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ORIGINAL ARTICLE

Effect of salinity on filtration rates of mussels *Mytilus edulis* with special emphasis on dwarfed mussels from the low-saline Central Baltic Sea

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Abstract The effect of salinity on the filtration rate of blue mussels, *Mytilus edulis*, from the brackish Great Belt (Denmark) and the low-saline Central Baltic Sea, respectively, was studied. First, we measured the effect of long-term (weeks) constant ambient salinities between 5 and 30 psu on the filtration rate of *M. edulis* collected in the Great Belt where the mean salinity is 17 psu. At salinities between 10 and 30 psu, the filtration rates did not vary much, but at 5 psu the filtration rates were significantly lower. Next, we studied dwarfed *M. edulis* (<25 mm shell length) from Central Baltic Sea (Askö, Sweden) where the mean salinity is 6.5 psu. The maximum filtration rate (F, ml min^{-1} ind.$^{-1}$) as a function of shell length (L, mm) and dry weight of soft parts (W, mg) were found to be: $F = 0.003L^{2.71}$ and $F = 0.478W^{0.92}$, respectively, and these results indicate that the filtration rates of dwarfed Baltic Sea mussels are comparable to filtration rates of Great Belt mussels of similar size exposed to salinities >10 psu. When Baltic Sea mussels acclimatized to 20 psu in the laboratory were exposed to 6.5 psu this caused a drastic reduction in the filtration rate, but after about 2 days the previous high filtration rate was regained at 6.5 psu, and further, a similar pattern was observed when the 6.5 psu exposed mussels were finally re-exposed to 20 psu. The observed lack of Great Belt mussels to completely adjust to 5 psu, in contrast to the ease of Baltic Sea mussels to adjust back and forth between 6.5 and 20 psu, is remarkable and may perhaps be explained by different genotypes of Great Belt and Baltic Sea mussels.

Keywords Salinity change · Long-term acclimation · Acute effects · Adjustment of filtration rate

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Introduction

The blue mussel, *Mytilus edulis*, is dwarfed in the inner Central Baltic Sea where the salinity is 6–8 psu (Kautsky 1982; Tedengren and Kautsky 1986; Vuorinen et al. 2002). In the Northern Baltic Sea along the southern coast of Finland, where the salinity decreases from 6.5 psu in the west to become only 3 psu in the east, *M. edulis* lives at the margin of its salinity tolerance and here there is a pronounced decrease in mussel size along the decreasing salinity gradient (Westerbom et al. 2002). Permanent low salinities, frequency and amplitude of salinity changes, as well as the changing rate of salinity may influence the filtration and growth rates, maximum shell length, and early development and survival of mussels (Theisen 1978; Davenport 1979a, b; Almada-Villela 1984; Gruffydd et al. 1984; Kautsky et al. 1990; Tedengren et al. 1990; Westerbom et al. 2002; Qiu et al. 2002), and recently, Hiebenthal et al. (2012) found that temperature may interact with these salinity effects. Acclimation to changing salinities can take place (Davenport 1979a, b; Sundaram and Shafee 1994; Gardner and Thompson 2001; Qiu et al. 2002; Marsden 2004; Suja and Muthiah 2006; Hamer et al. 2008), but due to acute salinity-induced valve closure and reduced filtration rate in the acclimation period, the resulting temporarily effects may blur the true ability of mussels to filter and grow at low salinities as recently shown by Riisgård et al. (2012b). Therefore, knowledge on potential ability

and actual acclimation time for partly or fully acclimation to new salinities is of basic importance for our understanding of feeding and growth of mussels in estuarine systems.

The allozyme frequencies in *M. edulis* collected at locations in the transition zone between the Baltic Sea and the North Sea has been studied by Theisen (1978) who observed a very conspicuous cline for the 3 allozyme loci studied, and due to the about 4 weeks long pelagic stage of *M. edulis* larvae Theisen suggested that the differentiation was not caused by geographic isolation but by the salinity level being "the most evident selective agent". Subsequent studies have confirmed that there are large genetic differences between Baltic and North Sea populations of *M. edulis* (e.g. Bulnheim and Gosling 1988; Johannesson et al. 1990). More recent studies on allozyme, nuclear DNA and mitochondrial DNA (mtDNA) markers have shown that the entire Baltic Sea is inhabited by a peculiar member of the *M. edulis* complex of blue mussels, that is, *Mytilus trossulus* which shows some genetic introgression from *M. edulis* and whose mtDNA has been almost completely replaced by *M. edulis* mtDNA (Riginos and Cunningham 2005; Zbawicka et al. 2007; Stuckas et al. 2009; Väinölä and Strelkov 2011). Studies on the effects of gene flow across the Baltic *Mytilus* hybrid zone, characterized by multilocus clines between *M. edulis* and *M. trossulus*, provide intriguing perspectives. Thus, a number of studies have attempted to assess the effects of the genotypic differences on growth, morphology and physiological performance of mussels from the two populations (Kautsky et al. 1990; Tedengren et al. 1990; QueryGilek et al. 2001). However, the effect of salinity on the filtration rate of mussels from the two populations has not yet been clarified (cf. Tedengren et al. 1990; Gilek et al. 1992).

In the present work, we studied the effect of constant ambient salinities between 5 and 30 psu on the filtration rate of *M. edulis* in long-term (weeks) laboratory acclimation experiments performed with mussels collected in the Great Belt (Denmark) where they were locally acclimated to 17 psu, and further, we measured the filtration rate and effects of salinity changes between 20 and 3.7 psu on dwarfed *M. edulis* collected in the Central Baltic Sea where they were locally adapted to 6.5 psu.

Materials and methods

Part I: mussels from Great Belt

Mussels of different size were collected from farm ropes in Kerteminde Bay (17.2 psu) 2 weeks before experimentation. Kerteminde Bay is part of the Great Belt, Denmark, where the salinity in the brackish water above the permanent halocline (Kullenberg and Jacobsen 1981; Jürgensen 1995; Møller 1996; Fyn County 2001; Bendtsen et al. 2009) has a mean (±SD) of 16.6 ± 0.6 psu and range of 10.3–24.4 psu for the period 2000–2010 (Riisgård et al. 2012b, Table 1 therein). Mussels were sorted into shell length size groups for every millimetre, and 240 individuals of 30–33 mm shell length were selected and divided into the 6 aquaria each with 40 mussels randomly selected from the 30 to 33 mm pool. Mussels were acclimated in the laboratory for 2 weeks to 5.3 ± 0.2, 10.4 ± 0.2, 15.4 ± 0.2, 20.0 ± 0.1, 25.0 ± 0.3 and 29.6 ± 0.1 psu in 16 l aquaria fully mixed by means of air stones before the filtration rate was subsequently measured during the next 21 days. Salinities were produced by either diluting natural Great Belt seawater with ion-exchanged water or adding sea-salt (Tetra Marine Salt). For the lowest salinity, mussels were initially exposed to 10 psu for 1 week before the salinity was further decreased to 5 psu. The bottom of the aquaria was cleaned every day, and all seawater in the aquaria was changed every 3 days. Mussels were exposed to a mean algal concentration of about 4,000 *Rhodomonas salina* cells ml^{-1} for 7 h per day (manually by repeated additions), and the filtration rate was measured two times daily by means of the clearance method. On day 0, 7, 14 and 21, 10 mussels were removed for determination of shell length, dry weight of soft parts (90 °C, 24 h) and condition index.

In a supplementary experiment, the acute effect of low salinity was studied. Here, the mean individual filtration rate in two groups of mussels (Group I: $L = 29.8 \pm 0.4$ mm; Group II: $L = 29.6 \pm 0.4$ mm; $n = 20$) was first measured at in fully mixed aquaria with 25 psu Great Belt seawater added sea salt (Tetra Marine Sea Salt). Subsequently, the mussels were exposed to low-saline seawater (about 7 psu) for 2 days, while being fed about 4,000 *R. salina* cells ml^{-1} before the filtration rate was measured.

Part II: mussels from Central Baltic Sea (Askö)

Mussels of different sizes were collected by means of scraping the bottom in the central Baltic Sea in the shallow waters around the island of Askö, about 70 km south of Stockholm, Sweden, where the salinity is low and stable, ranging from 6 to 7 psu (Gilek et al. 2001), and in this area, *M. edulis* is dwarfed (Kautsky 1982; Tedengren and Kautsky 1986; Vuorinen et al. 2002). The mussels were transported in a cooling box without water to the Marine Biological Research Centre, Kerteminde, where all experiments were performed. The mussels were kept in seawater collected at the collecting site (6.5 psu, 9 °C) and later in artificial seawater with 6.5 psu produced from ion-exchanged water added sea-salt (Tetra Marine Sea Salt). Mussels were fed once a day with *R. salina*.

First (Part IIa), the filtration rates of 6 size classes of mussels (#1 to #6, $n = 19$–29) were measured in 16 l aquaria in parallel using the clearance method, and air stones ensured full mixing of the water. Afterwards, the gill area and dry weight of soft parts were determined. The gill area of mussels was measured according to Riisgård et al. (2011). The mussel was opened, and the two shells separated with a scalpel in such a way that the gill area remained intact. The two shells with the gills were placed together with a ruler under a stereomicroscope, and a photograph was taken. From an enlarged printout of the photograph the area of a single gill layer was cut out, weighted, and the weight compared to a reference paper with a known area and weight. For calculating the total gill area, the area of the single gill layer was multiplied with a factor 8 (2 W-shaped gills, each with 2 demibranchs and 2 lamellae of same size).

Next (Part IIb) in order to study the effect of acute salinity changes on the filtration rate, 2 groups of each 5 mussels (mean ± SD shell length = 14.7 ± 0.3 mm) were initially acclimatized to 20 psu at approximately 13 °C for 7 days and then subsequently exposed to 6.5 psu for about 6 days before the salinity was changed back to 20 psu again.

Finally (Part IIc), to investigate the filtration behaviour of 6.5 psu adapted mussels at even lower salinity, 5 mussels (mean ± SD shell length = 14.6 ± 0.4 mm) from Askö were exposed to a reduced salinity of 3.7 ± 0.2 psu and temperature of 8.7 ± 0.3 °C in an aquarium to study the filtration rate in mussels exposed to salinity lower than their naturally occurring salinity of 6.5 psu by using the clearance rate method. The mussels were first acclimated for 2 weeks to 6.5 psu and subsequently for 2 days to the 3.7 psu salinity before clearance rates were measured. Prior to every filtration rate measurement algae were added to the 4 l feeding aquarium to maintain an algae cell concentration of 3,000–5,000 cells ml^{-1}.

Filtration rate was measured by means of the clearance method (e.g. Coughlan 1969; Jørgensen 1990) using an aquarium with mussels and well-mixed seawater added algal cells that are 100 % efficiently retained by the gills of the mussels (i.e. diameter >4 μm). The filtration rate (F) was determined from the exponential decrease in algal concentration as a function of time using the formula: $F = V \times b/n$, where V = volume of seawater, b = slope of regression line in a semi-ln plot for the reduction in algal concentration with time in the aquarium, n = number of mussels. The algal concentration was measured by means of an electronic particle counter (Elzone 5380) or in some cases by a fluorometer (Aquafluor, Turner Designs).

Weight-specific growth rate of mussels can be estimated according to the equation (Riisgård et al. 2012a, Eq. 22 therein): $\mu = \ln(W_t/W_0)/\Delta t$, where W_t and W_0 are the corresponding dry weights of bivalve soft tissue at end and start, and Δt the growth period. In the present work, the slope of regression line for ln W versus t was used as an estimate of the mean μ during the experimental period.

Condition index (CI, mg cm^{-3}) was calculated from the dry weight of soft parts (W, mg) and the shell length (L, cm): $CI = W/L^3$.

The flagellate *R. salina* (about 6 μm in diameter) was grown in repeated batch cultures in 20-l bottles containing 15 l of seawater (20 psu) enriched with f/2-medium. Cultures were continuously illuminated by fluorescent light tubes. Aeration and mixing were ensured by injection of compressed air. Every day 5 l of algal suspension was withdrawn and replaced by fresh medium.

Statistical analysis of impact of salinity on filtration rate was carried out by one-way repeated measures analysis of variance (ANOVA) in SigmaPlot 12.

Results

Part I: mussels from Great Belt

The filtration rate of *M. edulis*, locally acclimated to the salinity in Great Belt and acclimated in the laboratory for 2 weeks to 5, 10, 15, 20, 25 and 30 psu prior to subsequent 7-h daily measurements during the following 21 days, are shown in Fig. 1 and Table 1. It appears that the filtration rates between 10 and 30 psu are nearly identical with a tendency towards slightly higher values during the experimental period, but the filtration rate at 5 psu remains lower. The increase in shell length and weight-specific growth rate during the experimental period is modest, but with a trend of slightly higher rates at salinities >10 psu.

In order to further evaluate the effect of low salinity on the filtration rate, two groups of mussels acclimated to about 25 psu were acutely exposed to 7 psu and the filtration rate measured (Table 3). As it appears from Table 3, the mean individual filtration rate measured at 7 psu was in both groups lower than the reference (control) filtration rate measured at 25 psu. ANOVA revealed that the filtration rates measured at 5 and 7 psu (Tables 1, 2) are significantly ($P < 0.001$) lower than filtration rates measured at 10–30 psu (Table 1).

Part II: mussels from Central Baltic Sea (Askö)

a. The measured filtration rate and gill area as a function of mussel size are shown in Fig. 2 and Table 3. The maximum shell length of the dwarfed Baltic mussels was about 24 mm, and the power functions of filtration rate (F, ml min^{-1} $ind.^{-1}$) as a function of shell length (L, mm) and dry weight of soft parts (W, mg) were

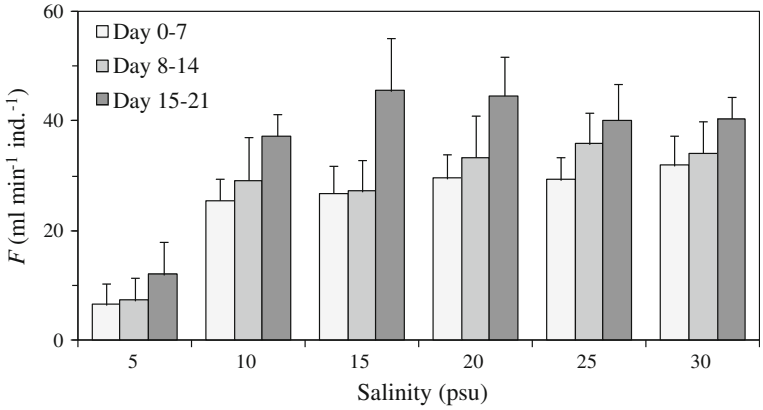

Fig. 1 *Mytilus edulis* (Great Belt, Table 1). Mean individual filtration rate (F) measured during 21 days, here split up into 3 periods: day 0–7, day 8–14 and day 15–21, with mussels exposed to 5, 10, 15, 20, 25 and 30 psu, respectively. ±SD indicated

Table 1 *Mytilus edulis* (Great Belt)

	Days	5 psu	10 psu	15 psu	20 psu	25 psu	30 psu
F (ml min^{-1} ind.$^{-1}$)	0–7	6.6 ± 3.8	25.5 ± 4.0	26.9 ± 5.1	29.6 ± 4.4	29.3 ± 4.1	31.9 ± 5.5
	8–14	7.3 ± 4.2	29.2 ± 8.0	27.2 ± 5.8	33.4 ± 7.7	35.9 ± 5.6	34.2 ± 5.7
	15–21	12.1 ± 5.8	37.3 ± 4.1	45.5 ± 9.6	44.7 ± 7.0	40.2 ± 6.5	40.5 ± 4.0
L (mm)	0	32.2 ± 0.4	32.0 ± 0.8	31.7 ± 0.5	32.2 ± 0.9	32.1 ± 0.6	32.0 ± 0.9
	7	31.0 ± 0.8	32.1 ± 1.0	32.2 ± 1.2	32.4 ± 0.9	32.9 ± 0.8	32.8 ± 1.2
	14	31.6 ± 0.8	32.0 ± 1.3	31.9 ± 0.8	32.8 ± 0.7	33.3 ± 1.1	33.0 ± 1.0
	21	32.0 ± 0.7	32.2 ± 1.1	32.6 ± 1.3	32.8 ± 1.1	32.7 ± 1.1	33.6 ± 0.8
W (mg)	0	130.8 ± 13.7	160.6 ± 10.7	151.6 ± 19.1	173.4 ± 31.1	158.6 ± 19.6	159.7 ± 17.4
	7	138.6 ± 24.0	165.0 ± 22.0	154.7 ± 24.2	175.8 ± 11.2	171.3 ± 34.1	176.5 ± 34.3
	14	141.3 ± 20.0	158.1 ± 20.5	157.4 ± 15.3	186.1 ± 32.0	203.1 ± 34.0	188.8 ± 19.8
	21	135.5 ± 4.3	168.0 ± 25.9	174.3 ± 20.7	190.3 ± 18.9	187.8 ± 21.2	193.0 ± 26.8
CI (mg cm^{-3})	0	3.9 ± 0.4	5.0 ± 0.6	4.8 ± 0.6	5.1 ± 0.8	4.7 ± 0.4	4.9 ± 0.5
	7	4.0 ± 1.0	5.0 ± 0.6	4.7 ± 0.7	5.1 ± 0.4	4.8 ± 0.7	4.9 ± 0.5
	14	4.5 ± 0.7	4.7 ± 0.7	4.8 ± 0.6	5.3 ± 0.8	5.5 ± 1.0	5.0 ± 0.4
	21	4.1 ± 0.4	4.8 ± 0.9	4.9 ± 0.5	4.5 ± 1.8	4.5 ± 1.9	5.1 ± 0.9
C (cells ml^{-1})	0–21	4,023 ± 647	3,431 ± 357	3,556 ± 291	3,627 ± 361	3,929 ± 359	3,559 ± 799
μ (% d^{-1})	0–21	0.18	0.13	0.62	0.48	0.97	0.91

Mean individual filtration rate (F), shell length (L), dry weight of soft parts (W), condition index (CI), algal (*R. salina*) concentration (C) and estimated weight-specific growth rate (μ) of mussels exposed to 5, 10, 15, 20, 25 and 30 psu. ±SD indicated

Table 2 *Mytilus edulis* (Great Belt)

	Group I (L = 29.8 ± 0.4 mm)	Group II (L = 29.6 ± 0.4 mm)
S_{25} (psu)	25.2 ± 0.9	25.7 ± 0.2
F_{25} (ml min^{-1})	29.8 ± 2.7	21.9 ± 0.8
S_7 (psu)	6.6 ± 0.2	7.3 ± 0.4
F_7 (ml min^{-1})	7.4 ± 1.4	1.8 ± 1.2

Mean individual filtration rates (F_{25} and F_7) measured in 2 groups of 20 mussels (I and II) with nearly same shell length (L). The filtration rates were initially measured at salinities around 25 psu (S_{25}) and subsequently measured again after 2 days acclimation to about 7 psu (S_7). ±SD indicated

found to be: $F = 0.003L^{2.71}$ and $F = 0.478W^{0.92}$, respectively, whereas the gill area (G, cm^2) could be expressed as $G = 0.006L^{2.19}$. Finally, the F/G-ratio which expresses the approach velocity of water in the direction normal to the gill surface is about 0.3 mm s^{-1} in all size classes.

b. Figure 3 shows the effect of salinity changes on the filtration rate of Askö mussels initially acclimatized to 20 psu in the laboratory (Table 4, #7 and #8) and subsequently exposed to 6.5 psu before again exposed to 20 psu. It is seen that the initially acute exposure of 20 psu acclimated mussels to 6.5 psu caused a drastic

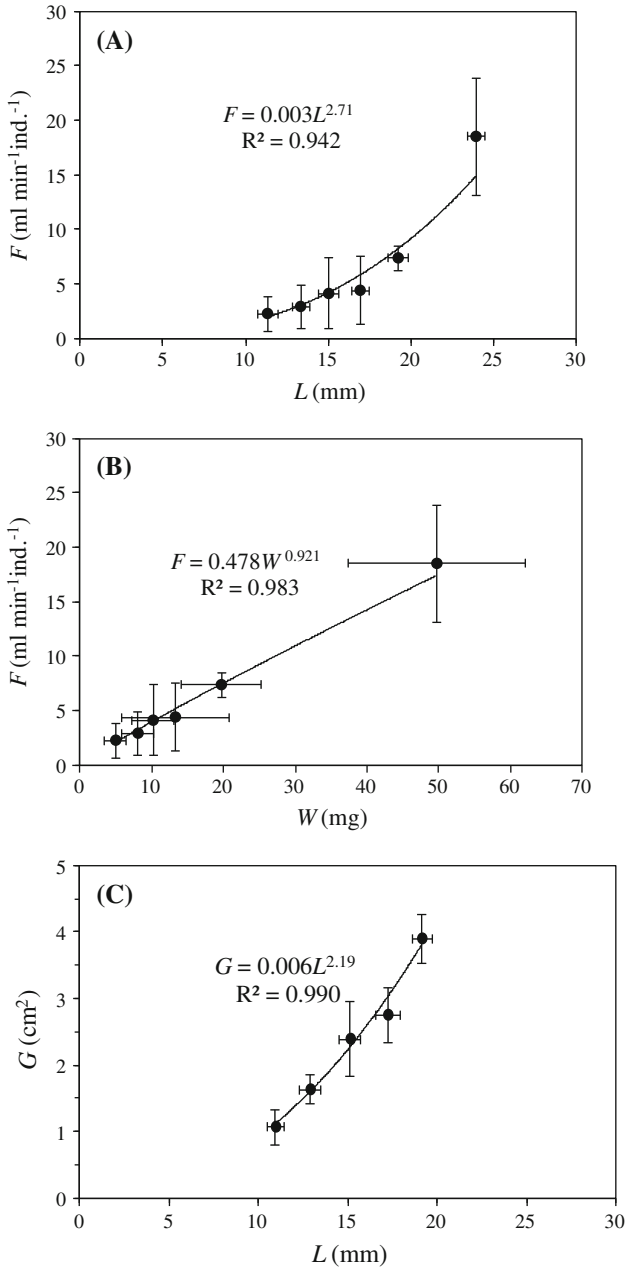

Fig. 2 *Mytilus edulis* (Askö, #1 to #6, Table 3). **a** Mean individual filtration rate (F) at 6.5 psu as a function of mean shell length (L). **b** Mean filtration rate as a function of mean body dry weight (W). **c** Gill area (G) as a function of shell length. ±SD indicated

reduction in filtration (valve closure), but after about 2 days, the high filtration rate was regained at 6.5 psu, and further, a similar pattern was observed when the 6.5 psu exposed mussels were finally re-exposed to 20 psu.

c. The filtration rate of 6.5 psu adapted Askö mussels exposed to a reduced salinity of 3.7 psu during 6 days before measurement was found to be 4.9 ± 1.3 ml min^{-1} for a 14.5 ± 0.5 mm mussel (Table 4).

Discussion

It is a new and interesting observation that Great Belt mussels were not able to adjust their filtration rate at 5 psu during the 3-week experimental period (Fig. 1), whereas Askö mussels were able to completely adjust their filtration rate within one to 2 days when they were first exposed to 20 psu and subsequently re-exposed to 6.5 psu (Fig. 3).

The present study is the first to lay down the filtration rate and gill area as a function of size of dwarfed Baltic mussels with maximum shell length of about 24 mm (Fig. 2). The power functions of filtration rate (F, ml min^{-1} $ind.^{-1}$) as a function of shell length (L, mm) and dry weight of soft parts (W, mg) were found to be: $F = 0.003L^{2.71}$ and $F = 0.478W^{0.921}$, respectively, whereas the gill area (G, cm^2) was found to be $G = 0.006L^{2.19}$. These equations may be compared to those recently presented by Riisgård et al. (2011, Figs. 7, 8 and 9 therein). For comparison a 20 mm shell length mussel, which has overlap with the lower size range of mussels studied by Riisgård et al. (2011), may be considered here. The estimated values using the present equations are $F = 9.3$ ml min^{-1} (8 °C) and $G = 4.2$ cm^2 which are in quite good agreement with the estimated values $F = 14.6$ ml min^{-1} (12 °C) and $G = 4.7$ cm^2 using the allometric equations reported by Riisgård et al. (2011). Finally, the F/G-ratio which expresses the approach velocity of water in the direction normal to the gill surface was in the present study found to be 0.31 ± 0.03 mm s^{-1} (mean ± SD of all size classes, Table 3) which may be compared to F/G = [(14.7/60) × 10/4.7 =] 0.52 mm s^{-1} estimated on basis of Riisgård et al. (2011) and 0.85 mm s^{-1} reported by Riisgård and Larsen (2000) using literature values, and about 1 mm s^{-1} (19 °C) measured by themselves using video recordings through the inhalant opening on an intact 15 mm shell length *M. edulis*. However, temperature differences may partly explain the different F/G-ratio. Using the relationship between filtration rate and temperature found for *M. edulis* by Kittner and Riisgård (2005), the F value for Askö mussels at 19 °C would for example be 36 % higher = (9.3 × 1.36 =) 12.6 ml min^{-1} and thus $F/G = 0.5$ mm s^{-1} in fairly good agreement with values obtained on mussels from areas with higher salinities. Therefore, it seems reasonably to conclude that the filtration rate, gill area and F/R-ratio of dwarfed Baltic Sea mussels are comparable to mussels from the Great Belt and other marine areas with substantially higher salinities, and this statement also seems to settle some of the open questions about possible differences between Baltic and North Sea *M. edulis* earlier pointed out by, for example, Tedengren et al. (1990).

Kautsky et al. (1990) found that the growth rate of *M. edulis* is much lower in the Baltic Sea (7 psu) than in the North Sea (28 psu), and reciprocally, transplanted mussels

Table 3 *Mytilus edulis* (Askö)

#	*n*	*T* (°C)	*L* (mm)	*W* (mg)	CI (mg cm^{-3})	*F* (ml min^{-1})	*G* (cm^2)	*F*/*G* (mm s^{-1})
1	26	8.5 ± 0.1	11.3 ± 0.6	4.9 ± 1.5	3.4 ± 1.1	2.3 ± 1.6	1.1 ± 0.3	0.35
2	29	8.3 ± 0.2	13.3 ± 0.5	8.0 ± 2.2	3.4 ± 1.9	3.0 ± 2.0	1.6 ± 0.2	0.32
3	29	8.3 ± 0.2	15.0 ± 0.6	10.1 ± 3.0	3.0 ± 0.9	4.2 ± 3.3	2.4 ± 0.6	0.30
4	22	8.2 ± 0.1	16.9 ± 0.5	13.2 ± 7.5	2.7 ± 1.4	4.5 ± 3.1	2.8 ± 0.4	0.27
5	22	8.4 ± 0.4	19.2 ± 0.6	19.6 ± 5.6	2.8 ± 0.8	7.4 ± 1.1	3.9 ± 0.4	0.32
6	19	8.5 ± 0.0	23.9 ± 0.5	49.6 ± 12.4	3.6 ± 0.9	18.6 ± 5.4		

Mean individual filtration rate (*F*), shell length (*L*), dry weight of soft parts (*W*), gill area (*G*), condition index (CI), temperature (*T*) and *F*/*G*-ratio (expressing the approach velocity of water in the direction normal to the gill surface) of 6 size classes (#1 to #6, *n* = number of mussels) of mussels locally adapted to 6.5 psu at Askö in the Central Baltic Sea. ±SD indicated

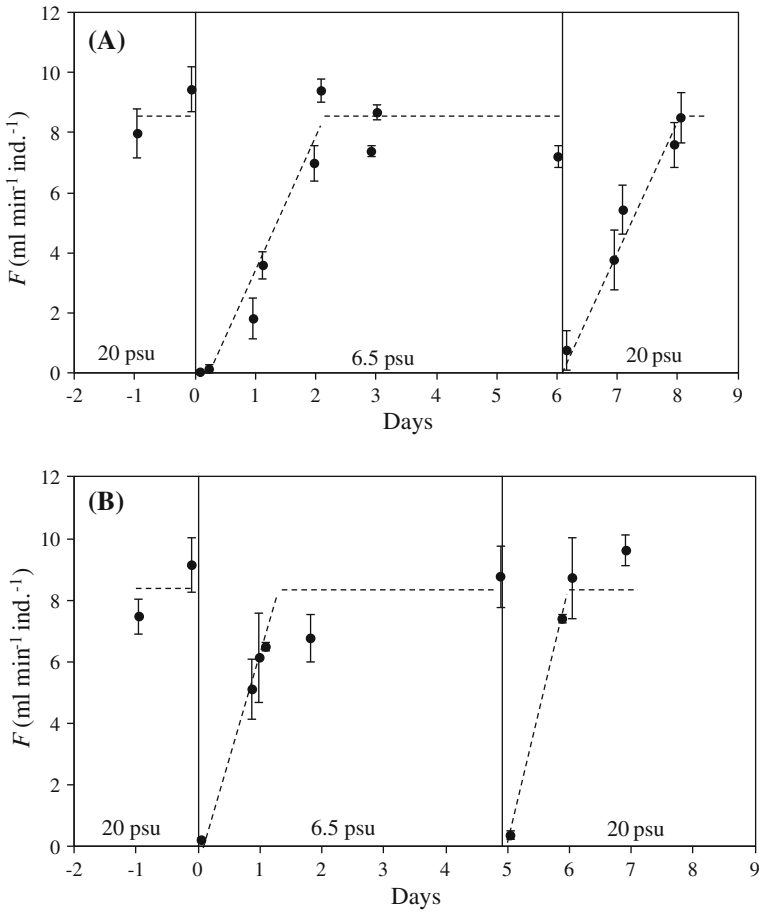

Fig. 3 *Mytilus edulis* (Askö). **a** Mean individual filtration rates (*F*, ml min^{-1}) of mussels (#7, Table 4) locally adapted to 6.5 psu at Askö and initially acclimatized to 20 psu for 7 days in the laboratory and then acutely re-exposed to 6.5 psu on day 0 (*vertical line*) before they again were exposed to 20 psu. **b** Repetition of the above experiment, but with a new group of mussels (#8, Table 4). The punctured lines fitted by eye indicate the behaviour of *F* during the experiments. ±SD indicated

Table 4 *Mytilus edulis* (Askö)

#	*n*	*S* (psu)	*T* (°C)	*L* (mm)	*W* (mg)	CI (mg cm^{-3})	*F* (ml min^{-1})
7	5	20	13.1 ± 0.6	15.0 ± 0.3	12.8 ± 3.6	3.8 ± 0.9	8.7 ± 1.1
8	5	20	13.4 ± 0.4	15.2 ± 0.5	12.9 ± 1.4	3.7 ± 0.7	8.3 ± 1.1
9	5	3.7	8.7 ± 0.3	14.5 ± 0.5	8.6 ± 0.9	2.8 ± 0.4	4.9 ± 1.3

Mean individual filtration rate (*F*), shell length (*L*), dry weight of soft parts (*W*), condition index (CI), temperature (*T*), salinity (*S*), number of mussels (*n*) in series (#). Size classes #7 and #8 were acclimated to 20 psu (before they were transferred back to 6.5 psu for 5 days and then returned to 20 psu, see Figs. 3 and 4). Size class #9 shows the mean filtration rate of mussels acclimated to 3.7 psu for 6 days. ±SD indicated

were found to grow at rates similar to those of native mussels, "indicating that this variation can largely be explained by physiological differences due to environmental salinity" rather than "regulated by non-genetic factors". 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. (1990) suggested that the different survival "probably have mainly genetic causes". Subsequently, Gilek et al. (2001) compared the filtration rates of *M. edulis* from the two populations and found that the weight-specific filtration rate was 7 ± 4 l g^{-1} h^{-1} for Baltic Sea (Askö) and for North Sea (Tjärnö) mussels somewhat lower filtration rates of 4 ± 1 l g^{-1} h^{-1} (Yttre Vattenholmen) and 3.8 ± 0.7 l g^{-1} h^{-1} (Strömstad) were found. However, considerably lower specific filtration rates were reported by Tedengren et al. (1990) for both native North Sea mussels and transplanted Baltic Sea mussels acclimated to North Sea conditions, and it was found that the two groups of mussels in 1987 had near identical filtration rates of 2.42 and 2.10 l g^{-1} h^{-1}, respectively, but not in 1988 when the North Sea mussels were found to have higher filtration rates (2.34 l g^{-1} h^{-1}) than the transplanted Baltic Sea mussels (0.84 l g^{-1} h^{-1}). A direct comparison of the above filtration rates with the filtration rates reported in the present study is not possible, because the filtration rates reported by both Gilek et al. (2001) and Tedengren et al. (1990) were converted to mass-specific rates for 1 g body dry weight mussels by using a weight exponent $b = 0.4$ in the allometric equation: $F = aW^b$. However, an Askö mussel with 50 mg body dry weight was in the present study found to have a filtration rate of about 17.5 ml min^{-1} (Fig. 2b), and using b value of 0.4, the weight-specific filtration rate is found to be $F/W^{0.4}$ $= (17.5 \times 60 \times 0.001/0.05^{0.4} = 1.1/0.3 =) 3.5$ l g^{-1} h^{-1}. But using a more appropriate b value of 0.66 (Riisgård 2001, Table 1 therein), the calculated specific filtration rate becomes $(1.1/0.05^{0.66} =) 7.95$ l g^{-1} h^{-1} which is close to 7.45 l g^{-1} h^{-1} reported by Møhlenberg and Riisgård (1979).

Recently, Riisgård et al. (2012b) studied the effect of different salinities (between 10 and 30 psu) on *M. edulis* from the Great Belt in laboratory feeding and growth experiments. They measured a tendency towards reduced growth with decreasing salinity, reflected as reduced shell growth rate and decreasing weight-specific growth rate with falling salinity, and the authors concluded that the observed effect of salinity could partly be explained by a temporary shell valve closure after an acute change in salinity. This seems to indicate that mussels that are well acclimated to different constant salinities between 10 and 30 psu may actually grow at comparable rates under otherwise identical conditions. The present study supports this hypothesis, because long-term salinity acclimated Great Belt mussels between 10 and 30 psu have near identical filtration rates (Fig. 1). But at 5 psu, the mean filtration rate from the Great Belt remains significantly reduced (Fig. 1), in striking contrast to the fast acclimation rate of mussels from the Baltic Sea (Fig. 3).

Apart from possible differences in phytoplankton biomass, the much lower growth rate of mussels in the Baltic Sea has been suggested to be due to salinity-dependent change in amino acid metabolism and nitrogen excretion causing a less favourable energy balance in low-saline areas (Tedengren and Kautsky 1986; Tedengren et al. 1990). Finally, it should be mentioned that there are large differences in allozyme frequencies between Baltic and North Sea mussels (Theisen 1978) and observed high initial mortality of North Sea mussels transplanted to the Baltic Sea has been found to be selective in certain enzyme loci so that only North Sea mussels of Baltic Sea genotype survived (Johannesson et al. 1990). The observed lack of Great Belt mussels to completely adjust to 5 psu (Fig. 1) in contrast to the ease of Baltic Sea mussels to adjust back and forth between 6.5 and 20 psu (Fig. 3) may thus be explained by different genotypes of the experimental mussels collected at two sites within the Baltic *Mytilus* hybrid zone (Bulnheim and Gosling 1988; Johannesson et al. 1990; Riginos and Cunningham 2005; Zbawicka et al. 2007; Stuckas et al. 2009; Väinölä and Strelkov 2011). Likewise, this may explain why the filtration rate of 14.5 mm Askö mussels exposed to an extremely reduced salinity of 3.7 psu was able to filter with a rate of 4.9 ± 1.3 ml min^{-1} (Table 3) which is comparable with $F = 3.9$ ml min^{-1} predicted from the equation shown in Fig. 2a, and $F = 6.1$ ml min^{-1} using the equation: F(ml min^{-1}) $= 0.02L$(mm)$^{2.14}$ given by Kiørboe and Møhlenberg (1981; equation corrected according to Kiørboe pers. comm.) for *M. edulis* exposed to 30 psu and 9–17 °C.

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