

Effect of Salinity-Changing Rates on Filtration Activity of Mussels from Two Sites within the Baltic *Mytilus* Hybrid Zone: The Brackish Great Belt (Denmark) and the Low Saline Central Baltic Sea

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Abstract

Mussels from two sites within the Baltic mussel (*Mytilus edulis* × *M. trossulus*) hybrid zone were used in a comparative study on the effects of salinity-changing rates on filtration activity. The acute effect of varying salinity-changing rates was found to be similar in *M. edulis* from the brackish Great Belt and in *M. trossulus* from the low saline Central Baltic Sea, and the relationships could be described by linear regression lines through 0.0 indicating that the acute effect of deteriorating conditions at decreasing salinities is the opposite as for improving conditions when the salinity is subsequently increased. Further, both *M. edulis* and *M. trossulus* acclimatized to 20 psu reacted to an acute salinity change to 6.5 psu by immediately closing their valves whereupon the filtration rate gradually increased during the following days, but only *M. trossulus* had completely acclimatized to 6.5 psu within 5 days which may be explained by different genotypes of *M. edulis* and *M. trossulus* which probably reflected an evolutionary adaptation of the latter to survive in the stable low-salinity Baltic Sea.

Keywords

Blue Mussels; *Mytilus edulis*; *Mytilus trossulus*; Acute Salinity Effects; Acclimatization; Filtration Rates

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1. Introduction

Permanent low salinity as well as frequency, amplitude and rate of salinity changes may influence feeding, growth, early development and survival of mussels and other filter-feeding bivalves [1]-[13].

The euryhaline blue mussel (*Mytilus edulis* L.) is able to live in both stable low salinity water areas and in estuaries with extreme salinity fluctuations. The immediate reaction of *M. edulis* to acute exposure to strongly reduced salinity water is closure of the valves whereby high saline water is retained within the mantle cavity [14], but also closure of the exhalant siphon and cessation of through-flowing water that prevents the gills and body against exposure to low-saline water may be part of the behavioral response to reduced salinity [1] [15]. The effect of salinity changes on the filtration rate of *M. edulis* from the brackish Great Belt (Denmark), which is one of the Danish Straits connecting the North Sea with the Baltic Sea and characterized by frequently changing salinities, was recently studied by Riisgård *et al.* [16]. Thus, at salinities between 30 and 10 psu the filtration rate was not much influenced, but at 5 psu the filtration rate remained reduced during 3 weeks (see Figure 1 in Riisgård *et al.* [16]). However, when mussels from 6.5 psu in the Central Baltic Sea (Äskö, 70 km south of Stockholm) were initially acclimatized to 20 psu and subsequently re-exposed to 6.5 psu this initially caused a drastic reduction in the filtration rate, but the previous high filtration rate, comparable to that of Great Belt mussels, was regained after 1 - 2 days at 6.5 psu (see Figure 3 in Riisgård *et al.* [16]). This difference in ability to fully acclimatize the filtration rate may be explained by different genotypes of the experimental mussels collected at the two sites within the Baltic *Mytilus* hybrid zone that is characterized by multilocus clines between *M. edulis* and *M. trossulus* [17]-[23].

The effect of changing salinity on the filtration rate of mussels from Great Belt has recently been studied by Pleissner *et al.* [24] who found that the filtration rate was unaffected by decreasing salinity down to about 10 psu, but below this threshold the mussels begun to close their valves and reduce the filtration rate. When the salinity was subsequently increased, the normal filtration rate was soon after restored, and Pleissner *et al.* [24] concluded that the filtration activity is strongly influenced by the salinity-changing rate: the faster the salinity is either reduced or increased, the more pronounced is the change in the filtration rate.

In the present work, we have performed a comparative study on the effects of salinity-changing rates on the filtration activity of *Mytilus edulis* from Great Belt and on *M. trossulus* from the low saline Central Baltic Sea where the blue mussel is dwarfed [25]-[27].

2. Materials and Methods

2.1. Salinity-Changing Rate Experiment

The newly developed fluorometer controlled apparatus (FCA) constructed by Pleissner *et al.* [24] was used in the present study with a few modifications in order to establish filtration-rate measurements on mussels at controlled salinity-changing rates. The FCA maintains a constant defined algal concentration in an aquarium with mussels by adding concentrated algal suspension to replace the amount of algal cells removed. The volume of algal suspension added to the aquarium is determined by the filtration activity of the mussels and wash out of algal cells with outflow from the aquarium. Water from the aquarium with mussels is continuously recycled through a tube to the fluorometer containing a flow-through cuvette what enables a continuous measurement of the algal concentration. If the algal concentration is below a defined level a peristaltic pump starts to pump a suspension of concentrated algae from a bottle (algal stock) into the aquarium to keep the algal concentration constant. The filtration rates were estimated by means of the equation [24]:

$$F = \frac{P_a \times C_s - (P_a + P_d) \times C_a}{C_a \times n} \quad (1)$$

where P_a = pumping rate of algal-dosing pump; P_d = pumping rate of pump adding distilled water or salt water (see below; $P_a + P_d$ = outflow from aquarium), calculated from the total volume of well-mixed algal stock suspension added to the aquarium per unit of time, n = number of mussels, C_s = algal concentration in stock suspension, C_a = algal concentration in well-mixed aquarium. The FCA was used to keep a constant concentration of algae in the aquarium (5000 *Rhodomonas salina* cells·ml⁻¹) during the salinity-changing experiments. In order to cross-check the filtration rates estimated from the FCA, the algal dosing-pump was temporary stopped and the filtration rate was then measured as the volume of water cleared of algal cells per unit of time (*i.e.*

clearance rate). The reduction in the number of cells as a function of time was followed by taking water samples (10 ml) from the aquarium at fixed time intervals of 5 min and measuring the particle concentration with an electronic particle counter (Elzone 5380). Because the about 6.3 μm algal cells are 100% efficiently retained by the gills of the mussels (*i.e.* cell diameter larger than 4 μm [28]) the measured clearance rate equals the filtration rate (= pumping rate). The clearance rate (F_{CR}) was determined from the exponential decrease in algal concentration as a function of time using the formula (e.g. Riisgård *et al.* [29]):

$$F_{CR} = \frac{V \times b}{n} \quad (2)$$

where b = slope of regression line in a semi-ln plot for the reduction in algal concentration with time, V = water volume in aquarium, n = number of mussels. A control experiment without mussels showed that sedimentation of algal cells was insignificant, and in all cases good agreement was observed between F_{CR} and F measured by means of the FCA.

In order to measure the effect of decreasing and subsequent increasing of salinity on the filtration rate of mussels an adjustable peristaltic pump was activated to supply the mussel aquarium with distilled water from a tank resulting in decreasing salinity with a certain constant rate (ΔS , $\text{psu}\cdot\text{h}^{-1}$) in the aquarium down to about 2 psu whereupon the dosing pump was changed to supply the aquarium with 18 psu bio-filtered seawater from another tank. To predict the decrease of the salinity in the aquarium, the following equation was used:

$$S_{t+x} = \frac{S_t \times V_a + 20 \times x \times P_a}{V_a + P_a \times x + P_d \times x} \quad (3)$$

where S_t = salinity in the aquarium at the time t , S_{t+x} = salinity in the aquarium x min after t , V_a = volume of water in the aquarium, P_a = pumping rate of dosing pump supplying 20 psu algal culture to the aquarium, P_d = pumping rate of dosing pump adding distilled water. The estimated salinity values obtained with Equation (3) were cross-checked with actual measurements (YSI 30) made during the period with decreasing salinity.

For subsequently increasing the salinity in mussel aquarium the dosing pump was switched to supply the mussel aquarium with 18 psu seawater from a tank resulting in increasing salinity with a certain rate (ΔS , $\text{psu}\cdot\text{h}^{-1}$). To predict the increase of the salinity in the aquarium, the following equation was used:

$$S_{t+x} = \frac{S_t \times V_a + 20 \times x \times P_a + 18 \times x \times P_d}{V_a + P_a \times x + P_d \times x} \quad (4)$$

where P_d = pumping rate of dosing pump supplying the mussel aquarium with 18 psu seawater. The salinity-changing rates were calculated for the laps of time during which the mussels responded to changes in salinity. During this laps of time, the decrease (or increase) of the salinity was considered near linear so that the dilution rate (or strengthening rate) was given by the slope of a straight line for salinity versus time in the experimental period where the filtration rate was affected. The mussel shell opening degree (*SOD*), defined as the distance between the shells just below the exhalant siphon aperture [29], was measured manually from a digital photo by using a ruler placed on the glass wall of the experimental aquarium close to the mussel.

Blue mussels, *Mytilus edulis*, were collected in Great Belt, Denmark, and kept in the nearby Marine Biological Research Centre (SDU) in aerated flow-through tanks supplied with seawater (18 ± 1 psu) until the experiments were performed. Two size groups of mussels were used: one group mussels ($n = 5$) collected 12 June 2013 with a mean shell length of 48 ± 2 mm (Group: “*M. edulis*, 48 mm”), and a group mussels ($n = 10$) collected 8 July 2013 with a mean shell length of 20 ± 2 mm (Group: “*M. edulis*, 20 mm”). Further, in one series of experiments a group of dwarfed mussels, *M. trossulus* (collected 23 May 2013) from the low saline (6.5 psu) Central Baltic Sea near Åland (Finland) were used, and here a group of 10 mussels with a mean shell length of 20 ± 2 mm (Group: “*M. trossulus*, 20 mm”) were kept through-flowing seawater (18 ± 1 psu) until they were transferred to the experimental aquarium after 3 weeks of acclimation. All experiments were performed at 13°C - 15°C .

2.2. Acclimatization of Filtration Rate to Changed Salinity

In order to study the ability of mussels to acclimatize the filtration rate to changed salinity, one group ($n = 5$) of *Mytilus edulis* collected 10 August 2013 in Great Belt (shell length 16.8 ± 0.7 mm) and another group ($n = 5$) of

M. trossulus collected 23 May 2013 in the Central Baltic Sea near Åland (16.5 ± 1.1 mm) were initially acclimatized in the laboratory to 18 ± 1 psu at 14°C for 3 weeks in aquaria with through-flowing natural seawater. The mean individual filtration rate of the two groups of mussels was measured in separate aquaria ($V = 2000$ ml) with air-mixed seawater by means of the clearance method using Equation (2). After initial measurement of the filtration rate at 20 psu, the mussels were subsequently exposed to 6.5 psu seawater from the collecting site near Åland for about one week before the salinity was again changed to 20 psu. Seawater with required salinity was obtained by adjusting the natural seawater with distilled water or salt (Red Sea Marine Salt).

2.3. Cultivation of Algae

The algae used was the flagellate *Rhodomonas salina* (about $6.3 \mu\text{m}$ diameter), grown in repeated batch cultures at 20°C in 10 l glass bottles containing 9 l of seawater (20 psu) enriched with f/2-medium. Cultures were continuously illuminated by light tubes and aeration and mixing were ensured by injection of compressed air. Every day 3 l of algal suspension was withdrawn and replaced by new medium.

2.4. Statistical Analysis

The influence of mussel size for sensitivity of filtration activity to varying salinity-changing rates was evaluated by statistically testing the effect of shell length of mussels on experimentally measured ΔF , after controlling for effects of ΔS , by using analysis of covariance (ANCOVA) in SPSS 12.

3. Results

Figure 1 shows an example of a salinity-changing experiment performed with a group of 48 mm *Mytilus edulis*. In this case the ΔF -values were found to be $-9.73 \text{ ml}\cdot\text{min}^{-1}\cdot\text{h}^{-1}$ for decreasing salinity ($\Delta S = -0.86 \text{ psu}\cdot\text{h}^{-1}$) and $12.67 \text{ ml}\cdot\text{min}^{-1}\cdot\text{h}^{-1}$ for increasing salinity ($\Delta S = 0.98 \text{ psu}\cdot\text{h}^{-1}$). The results from 7 similar experiments with varying salinity-changing rates are shown in **Figure 2** along with two other experiments performed with 20 mm shell length *M. edulis* from Great Belt and *M. trossulus* from the Central Baltic Sea, respectively. In all cases, the relationships can be described by linear regression lines through 0.0 which indicate that the acute effect on filtration rate to salinity-changing rates for deteriorating conditions at decreasing salinities is the opposite as for improving conditions when the salinity is subsequently being increased. The slope of the regression line for the individual size group of mussels is an expression for the sensitivity of the mussels, but slopes of regression lines for ΔF -values versus ΔS -values for mussels of different size (and thus different levels of filtration rate) cannot be directly compared. Statistical tests show that there is no difference in effect of ΔS on ΔF between 20 mm *M. edulis* and *M. trossulus* mussels from the two locations ($F_{1,14} = 0.595$; $p = 0.453$), between 20 and 48 mm *M. edulis* from Great Belt ($F_{1,19} = 0.954$; $p = 0.341$), and further no difference ($F_{1,20} = 0.668$; $p = 0.423$) between 20 mm *M. trossulus* and 48 mm *M. edulis*.

Figure 3 shows the effect of salinity changes on filtration rates of *Mytilus edulis* collected in Great Belt and in *M. trossulus* collected the Central Baltic Sea. In both cases the mussels reacted to the acute salinity changes by immediately closing their valves, thus reducing the filtration rate by some 90%, whereupon the filtration rate gradually increased during the following days. It is notable that *M. trossulus* had completely acclimatized to 6.5 psu within 5 days whereas *M. edulis* had only partly acclimatized within 7 days. The ability of the two groups of mussels to recover (*i.e.* filtration rate fully acclimated) from exposure to 6.5 psu when re-exposed to 20 psu was one day for the Central Baltic Sea mussels and two days for the Great Belt mussels. It may be concluded that only *M. trossulus* from the low saline Central Baltic Sea are able to fully acclimatize to a sudden, strongly reduced salinity (from 20 to 6.5 psu) within 5 days (**Figure 3**), and further, these mussels are able to fully recover within only one day when re-exposed to increased salinity (20 psu), whereas *M. edulis* from Great Belt need two days. But the acute effect of varying salinity-changing rates is similar in the two groups of mussels (**Figure 2**) and this indicate that the ability of dwarfed Central Baltic Sea mussels to re-acclimatize and filter at maximum rates at very low salinities may be a unique ability that is not correlated with a reduced sensibility of the filtration rate to acute changes in salinity compared to Great Belt mussels.

4. Discussion

The present results may be compared to recent preliminary data presented by Pleissner *et al.* ([24], Figure 9

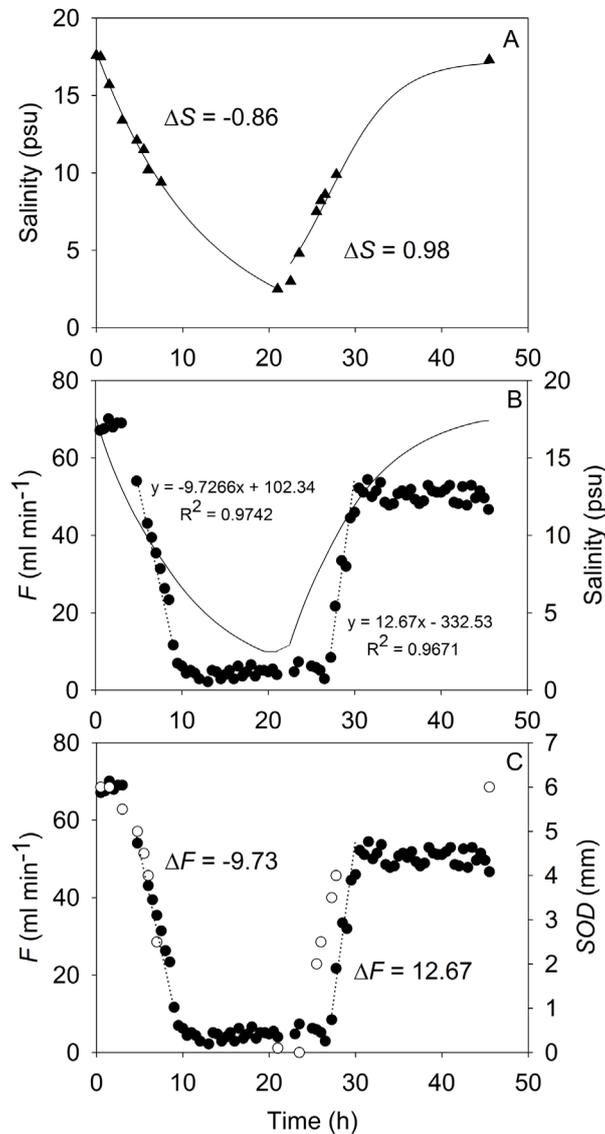


Figure 1. (A) Actually measured salinity (closed triangles) and estimated decreasing and increasing salinities during an experiment using Equations (3) and (4) respectively; (B) Measured mean filtration rates of a group ($n = 5$) of 48 mm shell length mussels (*Mytilus edulis*) using the FCA during an experiment with initially decreasing salinity followed by a period with increasing salinity (inserted curve). The equations for regression lines for decreasing and increasing filtration rates are shown; (C) Mean filtration rates (closed symbol) and shell opening degree (SOD, open symbol) during a salinity-changing experiment. The negative (ΔF , ml min⁻¹·h⁻¹) and positive (ΔF) filtration-changing rates are indicated (*i.e.* slopes of regression lines for shell closing/opening periods indicated in figure B).

therein) who found that the filtration-changing rate (ΔF) of 29 mm *Mytilus edulis* from Great Belt was strongly influenced by the salinity-changing rate (ΔS): “the faster the salinity was either reduced or increased, the more the change was pronounced in the filtration rate”. In the present study we have shown that this relationship can be described by a linear regression line through 0.0.

The ability of blue mussels from the Central Baltic Sea to fully acclimatize their filtration rate to a suddenly

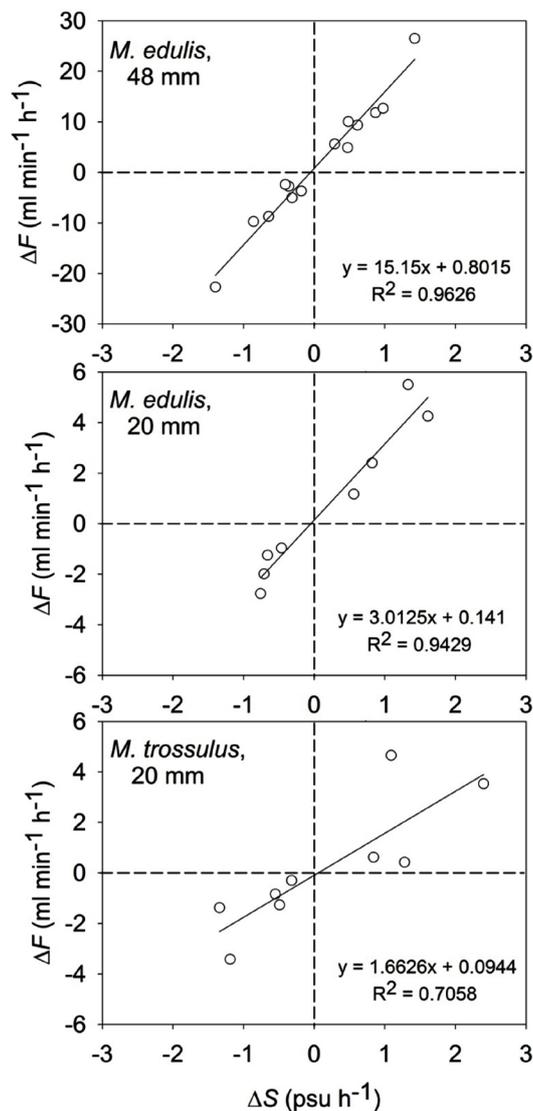


Figure 2. Filtration-changing rate (ΔF) of mussels as a function of salinity-changing rate (ΔS) in experiments with two groups of mussels from Great Belt (*Mytilus edulis*: 48 mm, 20 mm) and one group of mussels from the coastal waters of Åland in the Central Baltic Sea (*M. trossulus*: 20 mm).

reduced salinity from 20 to 6.5 psu within 5 days (Figure 3) is in good agreement with the recent findings by Riisgård *et al.* ([16], Figure 3 therein) who suggested that the ease of Baltic Sea mussels to adjust back and forth between 6.5 and 20 psu may be explained by different genotypes of the experimental mussels collected at two sites within the Baltic mussel (*Mytilus edulis* \times *Mytilus trossulus*) hybrid zone [5] [7] [13]-[17]. Kautsky *et al.* [5] found that the growth rate of *M. edulis* is much lower in the stable low-salinity Baltic Sea than in the North Sea (28 psu), and reciprocally transplanted mussels were found to grow at rates similar to those of native mussels, and further, the survival of Baltic Sea mussels was very high in contrast to mortality over 90% among North Sea mussels transferred to the Baltic Sea, and therefore Kautsky *et al.* [5] suggested that the different survival had mainly “genetic causes”.

The relevance of the present study for actual salinity changes in Great Belt may be evaluated by comparing laboratory data with frequency and amplitude of salinity-changing rates measured above the permanent halocline in the northern Great Belt in the period 2000-2010 (Riisgård *et al.* [11], Table 1 therein). The mean salinity in

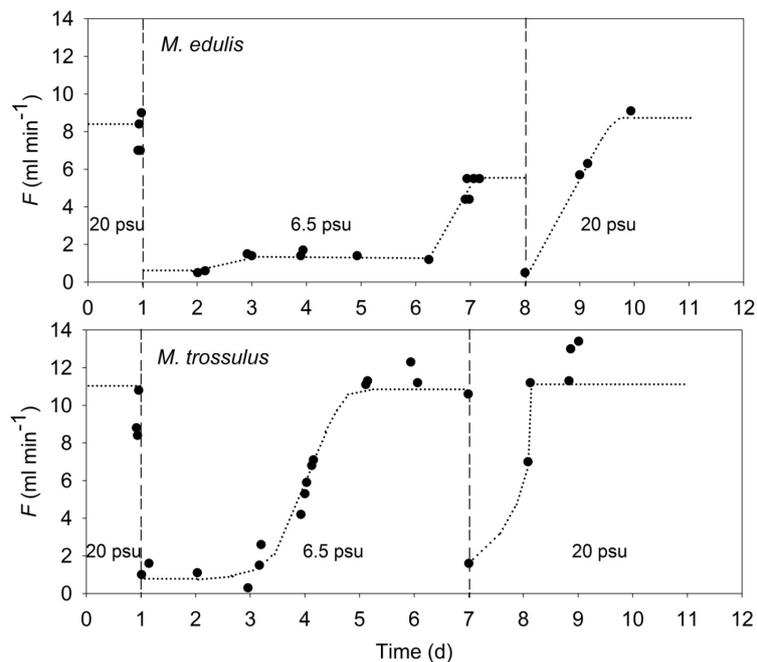


Figure 3. Mean individual filtration rates (F) of mussels collected in Great Belt and locally adapted to 20 psu (*Mytilus edulis*), and mussels collected in the Central Baltic Sea (near Åland) and locally adapted to 6.5 psu (*M. trossulus*). The mussels were in both filtration-rate experiments initially acclimatized for 3 weeks to 20 psu and then acutely exposed to 6.5 psu on Day 1 (left vertical dash line) before again exposed to 20 psu after 7 and 8 days, respectively (right vertical dash line). Dotted lines fitted by eye indicate the behavior of F during the experiments.

Great Belt is about 17 psu, major salinity changes of about 8.5 psu take place with an annual frequency of about 10, a mean duration time of 21 d, and with a mean salinity-changing rate of $0.4 \text{ psu}\cdot\text{d}^{-1} = 0.017 \text{ psu}\cdot\text{h}^{-1}$, which may be compared to the ΔS -values used in the present study (Figure 2). Here, the lowest salinity-changing rate was $\Delta S = 0.18 \text{ psu}\cdot\text{h}^{-1}$, or about 10 times higher than the mean changing rate in Great Belt, but it remains to be shown if salinity-changing rates of that order may have any notable acute effects on the filtration rate, or if the acclimatization ability of the mussels (e.g. [30] [31]) may prevent, or blur such effects.

It may be concluded that the acute effect of varying salinity-changing rates is similar in *Mytilus edulis* from Great Belt and *M. trossulus* from the Central Baltic Sea, i.e. the changes in filtration rates are linearly proportional to the acute changes in salinity (Figure 2), and further, the ability of *M. trossulus* to fully re-acclimatize to very low salinities (Figure 3) is likely to be genetically determined, reflecting an evolutionary adaptation to survive in the stable low salinity waters of the Baltic Sea.

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