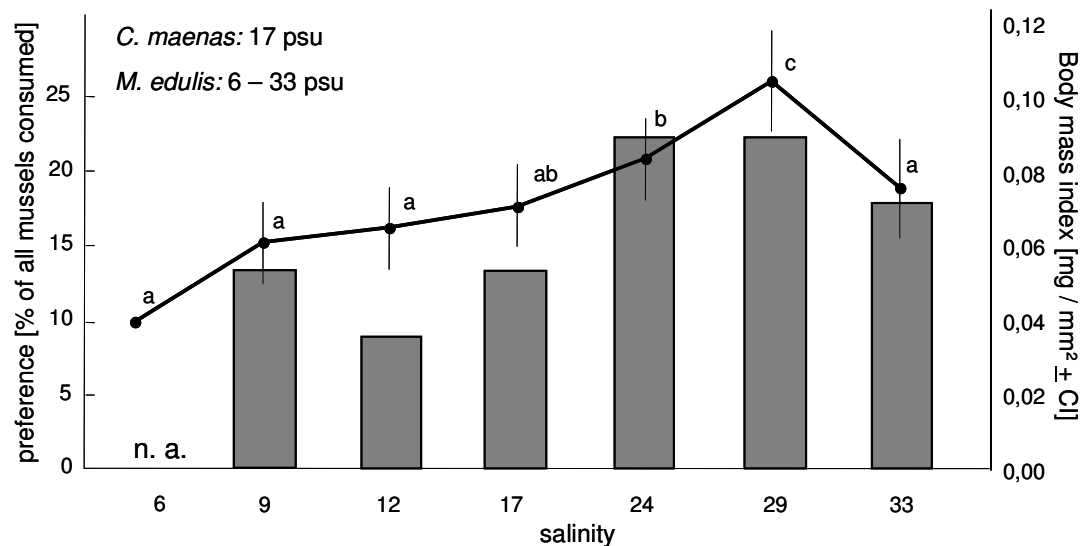
*Does preferred prey size differ between crabs adapted to different salinities?*

Crabs adapted to salinities from 12 to 33 psu showed a preference for medium size classes (between 15 and 25 mm) in mussels raised at 17 psu. We could not detect significant differences in the preferred mussel size between salinity treatments.

**Experiment II (*C. maenas*):**

*Is the preferred prey size dependent on the salinity where mussels were grown?*

The majority of the crabs (all kept at 17 psu) tended to choose a mussel that was grown at 24 or 29 psu. This preference was not statistically significant at the replication level we used, though, it is interesting to note that mussels in this salinity range showed highest growth rates (Chapter II) and highest body-mass indices (tissue dry weight\*shell length<sup>2</sup>, Figure 23).



**Figure 23:** Mussel preference in *C. maenas* from the Kiel Fjord (17 psu). *M. edulis* raised in different salinities. Grey bars are the percentage of all mussels consumed by crabs. Black line indicates the body-mass-indices (BMI) of mussels at different salinities. a, b, c relate to BMIs and indicate significant differences (posthoc Tukeys HSD).

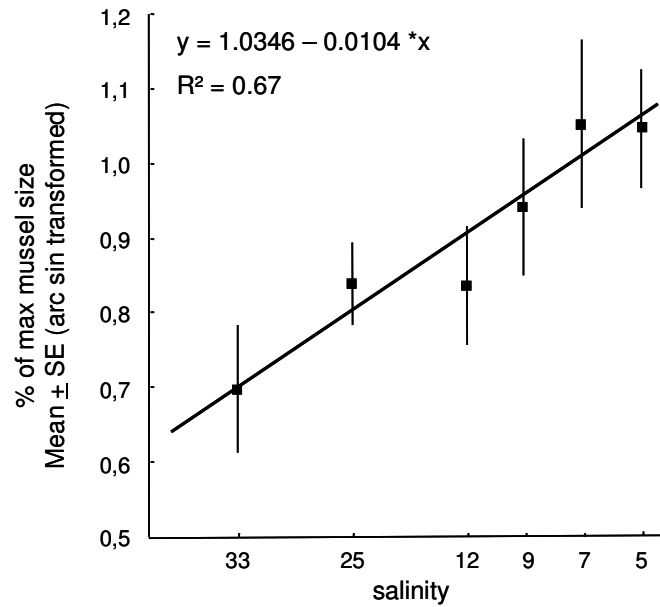
**Experiment III (*C. maenas* & *R. harrisi*):**

*Does ambient salinity affect the prey selection?*

Crabs and mussels were adapted to and grown in 5, 7, 9, 12, 24 and 33 psu. *R. harrisi* at 12 and 7 psu were feeding more often than did the animals at 5 and 9 psu, however, none of the animals seemed to be negatively affected by the salinity treatment, since all of them were active and reacted to disturbance (as for example during the water exchange process). Relative to body size, *R. harrisi* preferred mussels that were much larger than the prey preferred by *C. maenas*: mud crabs opened mussel that were as long as the predator's carapax width (CW) while shore crabs preferred prey that was only slightly longer than half their CW.



Preferred mussel size (corrected for the respective consumer species and given as percentage of max prey size) increased with decreasing ambient salinity, the results of a regression analysis is shown in Figure 24 (linear regression,  $F_1 = 8.11$ ,  $p < 0.05$ ,  $R^2 = 0.67$ ).



**Figure 24:** Prey size preference in *C. maenas* and *R. harrisi*, adapted to different salinities. *M. edulis* raised in respective salinities. In percentage of max size (the largest mussel that was consumed by *C. maenas* or *R. harrisi*, respectively). Data were arc sin transformed.

## Discussion

From the literature we know that for *Carcinus maenas* of 60 mm carapax width (CW) the favourite mussel size is around 30 mm shell length (Elner 1978, Cunningham & Hughes 1984), and medium sized crabs (5.0 – 6.5 mm CW) preferred mussels of 15 - 24 mm shell length (Enderlein et al. 2003). Thus, our crabs with a CW of 45 to 55 mm were likely to express a similar preference, which is well covered by the range of mussel sizes that were offered in our experiments. Nothing was known of mussel size preferences of *Rhitropanopeus harrisi* in the Baltic Sea. In the course of this investigation it became evident that, relative to its body size, *R. harrisi* feeds on larger mussels than *C. maenas*. This is probably due to their claw morphology with extremely large chelae (Figure 21)

Mussel shell condition is not entirely determined by salinity, even though this parameter has consequences for both shell thickness and shell stability (Chapter I + II, Kautsky et al. 1990). Many other factors can influence the building and strength of the shells. Leonard et al. (1999) observed a positive correlation between growth rates and shell thickness, which was confirmed in chapter II, and there are many references indicating that mussel shell thickening and other defence features are induced by the presence or by waterborne cues of predators (Juanes 1992, Norberg & Tedengren 1995, Beadman et al. 2003).

From previous studies we know that mussel growth is significantly influenced by temperature, salinity and food availability, while shell stability is only related to temperature and salinity (Chapter I). A field study revealed that, besides salinity, mussel provenance is a major factor in determining growth rates and shell stability in *M. edulis* (Chapter II). Growth rates as well as shell stability are influencing prey profitability and hence the crabs' foraging behaviour (Boulding 1984, Mascaro & Seed 2001, Beadman et al. 2003), and both of these mussel features were influenced by predicted shifts in temperature and salinity. Thus, an ensuing impact on the crab-mussel interaction can be assumed.

In the first experiment of this study we tested the influence of salinity on the feeding behaviour of *C. maenas*. The crabs were kept at different salinities, while all mussels came from the same salinity. If salinity had directly influenced the crab, for instance the force of its chelae or its energy demand, animals kept at high and low salinities should have differed in their prey selection. Since there were no significant differences in crab behaviour we conclude that ambient salinity did not directly affect crabs foraging.

In order to investigate the crabs' ability to detect differences in mussel shell stability we offered *C. maenas* six mussels of the same size but grown at different salinities. In preceding studies (Chapter II), shell stability had been shown to relate inversely to ambient salinity. Prey from lower salinities should require less energy and time to be opened and therefore should be of higher profitability (Cunningham & Hughes 1984). Surprisingly,

*C. maenas* was selecting mussels of relatively high salinities (24 and 29 psu) instead of the less resistant low salinity prey. At 24 psu, mussels in previous studies had the highest shell stability (Chapter II), thus another factor must have determined the crabs' preference. We suggest that *C. maenas* preferred mussels with a high condition index: comparing the body-mass-indices (BMI) of *M. edulis* at different salinities with the preferred mussel prey in this experiment, it is apparent that highest BMI coincide with crab preference. This assumption is supported by the low correlation coefficient of feeding preference and RSS (Pearson's product moment correlation,  $R^2 = 0.005$ ,  $p = 0.89$ ), compared to feeding preference and BMI ( $R^2 = 0.186$ ,  $p = 0.19$ ). Since *C. maenas* is handling and exploring its prey before deciding (Hughes & Elner 1979, Jubb et al. 1983) the animals probably detected the prey's weight/size relation during the selection process. Probably crabs cannot differentiate between shell weight and tissue weight, but since shell thickness as well as body dry weight were highest in mussels from 24 and 29 psu these prey items would always be the heaviest.

While the first two experiments represent a rather unnatural composition since the crabs were confronted with mussels kept at salinities differing from the crab ambient salinity, the last experiment with *C. maenas* and *R. harrisii* where predator and prey were cultured at the same salinity while salinity varied among predator-prey group pairs, displays the natural conditions in the Baltic. The first two experiments provided the basis to separate specific influences of salinity on crabs from those related to the mussels, the latter one, in contrast, reflect the actual influence of salinity on the interaction of both species. When crabs and mussels were kept at the same salinity, ranging from 5 to 33 psu, it became evident that the preferred prey size along this salinity gradient was increasing when salinity decreased. *Carcinus maenas* as well as *Rhithropanopeus harrisii* chose larger mussels when salinity was reduced.

The observations made during this study confirmed that salinity indeed influences prey selection in crabs. Experiment II, however, demonstrated that mussel size and BMI can be of higher importance than shell stability. Since in nature both of these factors are influenced by salinity in similar manner and because growth and shell strength are positively related (Chapter II), we conclude that salinity indeed affects the predator-prey interaction of crabs and mussels in the Baltic Sea but not only via shell stability, as assumed, but also indirectly by affecting other foraging relevant parameters.

What other factors influence the crabs' preference? Elner (1978) suggested that crabs, while handling and exploring their prey, are seeking for a weak spot by trial and error. Naturally occurring small fractures in the shells (Currey & Kohn 1976) can be extended by the crabs, resulting in the predator's success. In other studies it has been shown that crab preference is influenced by prey shape and volume (Mascaro & Seed 2001), size, shell thickness, degree of inflation (Boulding 1984) or even by fouling organisms (Enderlein et al.

2003). However, shell damages and epibionts are occurring sporadically, while a shift in salinity will be of persistence. Therefore, we consider the impact of this environmental factor of higher importance.

Griffith and Hockey (1987) suggest that mussels are passing through a “window of vulnerability” which is limited by the mussels’ susceptibility towards predation. With increasing temperature, as predicted by the climate modellations (BACC 2006), growth rates and shell stability of the mussels will increase (Chapter I), and consequently *M. edulis* will leave the window earlier in life. This positive effect of the predicted rise in temperature will probably apply for Western Baltic *Mytilus* populations, where the simultaneous reduction in salinity has no detrimental effect (Chapter I). In Eastern populations, on the contrary, the desalination will lead to reduced growth rates and reduced shell stability, thus counteracting the favourable temperature effect. Since growth and shell stability are positively correlated (Chapter I), the negative effect on shell stability will even be enhanced. Thus, the critical size (the size of maximal vulnerability, Vermeij 1976) in Eastern *Mytilus* will be shifted toward larger mussels. In mussel populations at low ambient salinity, maximal size and size at maturity are reduced, while the age at maturity is higher (Kautsky 1982b). Large size classes contribute to a high degree to the reproduction (Kautsky 1982b) and, as we demonstrated with this study, will be subject to increased predation pressure when salinity is reduced. Hence, reproduction of Eastern *Mytilus* populations will decrease, while predation increases. Additionally, the salinity reduction will lead to decreases in the mussels’ BMI, therefore crabs may be forced to feed on a higher number of mussels to satisfy their energy demands with consequently higher predation pressure on mussel populations.

The optimal foraging theory (Hughes 1980) assumes that foraging in predators takes place in a way that net energy intake is maximized. Thus, prey should be ranked following profitability. With changing BMI and shell stability, profitability of mussel size classes is likely to be altered. According to Cunningham and Hughes (1984), transpositions of ranks in profitability are possible, but not probable for natural conditions because profitability strongly depends on the relative sizes of crabs and prey (Boulding 1984), and on the environmental conditions. For example, prolonged search time (Frandsen & Dolmer 2002), hypoxia (Brante & Hughes 2001) or increased byssus attachment (Cunningham & Hughes 1984) can result in lower profitability of a prey by reducing predation efficiency.

## Conclusions

Since benthic communities are not static assemblages of predators and prey but rather highly dynamic systems with their members simultaneously influencing each other's morphology, another arms race between crabs and their mussel prey is likely to be induced. Mussels have successfully evolved structures and characteristics that reduce the risk of predation (Côté 1995, Leonard et al. 1999, Frandsen & Dolmer 2002). Some of these features can be induced by the predator's presence, and these responses can occur over ecological and evolutionary time scales or even within weeks (Juanes 1992). Crabs, on the other hand, are also reacting to their prey. Smith and Palmer (1994) could show that diet toughness has significant influence on claw morphology and strength of *Cancer productus*, a brachyuran molluscivorous crab. Fed with fully shelled prey, the crabs developed larger and stronger claws than crabs feeding on pre-opened mussels. As usual in the ecology and evolution of predator-prey interactions, the ability to respond phenologically or genetically to shifts in challenges will be a critical feature in determining the future crab-mussel interactions.

To conclude, Western Baltic *Mytilus edulis* populations will benefit from the predicted rise in temperature, while the salinity reduction in their habitat is not likely to adversely affect growth rates and shell stability. Crab prey size preference will move towards larger mussels, but will not have disastrous consequences since reproductively important size classes will still reach sizes beyond crab predation. For Eastern populations, climate change and resulting impacts on the predator-prey interaction are likely to result in detrimental conditions, since reduced shell stability, inhibited growth and the negative feedback of these effects are adding up to adverse conditions. Knowing this we predict a reduction in mussel abundance in the Eastern Baltic, provided that all other parameters do not change.

# Synthesis and conclusions

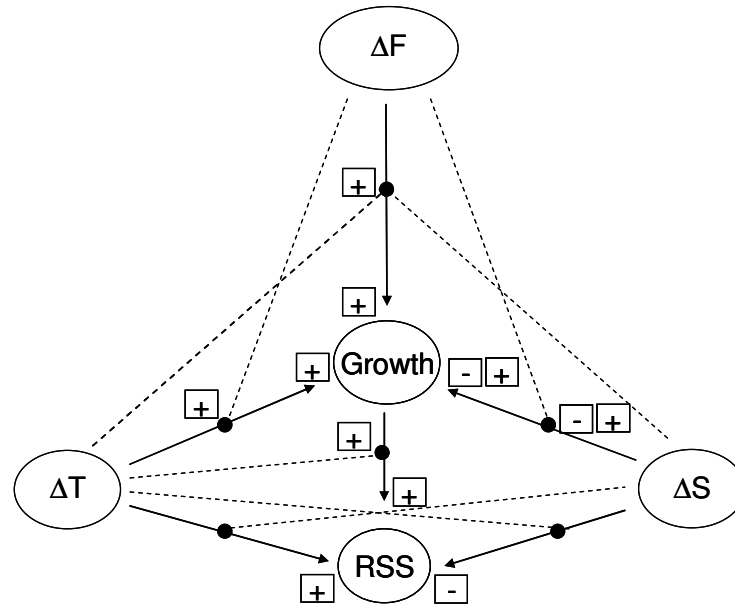
## Synthesis

Since the 1980, the dimension of human induced global change has gradually gathered worldwide public awareness. Though, we are still at the very beginning of understanding the resulting consequences. While high attention was paid to physical parameters such as increasing temperatures and rising sea level, it is only in the last years that investigations focus on the impacts of climate change on biological systems. Given their global economic and ecologic importance (Costanza et al. 1997), coastal marine environments should be of major concern, all the more as recent studies revealed that these systems are highly susceptible for any climate driven changes (Harley et al. 2006).

The Baltic Sea, as any other biological system, is not a static structure but a dynamic complex of many interactive processes. In its history, it has passed through several extensive changes (Niedermeyer 1996) with resulting physiological and ecological challenges for its inhabitants. Species in communities do not simply react to altered conditions but simultaneously influence each others' morphology and behaviour. Molluscs have evolved several ecological and structural characteristics which reduce the risk of predation, and many of these structures can be adapted when decapod predators are present (Leonard et al. 1999). Crabs, in particular *Carcinus maenas*, are also capable to deal with changed prey properties. They possess an adaptable variety of predatory skills (Cunningham & Hughes 1984), and Smith & Palmer (1994) showed that claw morphology and strength in *Cancer productus* can be adjusted to diet toughness even within a single moulting cycle. When fed with hard shelled mussels, the crabs developed larger and stronger claws than crabs feeding on soft prey. In this arms race, the ability to respond phenotypically is important for both predator and prey because phenotypical plasticity is a major factor in stabilizing population sizes and species co-existence (Miner et al. 2005).

Temperature in the Baltic Sea has already increased, and a further increase as well as a reduction in salinity are predicted (BACC 2006). Both factors are determinants for growth rates, maximal attainable sizes, and physiology (Schlieper & Remane 1971, Kautsky 1982a, Tedengren et al. 1990) with resulting consequences for competitiveness, reproductive success and species distribution (Riisgard & Randloev 1981, Kautsky 1982b, Riisgard et al. 2003, Bonsdorff 2006). Salinity is also suspected to influence mussel shell stability (Kautsky et al. 1990), and a reduction of this important prey feature due to predicted desalination would certainly affect the predator-prey interaction with regard to prey profitability (Elner & Hughes 1978).

This work has contributed substantially to a better understanding of the complexity and functioning of a key species' interaction in a Baltic benthic community. In accordance with the hypothesis that climate change affects prey properties, mussel growth rates are significantly increased by rising temperature and food availability, while the consequence of desalination depends on ambient salinity prior to the reduction. Shell stability is positively correlated to temperature and salinity, but not directly affected by food availability.



**Figure 25:** Effects of altered temperature  $\Delta T$ , salinity  $\Delta S$  and food availability  $\Delta F$  on growth rates and relative shell stability RSS of *M. edulis*. + positive effect, - negative effect, black circle and dotted line = interaction modulation.

The pattern of effects (Figure 25) is much more complicated than it was assumed. Intensity, and often even direction, of a single parameters' impact on a given property can be modified by other interacting factors. Interestingly, there were not only interactions between environmental factors but also between mussel features: high growth rates significantly increased shell stability, an observation that was also made by Leonard et al. (1999). Thus, while having no direct impact on shell stability, food availability affects this parameter indirectly via growth rates. The relationship between salinity and shell stability appears even more sophisticated: as mentioned above, the consequence of reduced salinity on growth rates can be positive if the former salinity was higher than 24 psu, but can also lead to decreased growth if the previous ambient salinity was lower than 20 psu. Desalination *per se* leads to reduced shell stability, but since growth rates affect shell stability, there is also an indirect effect of salinity that might even be in opposition to the direct impact.

When the study was extended to 6 mussel populations along the Baltic salinity gradient it became evident that the responses of *M. edulis* towards changes in salinity were strongly

dependent on both ambient salinity and mussel provenance. In populations from medium ambient salinities (Poel, Kiel, Kristineberg and Tjärnö), growth rates followed a monomodal regression line, with a peak at 25 psu and decreasing growth at very low as well as at very high salinities. This pattern was more prominent in the laboratory, but very similar in the field data. In mussels from Helgoland and Askö, growth increased linearly with salinity in the field, but also displayed the monomodal pattern in the lab. Shell stability increased with increasing salinity in the field, but unlike in growth rates, the laboratory results did not fully confirm these findings. I suspect that besides salinity another external factor such as food or water quality, excluded in the controlled laboratory conditions, influenced the shell building process in the field.

The general conformity of field and laboratory underscores the reliability of the outcomes. For the first time, a reliable data basis for predicting the future destiny of Baltic blue mussels has been generated. On the basis of these findings I predict that in the course of desalination by 5 psu there will be a significant reduction in the shell stability of all Baltic mussel populations and in the growth rates of mussels from Poel, Kiel and Kristineberg (Chapter II). For mussels from higher saline regions (Helgoland and Tjärnö), in contrast, conditions will improve since salinities between 24 and 29 proved to result in highest growth rates, high shell stability and high body-mass indices. Mussel populations that already exist at the edge of their distributional range will disappear upon further desalination since survival of *M. edulis* is not possible at salinities below 4-5 psu (Schlieper & Remane 1971, Westerbom et al. 2002, Bonsdorff 2006).

The reciprocal transplant experiment that was conducted in the field also provides useful and relevant knowledge on the invasiveness of the different Baltic *Mytilus* populations. By transferring the mussels over large distances and a considerable salinity gradient in a short time I simulated the transport via ship hull fouling (Gollasch 1996, 2002) which is another phenomenon of global change and can result in the invasion of species in new habitats. My results imply that mussels from Poel, Kiel, Kristineberg and Tjärnö show a wider ecological tolerance and, due to their higher growth rates, an enhanced competitiveness. A successful invasion of *M. edulis* originating from these populations is therefore more likely compared to specimens from Askö or Helgoland.

The central question of this work was whether the predator-prey interaction of crabs and mussels would be affected by the predicted climate changes. The results of chapter I and II demonstrated a significant decrease in mussel shell stability in the course of reduced salinity. With several prey selection experiments I could show that the preferred mussel size was negatively correlated to salinity: both crab species, *C. maenas* and *R. harrisii*, selected larger prey when salinity was reduced. However, when confronted with mussels of equal size crabs preferred prey with high body-mass indices over those with low shell stability.



## Conclusions

In this Eastern Baltic, the enhancing effect of higher temperature on mussel growth rates will be counteracted by the inhibiting impact of reduced salinity. Decreasing salinity also results in diminished shell thickness, and this weakening will be enhanced by the positive correlation between growth rates and shell stability. Thus, mussels in the East will be smaller and thinner shelled than today, resulting in enhanced vulnerability towards predation. In this context, the increase of preferred prey size is crucial: predation pressure is enhanced and simultaneously shifted towards larger mussels, hitting those size classes with major contribution to the population's reproduction (Kautsky 1982b). Since competitiveness is strongly related to both recruitment and growth rates, other species such as the invading zebra mussel *Dreissena polymorpha* (Orlova & Panov 2004, Bonsdorff 2006) could become an additional threat for the blue mussels. Based on these findings, I predict a reduction in abundance for Eastern Baltic *Mytilus* populations, mainly due to reduced reproduction and increased predation pressure, provided all other parameters remain unchanged.

Mussels in the Western Baltic, on the contrary, will not experience such harsh alterations. Desalination will result in reduced shell stability, and consequently the window of vulnerability (Griffith & Hockey 1987) is shifted towards larger mussels. But since growth rates will increase where the salinity shift entails 25 to 29 psu, *M. edulis* will be able to leave this window earlier in life and thus no change in the predator-prey relationship is suspected. Consequently, due to enhanced growth rates and diminished predation pressure, the results of this study imply higher future abundance for Western Baltic *Mytilus* populations.

In this study I elucidated the effects of climate change on the interaction between the blue mussel and its crab predators in the Baltic Sea. The work does not explore the impact on early life stages and ontogeny of the study organisms, and further investigations with regard to population dynamics would be of interest. However, since the results of the field and laboratory experiments presented here are highly consistent, they reveal one probable scenario for the consequences of climate change in the Baltic Sea.

## Danksagung

Ich möchte mich an erster Stelle bei Prof. Dr. Martin Wahl bedanken, der sich schon im Vorfeld dieser Arbeit viel Zeit für die Ausarbeitung des Projektes genommen hat. Ich habe in ihm einen sehr guten Betreuer gefunden, der stets ein offenes Ohr für Fragen und Probleme hatte und im Zweifel auch schnell mal selbst mit angepackt hat.

Die Unterstützung innerhalb der Arbeitsgruppe hat das Leben und die Organisation oft wesentlich erleichtert, und dafür möchte ich allen Kollegen sehr herzlich danken.

Valeria hat sicherlich nicht unwesentlich dazu beigetragen, daß ich nun endlich fertig geworden bin. Als Freundin, Kollegin und Zimmergenossin hat sie alle Höhen und Tiefen miterlebt, die von ausgelassener Heiterkeit über Tränen bis zur völligen Hysterie gereicht haben. Außerdem hat sie mit mir meine „extrem komplexen“ Ergebnisse diskutiert und mit vielen englischen Formulierungen die Manuskripte verbessert. Ein Arbeitsleben ohne sie kann ich mir im Moment gar nicht vorstellen. Ein privates übrigens auch nicht.

Penny hat mir in den ersten beiden Jahren sozusagen pausenlos zur Seite gestanden, und mit ihrer Unermüdlichkeit oft dazu beigetragen, die nötige Motivation für langweilige oder schwierige Aufgaben zu finden. In den letzten Monaten habe ich sie sehr vermißt, denn gute Laune und Humor sind gerade während der langen Stunden in der Klimakammer unersetzlich.

Meinem Vater möchte ich für die beiden wunderschönen Fahrten durch Schweden danken. Ohne seine Unterstützung hätte ich wohl schon bei der ersten Feldstation, die wir mit Versuchsanlagen bestückt haben, das Handtuch geworfen. Sein handwerkliches Geschick auch in schwierigster Lage (z.B. an einer Spundwand hängend) und die Fähigkeit zur Improvisation und Motivation haben mich durch die nervenaufreibende Anfangsphase der Feldversuche gebracht. Meiner ganzen Familie danke ich für die Unterstützung und das Verständnis in der letzten Zeit.

Markus war in der letzten heißen Phase als Fels in der Brandung und Herrscher über alle Formatierungs-Fallen meine Rettung. Er hat mit unglaublicher Ausdauer bis spät in die Nacht am Layout gebastelt. Ich danke ihm für die Geduld, die Unterstützung und die Geborgenheit, die er mir gibt. Diese Arbeit verdankt ihm außerdem die vielen schönen Fotos und den Entwurf der Titelseite.

Alex hat für den sportlichen und auch seelischen Ausgleich gesorgt und mir gegebenenfalls gesagt, daß ich es auf jeden Fall schaffe (und wenn ich dran gezweifelt habe mit Gewaltmaßnahmen gedroht... aber es hat ja funktioniert!).

Christian hat mich mit seiner Begeisterung für meine Arbeit immer wieder selbst überzeugt, daß ich an einem spannenden Projekt arbeite. Er ist auch glaube ich der Einzige, der sich

tatsächlich auf die Verteidigung freut. Auf jeden Fall ist es wunderbar, wenn jemand so viel Anteil nimmt.

Sabine und Philine waren immer für mich da, wenn der innere Schweinehund oder die Gemeinheiten des Universums zugeschlagen haben.

Randi hat noch in letzter Minute einen kritischen Blick auf die englischen Formulierungen geworfen und mir auch gute Vorschläge zur Strukturierung gemacht.

Peter und Katrin haben mir enorm geholfen, indem sie mit mir die Ergebnisse ausgiebig diskutiert und die Manuskripte durch Vorschläge verbessert haben.

Mark hat mir oft die Unterwasser-Einsätze abgenommen, in statistischen Fragen weitergeholfen und mich im richtigen Augenblick mit Nervennahrung versorgt.

Ich möchte mich bei Susanne Qvarfordt, Pia Norling, Penpag Reuter, Anne Wesche, Martina Löbl, Susann Ericsson, Stefan Andersson, Hans Ulrik Riisgaard und Kerstin Johannesson für die Hilfe bei der Betreuung meiner Feldversuche bedanken.

Die Biologische Anstalt Helgoland (GE), Tjärnö Marine Biological Laboratory (SE), Kristineberg Marine Research Station (SE), das Marine Biological Research Centre Kerteminde (DK), der Hafenmeister der Marina auf Poel (GE) und das Stockholm Marine Research Centre auf Askö (SE) haben mir während der Feldversuche Material und Räumlichkeiten zur Verfügung gestellt.

Die Besatzung der Littorina hat mich auf meiner ersten großen Fahrt sehr hilfsbereit unterstützt. Die Mannschaft der Polarfuchs, Norbert Hölcker und Michael Gruber haben beim Suchen von *Rhithropanopeus* großen Einsatz gezeigt. Matthias danke ich dafür, daß er sich stets zuverlässig und umsichtig um meine Versuchstiere gekümmert hat, und ich dadurch gerade in der letzten Phase den Kopf für andere Aufgaben frei hatte.

Der Deutschen Forschungsgemeinschaft danke ich für die dreijährige Finanzierung dieses Projektes WA 708/10-1+2.



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### **Origin of pictures:**

Kossak, Ute: Figure 11

panmap ([www.pangaea.de](http://www.pangaea.de)): front page, figure 10 (modified)

Qvarfordt, Susanne: front page Chapter II

Roth, Markus: Figure 4, figure 20 - figure 22, front page Chapter III

Wahl, Martin: front page Chapter I

## Curriculum Vitae

NAME: Kossak

VORNAME: Ute Hedi

GEBOREN AM: 18.05.1976

GEBURTSORT: Bad Homburg vor der Höhe

HEIMATORT: Friedrichsdorf im Taunus

NATIONALITÄT: deutsch

ELTERN: Hans-Jürgen Kossak, Sozialpädagoge  
Annegret Kossak, geb. Busse, Oberstudienrätin

### Ausbildung:

SEIT MAI 2003: Promotion am IfM-Geomar, Kiel

BIS MÄRZ 2003: Diplomarbeit im Bereich „limnisch-marine Ökologie“  
Thema: „Ernährungsökologische Parameter ausgewählter Gastropoden“  
Abschluß mit Diplom in Biologie

FEBRUAR 2002: Diplomprüfungen in den Fächern Zoologie (Hauptfach),  
Meereskunde und Geologie (Nebenfächer)

SS 2000: Auslandssemester, Università della Calabria, Cosenza, Italien

OKT. 1998: Vordiplom Biologie

SEIT WS 1996: Studium der Biologie an der CAU Kiel

SS 1996: Studium der Romanistik und Skandinavistik,  
Johann Wolfgang Goethe Universität Frankfurt am Main

JULI – DEZ. 1995: Praktikum im Ecomusée de la Crau, Südfrankreich

JUNI 1995: Abitur mit den Leistungskursen Französisch und Biologie

1986 – 1995: Phillipp-Reis-Gesamtschule in Friedrichsdorf/Taunus

1981 – 1986: Grundschule Dreieich in Köppern



## Erklärung

Hiermit erkläre ich, daß diese Arbeit, abgesehen von der Beratung durch meinen akademischen Betreuer, selbständig von mir angefertigt wurde und keine weiteren als die angegebenen Hilfsmittel und Quellen verwendet wurden. Ich habe bisher keinen anderen Promotionsversuch unternommen, und diese Arbeit hat weder ganz noch teilweise im Rahmen eines anderen Prüfungsverfahrens vorgelegen. Bei der Erstellung dieser Abhandlung habe ich mich an die Regeln guter wissenschaftlicher Praxis gehalten.

Teile dieser Arbeit wurden zur Veröffentlichung in Fachzeitschriften eingereicht: Kapitel I mit Penpag Reuter und Martin Wahl als Koautoren bei Marine Biology; Kapitel II und III mit Martin Wahl als Koautor bei Limnology & Oceanography bzw. bei Ecology.

Kossak, U., Reuter, P., Wahl, M. (2006). *Mussels Facing New Challenges: Some Effects of Climatic Changes on a Baltic Key Organism*. Submitted to Marine Biology.

Kossak, U., Wahl, M. (2006). *Mussels in a changing world: the effects of climatic changes on a Baltic Sea Key organism*. Submitted to Limnology & Oceanography.

Kossak, U., Wahl, M. (2006). *Salt in the soup – Will desalination affect a Baltic key predator-prey interaction?* Submitted to Marine Ecology Progress Series.

Kiel, den 01.11.2006

Ute Kossak