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Dwarfism of blue mussels in the low saline Baltic Sea — growth to the lower salinity limit

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ABSTRACT: Mussels within the Baltic *Mytilus edulis* × *M. trossulus* hybrid zone have adapted to the low salinities in the Baltic Sea which, however, results in slow-growing dwarfed mussels. To get a better understanding of the nature of dwarfism, we studied the ability of *M. trossulus* to feed and grow at low salinity (7 psu) compared with its performance at relatively high-salinity (20 psu) in controlled laboratory experiments, supplemented with field (Great Belt) growth experiments with *M. trossulus* and *M. edulis* in net-bags. Subsequently, the growth of *M. trossulus* transplanted in cages to various localities in the northern Baltic Sea was used to evaluate the effect of very low salinities, down to 3.4 psu. The laboratory feeding experiments with *M. trossulus* at 7 psu showed that the growth in shell length was negligible, whereas the body dry weight nearly doubled during the 15 d experiment, with a weight-specific growth rate of 3.7% d^{-1}. The same parameters measured at 20 psu showed a pronounced growth in both shell length and body dry weight, with a weight-specific growth rate of 2.2% d^{-1}. The growth rates of *M. trossulus* and *M. edulis* in suspended net-bags in the Great Belt (22 psu) were similar: 5.6 and 6.8% d^{-1}, respectively. *M. trossulus* in cage experiments had positive growth rates at locations with salinities above 4.5 psu, up to 2.60% d^{-1}, but negligible increase in the shell length, and at sites with salinities below about 4.5 psu, the somatic growth was negative, around −0.3% d^{-1}, which indicates valve closure and respiratory weight loss. A trend line in a plot of all available growth data for both mussel species as a function of salinity indicates that the growth of mussels is steadily hampered by reduced salinities from 30 psu down to about 10 psu, below which the growth is rapidly reduced to become negative below 4.5 psu. We suggest that reduced ability to produce shell material at extremely low salinity may explain dwarfism of mussels in the Baltic Sea. Reduced bio-calcification at low salinity, however, may impede shell growth, but not somatic growth, and this may at first result in an increased condition index, as seen in the benthic Baltic Sea mussels transferred to cages suspended in the water column.

KEY WORDS: *Mytilus edulis* · *Mytilus trossulus* · Filtration rate · Specific growth rate · Adaptation · Effect of salinity · Condition index · Bio Energetic Growth (BEG) model

INTRODUCTION

The Baltic *Mytilus* hybrid zone is characterized by multilocus clines between the Atlantic blue mussel *Mytilus edulis* and the Baltic *M. trossulus* (Theisen 1978, Bulnheim & Gosling 1988, Johannesson et al. 1990, Riginos & Cunningham 2005, Zbawicka et al. 2007, Stuckas et al. 2009, Väinölä & Strelkov 2011). Hybridization takes place wherever *M. trossulus* and *M. edulis* meet, but the extent of hybridization

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varies within the hybrid zone (e.g. Väinölä & Strelkov 2011). The Great Belt (Storebœlt) is in the steep transition zone between North Sea *M. edulis* and Baltic Sea *M. trossulus*, and therefore, it seems reasonable to discriminate between 'Great Belt *M. edulis*' and 'Baltic Sea *M. trossulus*'. Recent observations of the different abilities of the 2 mussels to acclimatize their filtration rates to low salinities (Riisgård et al. 2013) may be explained by different genotypes. The mussels within the *M. edulis* × *M. trossulus* hybrid zone have adapted to the low salinities in the Baltic Sea, although the low salinities have a detrimental effect on the growth, resulting in very slow-growing dwarfed mussels forming dense populations that dominate the hard bottoms in the Central Baltic Sea, where the salinity is about 6 to 7 psu (Remane & Schlieper 1971, Kautsky 1982, Tedengren & Kautsky 1986, Vuorinen et al. 2002, Kossak 2006). Hiebenthal et al. (2012) studied the effects of temperature and salinity on shell growth, physiological stress and mortality of young *M. edulis* in the Baltic Sea, but only for a limited salinity range (15 to 35 psu). Due to the absence of predators and competitors in the Baltic Sea, intraspecific competition is an important factor controlling the mussel population, and strong competition for food (phytoplankton) may partly explain the observed very slow growth rates (Kautsky 1982, Westerbom et al. 2002, Larsen et al. 2014, Fig. 9 therein). However, when exposed to 20 psu, the filtration rates of dwarfed mussels from the Central Baltic Sea (naturally adapted to 6.5 psu) are comparable to filtration rates of Great Belt (Denmark) mussels of similar size (adapted to salinities >10 psu), and further, Central Baltic Sea mussels easily adjust back and forth between 6.5 and 20 psu in contrast to Great Belt mussels (Riisgård et al. 2013, 2014a).

To get a better understanding of the nature of dwarfism of mussels in the Baltic Sea, we studied ability of Baltic Sea mussels to feed and grow at low salinity (7 psu) and to compare with their performance at relatively high (20 psu) salinity in controlled laboratory experiments. Further, to study the possible effect of preceding exposure of dwarfed mussels to low salinity in the Central Baltic Sea, the growth of *M. trossulus* and *M. edulis* of same size collected in the Central Baltic Sea and in the Great Belt, respectively, was simultaneously measured after placing the mussels in suspended net-bags in the Great Belt (mean salinity 17 psu). Finally, the somatic growth of Baltic mussels transplanted to various localities in northern Baltic Sea was used to evaluate the effect of salinities down to 3.5 psu.

MATERIALS AND METHODS

Laboratory feeding and growth experiments

Collection of mussels. Blue mussels *Mytilus trossulus* (denoted dwarfed or Åland mussels) were collected in coastal waters (6 to 7 psu) near the island of Kumlinge (Åland, Finland; Fig. 1A) on 4 December 2012 and 23 May 2013 and transported in a box cooled with ice to the Marine Biological Research Centre, Denmark.

Low salinity (7 psu) growth experiments. From a larger group of mussels collected on 4 December 2012, 42 mussels of similar size (between 15 and 16 mm) were selected and stored in an aquarium with artificially prepared 6.5 psu seawater for 2 d before the start of the experiment. During the experimental growth period, subsamples of mussels (n = 10) were collected on Day 0, 6, 11 and 15 for determination of shell length, dry weight of soft parts, dry weight of shells and condition indexes (*CI*). Because the algal suspension dosed by a pump to the mussels was 20 psu, the salinity in the experimental aquarium was adjusted early in the morning and late in the afternoon to remain near constant (7.2 ± 1.3 psu) by manually turning on and off a pump supplying the aquarium with distilled water. Every 2 d, the experimental aquarium was cleaned and the water replaced. The mean algal concentration during the growth period was 3018 *Rhodomonas salina* cells ml^{-1} (3.8 µg chl *a* l^{-1}).

High salinity (20 psu) growth experiment. From a larger group of mussels that had been transferred to a tank with through-flowing Great Belt seawater (~20 psu) after arrival at the laboratory, 72 mussels of similar size (between 15 and 16 mm) were selected and transferred to a well-mixed aquarium (10 l), 2 d before the start of the growth experiment. Subsamples of mussels (n = 10) were collected during the experimental growth periods on Day 0, 7, 14, 21, 28 and 35 to determine growth parameters for determination of shell length, dry weight of soft parts, dry weight of shells and *CI*. The mean algal concentration in the experiment was 2925 *Rhodomonas salina* cells ml^{-1} (3.7 µg chl *a* l^{-1}).

Fluorometer-controlled apparatus. The growth experiments were performed using the fluorometer-controlled apparatus (FCA) described by Pleissner et al. (2013). On a few occasions, one of the mussels collected during the experimental growth period proved to be empty closed shells, but the total mortality among the original 42 mussels used at low salinity (7 psu), for example, did not exceed 2 individuals.

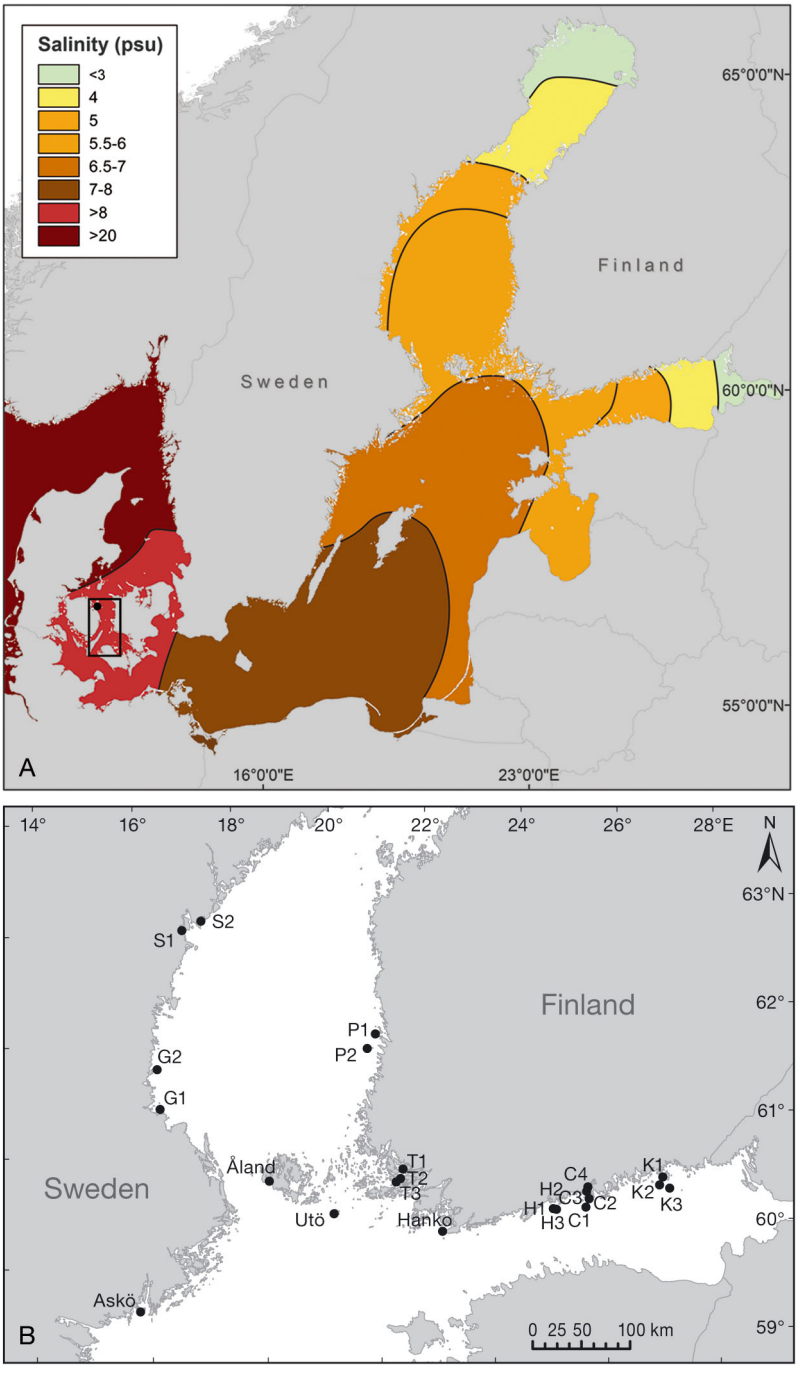

Fig. 1. (A) Salinity of surface water in the Baltic Sea (based on HELCOM data from http://balance-eu.org/publications/index.html), and the location of the Great Belt (rectangle) and Kerteminde Fjord (point). (B) Mussel collection sites, and locations for experimental growth studies with mussels in cages (see 'Materials and methods' and Table 5)

The FCA method ensures a certain narrow range of algal concentrations (C_a) in an aquarium with well-mixed water and filtering mussels. To this aquarium is added algal suspension from a culture with a certain high concentration (C_c) at a known rate (P) by means of a dosing pump. An overflow ensured a constant volume in the aquarium, and therefore, the mean individual filtration rate (F) can be calculated as follows (Pleissner et al. 2013):

$$F = P \times (C_c - C_a)/(n \times C_a) \quad (1)$$

where n = number of filtering mussels. During the experimental period, when the mussels may grow and increase their filtration rate, C_a is kept constant by the automatic fluorometer-control of the algal dosing rate (P).

As a supplementary check, the filtration rate of the mussels was also measured daily by the clearance method where the filtration rate is determined as the volume of water cleared of suspended particles per unit of time. By stopping the dosing pump and throughflow, the reduction in the number of algal cells as a function of time was followed by taking water samples at fixed time intervals from the aquarium with mussels and well-mixed seawater and measuring the algal cell concentration with an electronic particle counter (Elzone 180). The filtration rate (F) is determined by means of the 'clearance method' from the exponential decrease in algal concentration (verified as a straight line in a semi-log plot) as a function of time using the following formula (Riisgård et al. 2011a,b):

$$F = (V \times b)/n \quad (2)$$

where V is the volume of water in aquarium, n is the number of mussels, and b is the slope of regression line in a semi-ln plot for the reduction in algal concentration with time.

Equations for data analysis. The condition index (CI) and shell condition index (CI_{shell}) were calculated from the dry weight of soft parts (W, mg), dry weight of shell (W_{shell}, mg) and the shell length (L, cm):

$$CI = W/L^3, \quad CI_{shell} = W_{shell}/L^3 \quad (3)$$

For experimental data, the actual weight-specific growth rates of mussels ($\mu_{act} = W^{-1}dW/dt$, % d^{-1}) was calculated as follows:

$$\mu_{act} = \ln(W_2/W_1)/(t_2 - t_1) \times 100 \quad (4)$$

(or equivalently from the slope of the trend line in a plot of $\ln(W)$ versus time), where t_1 and t_2 refer to the start and end of a growth period, respectively, and W_1 and W_2 are the corresponding values of dry weight. The average value of μ_{act} obtained this way is taken to be valid at the average dry weight of soft parts defined as follows:

$$W_{avg} = (W_1 \times W_2)^{1/2} \quad (5)$$

The estimated weight-specific growth rate based on the BioEnergetic Growth (BEG) model (Riisgård et al. 2012a, Eq.18 therein) was calculated as follows:

$$\mu_{BEG} \equiv \mu_W = aW^b, \quad (a = 0.871 \times C - 0.986;\ b = -0.34) \quad (6)$$

where the units are μ_{BEG} in % d^{-1}, W in g dry weight of soft tissue and C in µg chl *a* l^{-1}. The notation μ_W implies µ to be based on an empirical filtration rate in terms of W (in the form $F_W(l\ h^{-1}) = 7.45W(g)^{0.66}$).

Because the relationship between gill area and shell length remains essentially constant, it may be expected that a filtration rate based on shell length (F_L) would be more accurate than one based on the dry weight of soft tissue (F_W) as the *CI* varies during growth. The influence of *CI* was recently examined by Riisgård et al. (2014b) using available and new experimental data on maximum filtration rates of *M. edulis* covering the *CI* range of 2.31 to 8.68 mg cm^{-3}, for which the following 'model' equations were found:

$$F_W(l\ h^{-1}) = 6.521W(g)^{2/3} \quad (7)$$

$$F_L(l\ h^{-1}) = 0.00183L(mm)^2 \quad (8)$$

$$F_L/F_W = (0.3562CI(mg\ cm^{-3})^{2/3})^{-1} \quad (9)$$

Since the filtration rate based on dry weight of soft tissue enters into the first term of *a* in Eq. (6), we arrive at the modified BEG model based on F_L by introducing the correction factor Eq. (9):

$$\mu_{BEG\text{-}corr} = aW^b, \quad (a = 0.871 \times C \times F_L/F_W - 0.986;\ b = -0.34) \quad (10)$$

or

$$\mu_{BEG\text{-}corr} \equiv \mu_L = aW^b, \quad (a = 2.445 \times C \times CI^{-2/3} - 0.986;\ b = -0.34) \quad (11)$$

The notation μ_L implies µ to be based on empirical filtration rate in terms of L (Eq. 8). The correction factor Eq. (9) is unity for $CI = 4.70$ mg cm^{-3} for which Eq. (11) reduces to Eq. (6), and it implies that F_W tends to underestimate the actual filtration rate (F_L) when $CI < 4.70$, and to overestimate it when $CI > 4.70$ mg cm^{-3}.

Statistical analysis. Since no experiment was replicated, we rely on correlation coefficients (R^2) to characterize goodness of regression equation fit in the figures, while 2-factor ANOVA without replication is used to measure significance of weight-specific growth rates (µ) from models relative to experimental values, with $p > 0.05$ implying statistical significance for agreement.

Field growth experiments

Great Belt. A growth experiment was conducted near the Great Belt (Denmark; Fig. 1A) in the inlet to Kerteminde Fjord by suspending net bags containing 9 to 11 individuals of either small mussels from the Central Baltic Sea (near the island of Askö, 70 km south of Stockholm, Sweden; Fig. 1B) or Great Belt at a depth of ~1 m. Prior to the growth experiment, a total of 38 and 41 mussels of the same size (~15 ± 0.5 mm) from Askö and Great Belt, respectively, were randomly selected and put in net bags. Each net bag was kept separately in a small tank for 7 d to allow the mussels to produce byssi and attach firmly to the net-bag material before the bags were suspended in the water at the growth site (the 'triangle' close to the Marine Biological Research Centre [SDU], Kerteminde). Subsamples (n = 5 to 11) were collected at Day 0, 7, 15 and 21 for determination of shell length and dry weight of soft parts, giving rise to periods I (Days 0–7), II (Days 7–15), III (Days 15–21), and IV (Days 0–21). Measurements of chl *a*, temperature and salinity were made daily (Yellow Springs Instruments, YSI 650) during the growth period.

Baltic Sea. The growth of dwarfed mussels from Hanko, southwest of Finland (5.9 to 6.0 psu), was investigated by caging the mussels at various locations along the salinity gradient in the Gulf of Finland (stations Helsinki, Porvoo, Kotka) and Gulf of Bothnia (stations Turku, Pori, Gävle, Sundsvall) in the northern Baltic Sea (Fig. 1B). Adult mussels (shell length 25 to 30 mm) were collected by SCUBA divers at Hanko, placed in aerated water from the collection site, transported to the RV 'Aranda' and kept at same ambient temperature until arrival at the caging locations. Mussels (n ≈ 400) were deployed in stainless steel cages (80 × 40 cm) at depths of 7 to 8 m. Cages were held in stable vertical position by submerged buoys and anchored to the bottom with a 350 kg weight. Chl *a*, temperature and salinity at the caging locations were either measured at the time of sampling or obtained from the regional monitoring data bank

(Baltic Sea Portal, Finnish Environment Institute, www.itameriportaali.fi/en/tietoa/algaline_seuranta/en_GB/algaline_seuranta/) and in 2 cases (Gävle, Sundsvall) from data loggers (Star-oddi DST-CTD) attached to the cages. Growth of dwarfed mussels was estimated from measured mean shell length and body dry weight of samples collected on first and last day of the growth period.

RESULTS

Laboratory feeding and growth experiments with Åland mussels

Fig. 2 and Tables 1 to 3 show the growth parameters measured in the low-salinity (7 psu) experiment. While the growth in shell length (Fig. 2A) and in shell weight (Fig. 2C) were negligible, the body dry weight nearly doubled during the 15 d experiment (Fig. 2B), and the mean weight-specific growth rate was μ = 3.7% d^{-1}. Consequently, the *CI* nearly doubled (Fig. 2D, Table 1). The same parameters for the high-salinity (20 psu) experiment are shown in Fig. 3 and Table 1, and indicate significant growth in shell length and shell weight and an actual weight-specific growth rate of μ_{act} = 2.2% d^{-1} of the somewhat larger mussels. Table 2 shows the estimated and actual weight-specific growth rates at specified algal concentrations for both salinity experiments. By the end of the low-salinity experiment, a pronounced reduction in the filtration rate was observed (F_{FCA} and F_C in Table 1). Thus, during the last 4 d, the filtration rate measured by both the FCA and clearance methods was reduced to about 45% of the values in the previous period, before the last 4 days.

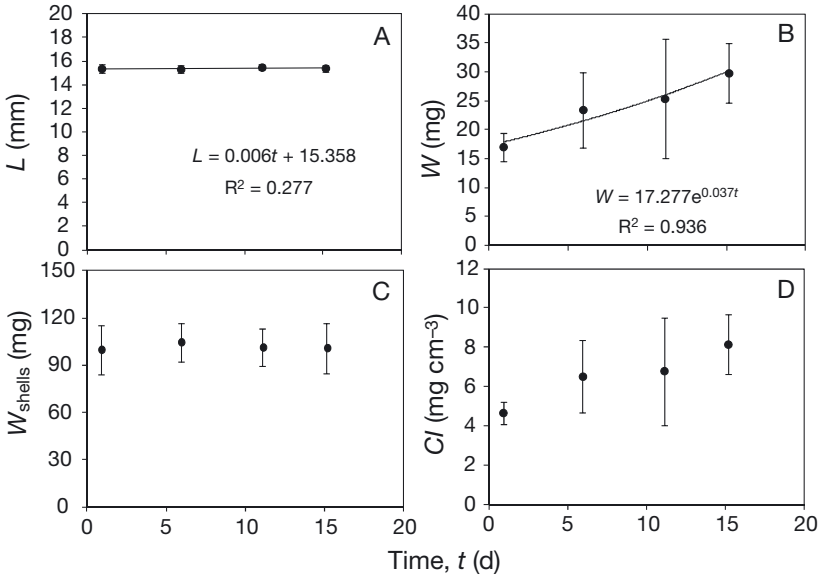

Fig. 2. *Mytilus trossulus* (Åland mussels, 7 psu, 'low-salinity' laboratory experiment). (A) Mean shell length (*L*), (B) body dry weight (*W*), (C) shell dry weight (W_{shells}), (D) condition index (*CI*) during steady-state feeding and growth experiment. Regression lines and their equations are shown for (A) and (B). The exponent in the equation in (B) indicates an actual weight-specific growth rate μ_{act} = 3.7% d^{-1} during the growth period. Bars: ±1 SD

Table 1. *Mytilus trossulus* (Åland mussels, 7 psu and 20 psu, laboratory experiments). Shell length (*L*), dry weight of soft parts (*W*), condition index (*CI*) from subsamples collected during the experiment, measured individual filtration rates using FCA (F_{FCA}) and clearance (F_C) methods, and estimated shell length (F_L, Eq. 7) and dry weight of soft parts (F_W, Eq. 8). n = 9 or 10 for each period. Mean values ± SD are shown

Time (d)	*L* (mm)	*W* (mg)	*CI* (mg cm^{-3})	F_{FCA} (ml min^{-1})	F_C (ml min^{-1})	F_L (ml min^{-1})	F_W (ml min^{-1})
7 psu							
0.9	15.4 ± 0.4	17.0 ± 2.4	4.7 ± 0.6	6.2 ± 0.5	4.9 ± 0.3	6.9 ± 0.3	8.4 ± 0.8
5.9	15.3 ± 0.3	23.4 ± 6.6	6.5 ± 1.8	4.7 ± 1.6	5.4 ± 1.3	6.9 ± 0.3	10.3 ± 1.9
11.1	15.5 ± 0.2	25.3 ± 10.3	6.8 ± 2.7	5.7 ± 1.5	5.9 ± 1.2	7.0 ± 0.2	10.8 ± 3.0
15.1	15.4 ± 0.3	29.8 ± 5.2	8.1 ± 1.5	2.6 ± 1.8	2.4 ± 0.6	7.0 ± 0.3	12.2 ± 1.4
20 psu							
0.8	17.8 ± 0.9	28.2 ± 8.6	5.0 ± 1.3	–	–	9.5 ± 1.0	11.7 ± 2.3
7.8	17.9 ± 1.0	32.9 ± 9.0	5.9 ± 1.5	7.7 ± 1.7	7.3 ± 2.4	9.6 ± 1.2	13.3 ± 2.5
14.8	17.9 ± 0.8	45.8 ± 12.4	8.0 ± 2.1	10.7 ± 3.2	10.1 ± 2.4	9.5 ± 0.8	15.1 ± 4.3
21.8	18.5 ± 1.3	45.7 ± 14.0	7.1 ± 1.1	13.8 ± 2.3	12.9 ± 1.5	10.2 ± 1.5	14.9 ± 4.6
28.8	18.9 ± 1.2	51.7 ± 15.9	7.5 ± 1.6	12.4 ± 5.0	11.9 ± 4.7	10.9 ± 1.5	17.4 ± 3.6
35.7	19.5 ± 1.5	61.9 ± 14.8	8.3 ± 1.5	16.4 ± 5.1	17.7 ± 4.7	11.7 ± 1.9	19.7 ± 3.1

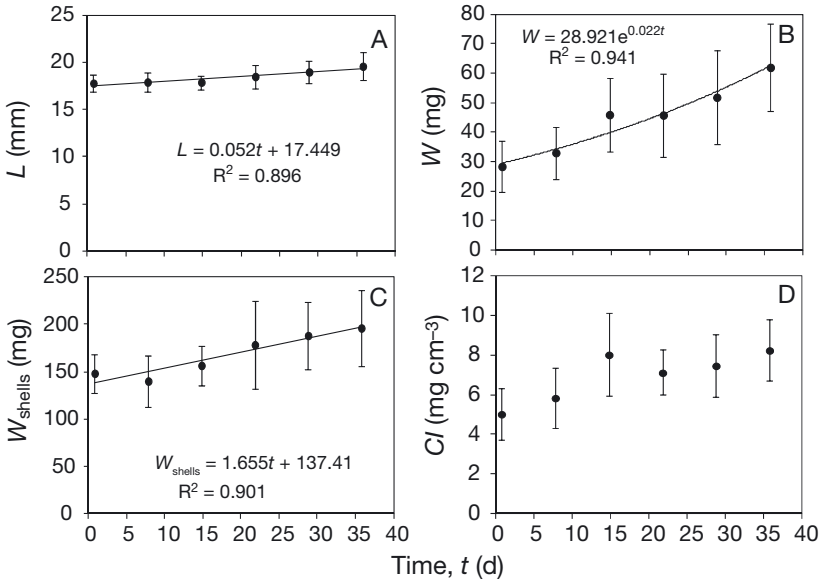

Fig. 3. *Mytilus trossulus* (Åland mussels, 20 psu, 'high-salinity' laboratory experiment). (A) Mean shell length (*L*), (B) body dry weight (*W*), (C) shell dry weight, (D) condition index (*CI*) during steady-state feeding and growth experiment. Regression lines and their equations are shown for (A) and (B). The exponent in the equation in (B) indicates an actual weight-specific growth rate, μ_{act} = 2.2 % d^{-1} during the growth period. Bars: ±1 SD

Table 2. *Mytilus trossulus* (Åland mussels, 7 and 20 psu, laboratory experiments). Estimated weight specific growth rates ($\mu_W = \mu_{BEG}$; $\mu_L = \mu_{BEG\text{-}corr}$) for specified algal (*Rhodomonas salina*) cell concentration (*C*) and equivalent chl *a* concentration, and the average temperature (*T*) for the period along with actual measured weight-specific growth rates (μ_{act})

t_0 (d)	t (d)	W_{avg} (g)	C (cells ml^{-1})	Chl *a* ($\mu g\ l^{-1}$)	T (°C)	μ_W (% d^{-1})	μ_L (% d^{-1})	μ_{act} (% d^{-1})
7 psu								
0.9	5.9	0.020	3092	3.9	10.4	9.1	5.7	5.4
5.9	11.1	0.024	2926	3.7	11.0	7.8	3.8	1.5
11.1	15.1	0.027	2956	3.7	11.3	7.6	3.3	4.0
0.9	15.1	0.023	3018	3.8	10.8	8.4	4.6	3.7
20 psu								
0.8	7.8	0.030	2868	3.6	9.7	7.0	4.6	2.0
7.8	14.8	0.039	2874	3.6	11.0	6.5	3.3	4.7
14.8	21.8	0.046	3022	3.8	10.8	6.6	2.7	0.0
21.8	28.8	0.049	2969	3.7	9.8	6.3	2.8	1.8
28.8	35.7	0.057	2913	3.6	10.1	5.8	2.3	2.6
0.8	35.7	0.042	2925	3.7	10.2	6.5	2.9	2.2

Field growth experiments

Great Belt

Fig. 4 shows that the growth rates of Askö and Great Belt mussels in the high-salinity field experiment are very similar during the growth period (Table 4). The exponents in the equations for the exponential regression lines in Fig. 4B show that the actual weight-specific growth rates, cf. Eq. (4), are μ_{act} = 5.6 and 6.8 % d^{-1} for Askö and Great Belt mussels, respectively.

As another indicator, Fig. 5 shows the shell condition index (CI_{shell}) during growth in the field (20 psu) and in the laboratory experiments (20 and 7 psu), with approximately the same rate of increase at 20 psu but a decrease at 7 psu, and a slightly lower CI_{shell} for the dwarfed Åland mussels. The level of CI_{shell} is also lower for Askö mussels than for Great Belt mussels.

Baltic Sea

Table 5 shows the data for the mussel cage experiments performed in the northern Baltic Sea. The weight-specific growth rates at sites with positive growth vary between 0.02 and 2.60 % d^{-1}, whereas no significant increase in shell length takes place; therefore, the *CI* increases in these mussels. It is notable that the salinities at sites with negative growth (Kotka K1, K2, K3; Sundsvall S1) are below 4.5 psu.

DISCUSSION

Laboratory feeding and growth experiments

In the laboratory experiment with Åland mussels *Mytilus trossulus*, the actual weight-specific growth rate was μ_{act} = 3.7 % d^{-1} at low salinity (7 psu) (Fig. 2B), compared to μ_{act} = 2.2 % d^{-1} at high salinity (20 psu) (Fig. 3B) obtained with mussels from the same collection site and at nearly the same chl *a* concentration, listed in Table 2 along with the estimated weight-specific growth rates at specified algal concentrations. The agreement between actual measured weight-specific growth rate (μ_{act}) and the estimated value based on shell length (μ_L) is reasonably good (ANOVA 2-factor without replication, p = 0.547 for

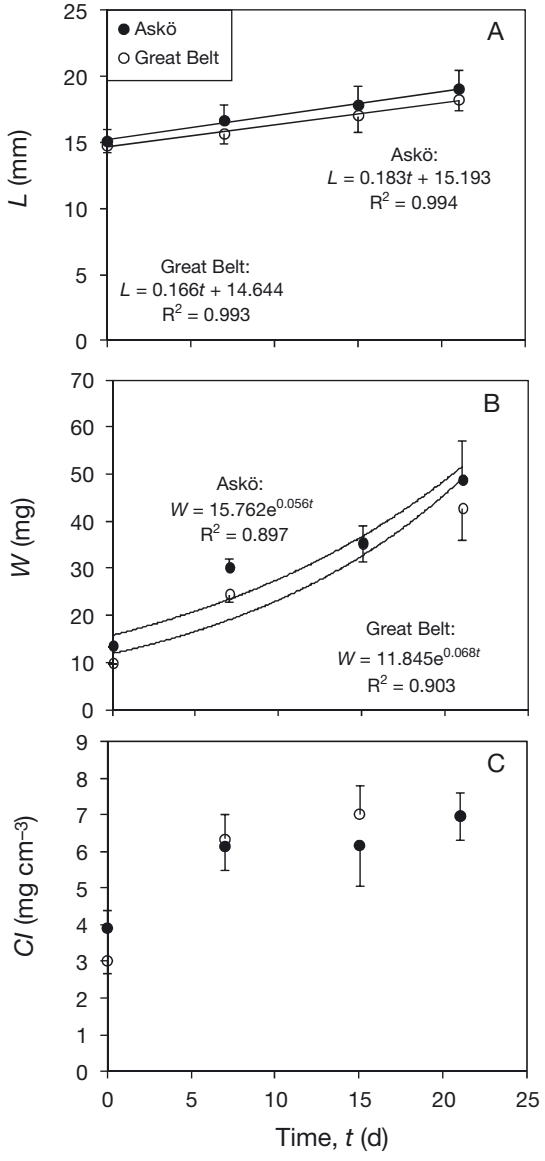

Fig. 4. *Mytilus trossulus* (Askö) and *M. edulis* (Great Belt). Field mussel growth experiment. Mean ± SD growth in (A) length (*L*), (B) dry weight of soft parts (*W*) and (C) condition index (*CI*) of mussels in suspended net bags in September–October 2012. Subsamples were collected on Day 0, 7, 15 and 21. Regression lines and corresponding equations are shown, except for *CI*. In (B), the weight-specific growth rate (μ_a) is expressed by the exponents (i.e. 5.6 and 6.8% d^{-1} for Askö and Great Belt mussels, respectively)

7 psu and p = 0.315 for 20 psu), but the estimated specific growth rate based on the body dry weight (μ_W) is poor (p = 0.036 for 7 psu and p = 0.007 for 20 psu), being 2- to 3-fold higher than the actual growth rate (Table 2). This agrees with the fact that *CI* > 4.7 mg cm^{-3} (Table 1). It may (tentatively) be concluded that mussels grow in body weight at comparable rates at low (7 psu) and high (20 psu) salinity, but the minimal or lack of growth in shell length or shell weight observed in the low-salinity experiment (Fig. 2A,C) suggests that reduced ability to produce shell material at low salinity may be a main factor explaining dwarfism of blue mussels in the Central Baltic Sea. During the last 4 d of the experiment, the filtration rate of Åland mussels at low salinity became reduced to about 45% of values in the previous period (Table 1). The reason for this change is unknown, but it might be linked to the lack of shell growth at the very low salinity, possibly caused by reduced bio-calcification (Malone & Dodd 1967, Almada-Villela 1984).

In the low salinity experiment (Table 1), the increase in soft body dry weight (*W*) combined with the lack of increase in shell length (*L*) resulted in a ~170% (8.1 vs. 4.7) increase in the *CI*, and although the estimated filtration rate (F_L) using the shell length and Eq. (7) was in reasonably good agreement with the

Table 3. *Mytilus trossulus* (Askö) and *M. edulis* (Great Belt) field growth experiments. Collection date in 2012, time (*t*) since first collection date, measured shell length (*L*) and dry weight of soft parts (*W*), and condition index (*CI*) of collected samples. Chl *a*, temperature (*T*) and salinity (S) and *CI* are mean ± SD values measured between the collection dates

Date	*t* (d)	*L* (mm)	*W* (mg)	*CI* (mg cm^{-3})	Chl *a* (µg l^{-1})	*T* (°C)	S (psu)
Askö							
17 Sep	0	15.1 ± 1.0	13.5 ± 2.0	3.9 ± 0.5	–	–	–
24 Sep	7	16.7 ± 1.3	30.1 ± 3.7	6.2 ± 0.7	2.7 ± 0.5	14.0 ± 0.8	23.4 ± 0.6
02 Oct	15	17.8 ± 1.5	35.4 ± 8.6	6.2 ± 1.1	2.7 ± 0.6	13.1 ± 0.4	22.5 ± 0.9
08 Oct	21	19.1 ± 1.4	48.7 ± 9.6	7.0 ± 0.6	2.6 ± 0.5	12.7 ± 0.7	21.3 ± 0.3
Great Belt							
17 Sep	0	14.8 ± 0.4	9.8 ± 1.5	3.0 ± 0.3	–	–	–
24 Sep	7	15.7 ± 0.7	24.5 ± 3.7	6.3 ± 0.7	2.7 ± 0.5	14.0 ± 0.8	23.4 ± 0.6
02 Oct	15	17.1 ± 1.2	35.1 ± 6.7	7.0 ± 0.8	2.7 ± 0.6	13.1 ± 0.4	22.5 ± 0.9
08 Oct	21	18.2 ± 0.8	42.7 ± 7.0	7.0 ± 0.4	2.6 ± 0.5	12.7 ± 0.7	21.3 ± 0.3

Table 4. *Mytilus trossulus* (Askö) and *M. edulis* (Great Belt) field growth experiments. Mean shell length (L), dry weight of soft parts (W_{avg}), salinity (S), temperature (T), and chl *a* concentration in the growth periods, along with estimated weight-specific growth rate, μ_{BEG} (= μ_W), and the actual measured weight-specific growth rate, μ_{act}. n = 5 to 11 for each period. Period IV spans the entire Period I to III

Period no.	Period length (d)	n	L (mm)	W_{avg} (mg)	S (psu)	T (°C)	Chl *a* (µg l^{-1})	μ_{BEG} (% d^{-1})	μ_{act} (% d^{-1})
Askö									
I	7	(9)	15.9	20.1	23.4	14.0	2.7	5.1	11.5
II	8	(8)	17.2	32.6	22.5	13.1	2.7	4.5	2.0
III	6	(7)	18.4	41.5	21.3	12.7	2.6	3.7	5.3
IV	21	(7)	17.1	25.6	22.5	13.3	2.7	4.7	6.1
Great Belt									
I	7	(9)	15.2	15.5	23.4	14.0	2.7	5.6	13.1
II	8	(11)	16.4	29.3	22.5	13.1	2.7	4.6	4.5
III	6	(7)	17.6	38.7	21.3	12.7	2.6	3.8	3.3
IV	21	(5)	16.5	20.5	22.5	13.3	2.7	5.0	7.0

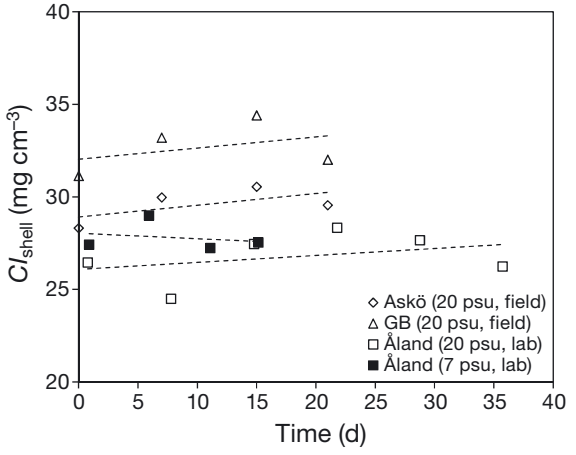

Fig. 5. *Mytilus trossulus* (Askö, Åland) and *M. edulis* (Great Belt). Shell condition index ($CI_{shell} = W_{shell}/L^3$; Eq. 3) as a function of time in field and laboratory growth experiments with mussels from Askö, the Great Belt (GB) and Åland exposed to high (20 psu) and low (7 psu) salinities. Linear regression lines are shown

experimentally measured filtration rates (F_{FCA} and F_C; Table 1), it is notable that the estimated filtration rate (F_W) using W and Eq. (8) increasingly overestimated the actual filtration rate. The latter phenomenon probably can be ascribed lack of growth of the gills, which is likely to be closely correlated with a simultaneous growth in shell length (Riisgård et al. 2011b, Figs. 7 & 8 therein). However, more experimental work is needed to clarify how low salinity may affect not only shell growth, but also feeding ability, when the *CI* of dwarfed mussels exceeds a certain level.

In the laboratory growth experiments, the BEG model ($\mu_{BEG} = \mu_W$) over-estimated the actual growth (μ_{act}) by 215% (8.4 vs. 3.9) and 296% (6.6 vs. 2.2) for Åland mussels at 7 psu and 20 psu, respectively (Table 2). However, the corrected BEG model, Eq. (11), based on calculating the filtration rate from shell length, gives weight-specific growth rates ($\mu_{BEG\text{-}corr} = \mu_L$) in better agreement with the actual specific growth rates. Specifically, μ_L and μ_{act} take values of 4.6 and 3.9% d^{-1} at 7 psu and 2.9 and 2.2% d^{-1} at 20 psu, respectively, as seen from Table 2. This example emphasizes that the BEG model is sensitive to changes in the *CI* and that the model may be improved by using Eq. (11). Future data should therefore include values of the *CI*.

Field growth experiments

Great Belt

The actual growth rates (μ_{act}) of mussels in net-bags in the Great Belt were 6.1 and 7.0% d^{-1} for Askö and Great Belt mussels, respectively, and the mean chl *a* concentration was 2.7 µg l^{-1} (Table 4). It is notable that the growth rate of Askö and Great Belt mussels are very similar (Fig. 4), and this is in agreement with earlier observed growth rates of Baltic Sea (7 psu) mussels transplanted to the North Sea (28 psu) by Kautsky et al. (1990) and Tedengren et al. (1990). Further, the actual weight-specific growth rates are in reasonable agreement with the predicted growth from the BEG model (Table 4) (ANOVA; p = 0.550 for Askö and p = 0.470 for Great Belt), as also noted by Larsen et al. (2014) using the same data for a comparison of various growth models. It is notable that the high-salinity (20 psu) laboratory experiment with mussels from the same collecting site showed substantially lower growth (Table 2) despite the higher chl *a* concentration of 3.7 µg l^{-1}, a phenomenon probably caused by suboptimal conditions in the growth aquarium, with only slow through-flow of fresh seawater to reduce the wash-out of algal cells.

Baltic Sea

The actual growth rates (μ_{act}) of mussels in cages in the Baltic Sea were considerably lower than those of mussels in net-bags in the Great Belt, although the chl *a* concentrations measured at the mussel-cage loca-

Table 5. *Mytilus trossulus.* Date, site, salinity (S), chl *a* (measured value or range), temperature (*T*; on date of sampling), time (*t*), shell length (*L*), body dry weight (*W*), condition index ($CI = W/L^3$, Eq. 3, n = 15 to 20), and weight specific growth rate (μ_{act}, Eq. 4) of mussels in cages at various Baltic Sea sites during certain time periods (*t*). At Hanko (and in 1 case, Utö) mussels were collected from the native population; some mussels were used as start group on Day 0 (*t* = 0), while other mussels were put into the cages and transplanted for measurement of growth parameters at the sites (Fig. 1B). Where applicable, values are mean ± SD

Date	Site name, symbol on map	S (psu)	Chl *a* (µg l^{-1})	*T* (°C)	*t* (d)	*L* (mm)	*W* (mg)	*CI* (mg cm^{-3})	μ_{act} (% d^{-1})
2006 Apr 26	Utö	6.0	6–15	2.0	0	31.3 ± 2.7	64.7 ± 23.4	2.2 ± 1.0	
Jul 6	Turku 1, T1	5.6	3–6	15.3	71	28.8 ± 2.4	121.1 ± 34.9	5.1 ± 1.3	0.88
	Turku 2, T2	5.7	3–6	15.0	71	30.0 ± 1.9	108.7 ± 43.7	4.0 ± 1.6	0.73
	Turku 3, T3	5.6	3–6	16.8	71	29.6 ± 2.3	175.1 ± 31.3	6.8 ± 1.0	1.40
2007 Sep 9	Hanko	5.9	5.3	15.9	0	21.7 ± 1.5	68.9 ± 17.0	6.9 ± 1.6	
Oct 9	Porvoo, C1	4.8	3.5	14.1	29	24.1 ± 1.3	114.2 ± 38.0	8.4 ± 3.1	1.68
	Porvoo, C2	4.8	3.5	13.2	29	24.4 ± 1.2	129.4 ± 18.2	8.9 ± 0.8	2.11
	Porvoo, C3	4.8	6.0	13.0	29	25.3 ± 1.7	148.8 ± 35.3	9.4 ± 2.6	2.60
	Porvoo, C4	4.8	6.0	13.3	29	24.7 ± 1.9	123.3 ± 32.7	8.2 ± 1.5	1.95
2008 Jun 7	Hanko	5.7	4.5	12.0	0	32.1 ± 2.6	143.8 ± 36.9	4.4 ± 1.3	
Aug 18	Pori, P1	5.4	4–6	13.9	72	34.1 ± 2.6	146.1 ± 47.6	3.8 ± 1.3	0.02
	Pori, P2	5.5	5–8	12.5	72	32.8 ± 3.2	176.3 ± 69.7	4.9 ± 1.6	0.28
2009 Jul 31	Hanko	6.0	4.1	16.3	0	30.4 ± 2.4	116.8 ± 31.4	4.2 ± 1.0	
Aug 25	Kotka 1, K1	4.3	6.9	17.0	25	30.9 ± 3.0	93.6 ± 30.7	3.3 ± 1.3	−0.47
	Kotka 2, K2	4.3	6.9	17.0	25	29.6 ± 2.5	116.4 ± 40.6	4.6 ± 1.7	−0.01
	Kotka 3, K3	4.3	6.9	16.7	25	30.8 ± 1.4	100.3 ± 25.9	3.5 ± 0.9	−0.32
2010 Jun 1	Hanko	5.9	3.6	12.9	0	30.7 ± 2.5	76.9 ± 25.8	2.7 ± 1.1	
Sep 2	Gävle 1, G1	4.2	3–6	15.5	94	30.3 ± 3.0	83.8 ± 29.8	3.2 ± 1.4	0.09
	Gävle 2, G2	4.5	3–6	15.6	94	30.3 ± 3.8	105.2 ± 28.1	3.9 ± 1.2	0.33
Sep 1	Sundsvall 1, S1	3.4	3–6	15.5	93	27.8 ± 1.9	53.4 ± 28.3	2.4 ± 1.1	−0.39
	Sundsvall 2, S2	4.5	3–6	14.7	93	29.7 ± 2.2	92.8 ± 17.7	3.6 ± 0.9	0.20
2011 Sep 1	Hanko	6.0	3.8	15.0	0	27.1 ± 1.7	88.2 ± 24.7	4.5 ± 1.2	
Oct 4	Helsinki 1 H1	5.7	5.1	13.0	34	27.4 ± 1.8	117.2 ± 33.0	5.6 ± 1.2	0.84
	Helsinki 2 H2	5.7	6.3	13.0	34	27.3 ± 2.0	134.0 ± 29.7	6.7 ± 1.7	1.23
	Helsinki 3 H3	5.7	16.4	13.0	34	28.3 ± 2.5	163.1 ± 59.6	7.3 ± 2.9	1.81

tions in the Baltic Sea were higher, 3 to 6 µg l^{-1} or more (Table 5). In general, the *CI* tends to increase when mussels are transferred from relatively meager to better food conditions (Riisgård et al. 2012a,b, Larsen et al. 2014), and the same phenomenon could be observed in most cases of the present study when mussels from a dense bed were transferred to cages in the water column (Table 5). However, at locations with very low salinity (<4.5 psu), the actual growth rates were negative, and therefore the *CI* decreased. It is notable that no increase in shell length (from initial values of 25 to 30 mm) took place at any of the mussel-cage locations (Table 5), and this phenomenon implies a close correlation between *CI* and μ_{act} as seen from Fig. 6. Because the weight-specific growth rates were considerably lower in the Baltic Sea (Table 5) than in the Great Belt (Table 4), it may be concluded that salinity, and not shortage of food, is the main factor causing reduced growth of mussels suspended in cages in the Baltic Sea, where the lowest salinity that allows positive somatic growth of mussels seems to be 4.5 psu; although all caging sites were probably influenced by natural salinity fluctuations taking place in the coastal areas due to variations in fresh-water runoff from land (Westerbom et al. 2002).

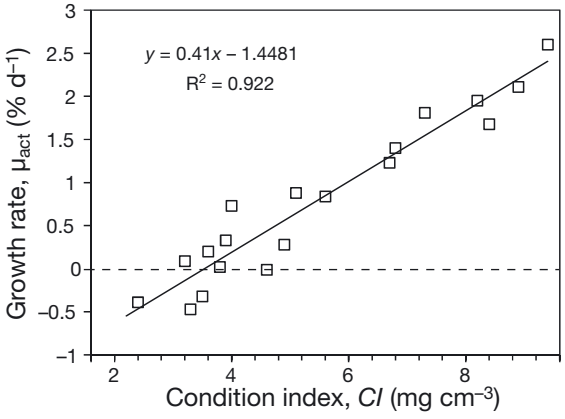

Fig. 6. *Mytilus trossulus*. (Åland mussels in the Baltic Sea, Table 5). Weight-specific growth rate versus condition index

In addition to variations in salinity, temperature varied between the different experiments. For the weight-specific growth rate, for example, tempera-

tures ranged from 12.7 to 14°C (Table 4). To estimate the resulting variation of weight-specific growth rate, we consider the temperature corrections to filtration rate and respiration introduced by Larsen et al. (2014, Eq. 5 therein) to their BEG model. Relative to the value of μ_{BEG} at the mean temperature of 13.35°C, μ_{BEG} varied from −0.8% to +0.7% in the temperature range of 12.7 to 14°C at the chl *a* concentration of 2.7 µg l^{-1}, which is negligible compared to the variations seen in Table 4.

For the data of Table 5, temperature varies from a low of 12°C (ignoring the 2.0°C of Utö) to a high of 16.8°C, but also the chl *a* concentration varies between sites. For an estimate of the temperature effect, we assume the same reference temperature of 13.35°C as for Table 4 and a chl *a* concentration of 4.5 µg l^{-1}, which gives a variation of μ_{BEG} of −2.5% to +5.9% for the temperature range.

For the data of Fig. 5 (CI_{shell} versus time), there is a decreasing temperature pattern for Askö and the Great Belt (from about 14 to 12.7°C), but data on temperature changes for Åland (20 psu and 7 psu) are not available. Hiebenthal et al. (2012) found the mass-based *CI* (ratio of soft tissue weight to shell weight) to decrease with increasing temperature (5 to 25°C) but not to be significantly affected by salinity (15 to 35 psu), which is contrary to the present results (Fig. 5), although covering a rather narrow temperature range (9.7 to 14°C).

Fig. 7 shows available growth data for both mussel species as a function of salinity. To judge from the inserted trend line, the growth of mussels is steadily hampered by reduced salinities from 25 to 30 psu down to about 7 to 10 psu, below which growth is rapidly reduced, becoming negative below 4.5 psu.

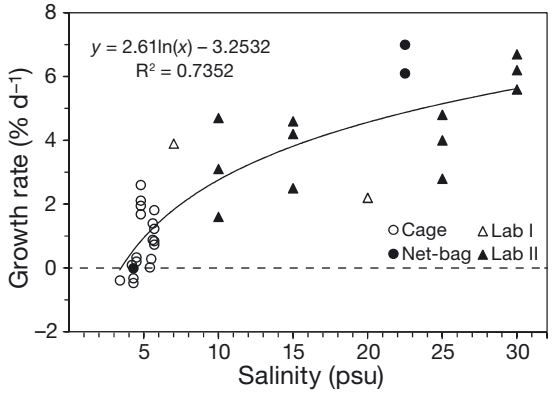

Fig. 7. *Mytilus trossulus* and *M. edulis*. Weight-specific growth rate (μ_{act}) of mussels in field studies using cages (our Table 5) or net-bags (our Table 3) and in laboratory studies (Lab I = our Table 2; Lab II = Riisgård et al. 2012b, their Tables 2, 3 & 4) as a function of salinity of the ambient water

Shell *CI*

Since some of the datasets include the dry weight of shells, we also explore the variation during growth of the shell *CI* (CI_{shell}, Eq. 3). Fig. 5 shows that CI_{shell} increases during growth (0.0602, 0.0632 and 0.0375 mg cm^{-3} d^{-1} for Askö, GB and Åland mussels, respectively) at high salinity (20 psu) but decreases (−0.0289 mg cm^{-3} d^{-1}) at low salinity (7 psu). The magnitude of the index may be thought of as a geometric form factor (assuming shell material to have a fixed mass density), which might include a measure such as the ratio of shell thickness to length, in which case a lower value would imply a thinner shell. Further, since shell length increases during growth in all cases shown in Fig. 5, the decrease of CI_{shell} at low salinity would imply that Åland mussels at 7 psu grow thinner shells than normal. This suggestion is in agreement with Kautsky et al. (1990), who found that the shell weight was about 2-fold heavier in North Sea mussels than in Baltic Sea mussels, and it agrees with the decreasing shell breakage pressure ('shell stability') found by Kossak (2006, Fig. 6 therein) for decreasing salinity. The process of calcification and shell deposition is depressed below 12.8 psu (Almada-Villela 1984), and this may partly explain the differences in shell thickness, but thinner shells remained in Baltic Sea mussels transplanted to the North Sea (Kautsky et al. 1990), indicating possible genetic causes.

CONCLUSIONS

All our studies indicate that the growth rates of *Mytilus edulis* and *M. trossulus* under same conditions at high salinity (20 psu) are nearly identical. Both species have the ability to grow fast under optimal conditions, including relatively high salinity (Fig. 4), and both species respond by valve closure (reduced filtration rate) to acutely changed salinities, but only *M. trossulus* is able to completely acclimate its filtration rate to salinities below 7 psu and to tolerate extremely low salinities over extended time periods (Riisgård et al. 2013, 2014a). Thus, when North Sea (28 psu) mussels are transplanted to the Baltic Sea, they have a high initial mortality, and enzyme analyses by Johannesson et al. (1990) have shown that the mortality is selective, so that only North Sea mussels of the Baltic Sea genotype survive. Filgueira et al. (2013) found that the weight-based *CI* (CI_{weight} = dry meat weight (g)/dry shell weight (g) × 100, which may be nearly proportional to the present *CI*), was a good indicator of aquaculture intensity for *M. edulis*

and the oyster *Crassostrea virginica* across different bays in Atlantic Canada. The underlying premise was that overstocking of bivalves leads to increased competition for food resources, which might ultimately have a significant effect on bivalve growth performance and the *CI*. Despite the present low salinity, we interpret this to imply that increasing *CI* reflects increasing growth rates, as depicted in Fig. 6.

In a related study, Kossak (2006) collected juvenile blue mussels at 6 sites with different salinities within the 'Baltic Sea salinity gradient' without attempting to differentiate between the *M. edulis* type entering from the North Sea and the *M. trossulus* type from the inner Baltic Sea. The mussels were then reciprocally transplanted between sites with salinities varying between 6 and 33 psu. Shell length growth rates and shell breakage pressure ('shell stability') were used to compare the performance of the mussels at different sites. Shell growth rates increased with increasing salinity from 6 to 25 psu, with a sharp increase from 6 to 17 psu (Kossak 2006, Figs. 12 & 18 therein), and increasing salinity resulted in increasing shell stability. These observations are consistent with the present weight-specific growth rates of mussels in field studies (Fig. 7) and measured CI_{shell} (Fig. 5).

To what extent the observed changes in *CI* and *W* of mussels in cages might have been influenced by spawning remains unknown. According to Sunila (1981), who studied the reproductive cycle of mussels collected in the Gulf of Finland (6 to 7 psu), spawning occurs mainly in July, and the most inactive time is from August to October. Therefore, the observed *CI* and μ_{act} in Table 5 should be considered as minimum values.

The salinity limit of 4.5 psu for positive growth (Fig. 7) is in agreement with the actual distribution of mussels in the central Gulf of Finland (Segerstråle 1944). Further, Westerbom et al. (2002) observed a marked decline in mean mussel shell length along a salinity gradient from the Archipelago Sea in the northern Baltic proper (Utö, 6.5 psu) to the Gulf of Finland (Tvärminne, 6 psu and Sönderskär, 5 psu). By studying growth marks in the shells, Westerbom et al. (2002) found that the shell length increases nearly linear to an age of about 6 to 7 yr, whereupon the growth eases off to result in a maximum attainable shell length characteristic of the locality. Thus, at 6.5 psu (Utö), the maximum size was 35 mm; at 6 psu (Tvärminne), it was 30 mm; and at 5 psu (Söderskär), the maximum shell length was only 25 mm. The bioenergetic factors controlling the maximum size of dwarfed mussels at extremely low salinities remain obscure — as they are for mussels in general (Barker Jørgensen 1976).

The biology of brackish waters has been thoroughly reviewed by Remane & Schlieper (1971), who had worked extensively on the Baltic Sea coast of Germany, and this review provided an overview of the present knowledge on the special ecological and physiological features of brackish-water organisms, such as species poverty, changes in forms, osmotic resistance (including non-genetic and genetic adaptation of organisms), osmoregulation, oxygen requirements and reduction in size and mussel shell stability, which was postulated to be affected by salinity and temperature. According to Kautsky et al. (1990, p. 208 therein), and also referring to Tedengren & Kautsky (1986) and Tedengren et al. (1990), the main reason for the low growth rate of mussels in the Baltic Sea 'is likely to be a salinity-dependent change in amino acid metabolism and nitrogen excretion resulting in a less favorable energy balance in low saline areas'. Reduced bio-calcification at low salinity, resulting in impeded shell growth (Malone & Dodd 1967, Almada-Villela 1984), but not in reduced somatic growth, may at first result in an increased *CI*, as seen in benthic mussels transferred to net-bags (Fig. 4C) or cages (Table 5) suspended in the water column. However, insufficient space between the valves might subsequently lead to valve closure in order to reduce the filtration rate and thus food ingestion and further somatic growth. Future studies using e.g. underwater video may clarify whether such an explanation of the phenomenon of mussel growth at the limit of salinity tolerance is credible.

In a recent study on long-term starvation of *Mytilus edulis*, Riisgård & Larsen (2014) found that partial valve-closure (and strong reduction of the ventilation rate) is an efficient mechanism to reduce respiratory weight loss, and typically, the weight-specific negative growth rate during starvation was about –0.3 % d^{-1}. An inspection of the present Table 5 reveals negative growth rates of this order for mussel-cage growth sites Kotka K1, K2, K3 and Sundsvall S1 with salinities of 4.3 and 3.4 psu, respectively. This suggests that the mussels at these caging sites may have had their valves more or less closed in response to low salinity. Obviously, such a behavioral response is also highly relevant for monitoring studies using transplanted filter-feeding mussels to identify the accumulation and effects of hazardous substances (Turja et al. 2013, 2014).

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