



# Disentangling the biological and environmental control of *M. edulis* shell chemistry

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[1] Blue mussel individuals (*Mytilus edulis*) were cultured at four different salinities (17, 20, 29, and 34). During the course of the experiment, temperature was gradually increased from 6°C to 14°C. Mg/Ca and Sr/Ca ratios of the shell calcite portions produced during the 9 weeks of experimental treatment as well as parts that were precipitated before the treatment phase were measured by laser ablation–multicollector–inductively coupled plasma–mass spectrometry. Mg/Ca ratios show a positive correlation with temperature for individuals cultured at salinity 29 and 34 ( $\text{Mg/Ca (mmol/mol)} \sim (0.2\text{--}0.3) \cdot T (\text{°C})$ ), while for individuals cultured at low salinities (17, 20) no trend was observed. Sr/Ca ratios were not affected by temperature but strongly by salinity. The data show very strong biological influence (“individual differences” and “physiological variability”) on elemental ratios (79% on Mg/Ca and 41% on Sr/Ca) in *M. edulis* calcite. The results challenge the use of blue mussel shell data as environmental proxies.

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## 1. Introduction

[2] Understanding climate history helps interpreting fluctuations or directional shifts of parameters like temperature or CO<sub>2</sub> in the context of global change. Biological climate archives are valuable records of environmental conditions during the lifetime of the organism. Mussels have the potential to provide high resolution records of a large variety of environmental regimes due to their high growth rate, global distribution [Gosling, 1992] and tolerance to a broad range of environmental conditions [Seed and Suchanek, 1992] and some bivalves are

extremely long-lived [e.g., Schöne et al., 2005]. Trace metal distributions (e.g., Mg and Sr) in bivalve shells are a field of current interest because as a proxy archive [e.g., Klein et al., 1996a, 1996b; Lazareth et al., 2003; Immenhauser et al., 2005; Freitas et al., 2008; Wanamaker et al. 2008], they may help reconstructing (paleo)environmental conditions and thus deliver the data necessary to construct and improve models of past climate.

[3] However, several recent studies [e.g., Klein et al., 1996b; Vander Putten et al., 2000; Gillikin et al. 2005; Carré et al., 2006; Freitas et al. 2006; Heinemann et al., 2008] on elemental ratios

in bivalve shells failed to show unambiguous relationships between elemental ratios and environmental factors (e.g., temperature and salinity). The reasons are often referred to as “biological control” or “vital effects” meaning elemental ratios in the mussel shell (e.g., Mg/Ca, Sr/Ca) are not exclusively controlled by inorganic thermodynamic principles but also by individual physiological processes. For example, Klein *et al.* [1996b] suggested that skeletal chemistry of *Mytilus trossulus* from the field is primarily controlled by rate of mantle metabolic activity (metabolic pumping of Ca to the extrapallial fluid (EPF)) and only secondarily modified by variation of seawater salinity. Also, in their study on the distribution of Mg, Sr and Pb in the calcite shell layer of *Mytilus edulis*, Vander Putten *et al.* [2000] showed that patterns of these elements cannot be explained by seasonal variations in seawater composition alone. According to the latter study the direct use of Mg as a proxy in *M. edulis* shells is hampered by the absence of a consistent Mg-temperature relationship over the year. Crystal growth rate in two aragonitic marine bivalve species (*Mesodesma donacium* and *Chione subrugosa*) was found to be the main factor influencing trace elements concentrations, especially for Sr (explaining up to 74% of the variance) [Carré *et al.*, 2006]. As a consequence, the environmental control on minor and trace elements in mollusks is often too weak to develop suitable proxies [Carré *et al.*, 2006]. The findings from recent bivalve studies corroborate the results of previous studies reporting a strong biological influence and the interaction among different environmental factors affecting elemental ratios in bivalve shells [e.g., Heinemann *et al.*, 2008].

[4] The ambiguity of results in recent studies raises the question as to whether the influence of a single environmental factor on bivalve shell composition can be strong enough to provide a reliable signal superimposing the “noise” produced by other environmental variables and/or by biological effects. Hence, it is important to quantify the influence of single environmental variables such as temperature or salinity as well as the combined effect of such factors on elemental ratios (i.e., Sr/Ca and Mg/Ca) relative to the biological background “noise” such as genetics, physiology, growth and reproductive cycles and infections, respectively. In the present study we investigated the influence of temperature, salinity, individual differences and physiological variability on element to calcium ratios in the calcite layer of

juvenile blue mussels (*M. edulis*) to critically assess its suitability as a proxy archive.

## 2. Materials and Methods

### 2.1. Culturing

[5] Young (6–9 mm) blue mussels, *Mytilus edulis*, collected in August 2003 from settlement panels deployed in the Kiel Fjord in spring of the same year, were first kept under identical and controlled conditions in a flow through system of filtered seawater (salinity around 17) in the laboratory at 12°C for 5 months. During this time, the bivalves were fed daily with natural plankton caught from Kiel Fjord (20–100  $\mu\text{m}$ ) at concentrations typical for the Baltic Sea ( $3 \times 10^3$  cells/mL) [Clausen and Riisgard, 1996].

[6] After this laboratory acclimatization phase, the juvenile *M. edulis* were partitioned into 4 treatment groups in 2 L aquaria. Subsequently, the bivalves were gradually adapted (salinity change by 5 units per week), to 4 different salinities (17, 20, 29, 34). Salinities higher than 17 (initial salinity) were obtained by adding artificial marine salt (Tropic Marin, Dr. Biener, Wartenberg) to natural Baltic Seawater. In this experimental setup, each experimental unit consisted of the 2 L aquarium (replicate) containing 20 mussel individuals of similar size (pseudo replicates) and 2 reservoirs. A pump placed in a lower reservoir filled an upper reservoir, allowing the water to flow through the culture tanks (2 L aquaria) back into the lower reservoir. The setup resulted in a total water volume of ~75 L for each experimental unit. The water was exchanged once per week.

[7] As in the Baltic Sea blue mussels’ growth rates are normally highest in early spring and summer [Kautsky, 1982a], the experiment was conducted from 4 February to 13 May 2004. In the course of the experiment temperature was continuously adjusted to the seasonal Kiel Fjord water temperature (20 year average of the experimental period February until May) [Lehmann *et al.*, 2002] and ranged from 6°C to 14°C. In this treatment phase, food consisted of cultured algae (*Dunaliella* sp. and *Rhodomonas* sp.) at a concentration of  $6 \times 10^3$  cells/mL. Prior to the daily feeding, the algal suspension was adjusted to experimental salinity and constantly dripped (20 mL/min) into the aquaria over a period of 2 h ( $72 \times 10^4$  cells/mussel). Light exposure was 10 h a day ( $\sim 150 \mu\text{E}/\text{m}^2/\text{sec}$ ). For more details on culturing technique used see the

**Table 1.** Instrument Parameters of the LA-ICP-MS Measurements

Parameters	Explanation of Parameters
<i>AXIOM MC-ICP-MS</i>	
Cool gas	14 L/min
Auxiliary gas	1.5 L/min
Nebulizer gas	0.6 L/min
RF power	1000 W
Reflected power	2 W
Ion energy	4968 V
Cones	R.A. Chilton RAC19/RAC705
Resolution	500 res
Integration time per scan	2 s
Measured isotopes (Faraday Cup used)	<sup>24</sup> Mg (L3), <sup>25</sup> Mg (Ax), <sup>26</sup> Mg (H3), <sup>44</sup> Ca (L4), <sup>46</sup> Ca (Ax), <sup>48</sup> Ca (H4), <sup>84</sup> Sr (L2), <sup>85</sup> Rb (L1), <sup>86</sup> Sr (Ax), <sup>87</sup> Sr (H1), <sup>88</sup> Sr (H2)
<i>UP193 Solid State Laser</i>	
Ablation gas	0.6 L/min (He)
Spot size/distance between spots	35 μm/100 μm
Fluence	3 J/cm <sup>2</sup>
Repetition rate	10 Hz
Ablation time	50 s
Washout time	120 s

study of *Kossak* [2006]. Growth for each individual mussel was monitored by measuring shell length (from umbo to shell margin, longest distance) at five dates (4 February, 9 and 25 March, 22 April,

**Table 2.** Means and Variances of Shell Parts Grown in Nature Under Similar Conditions Before the Actual Treatment Started<sup>a</sup>

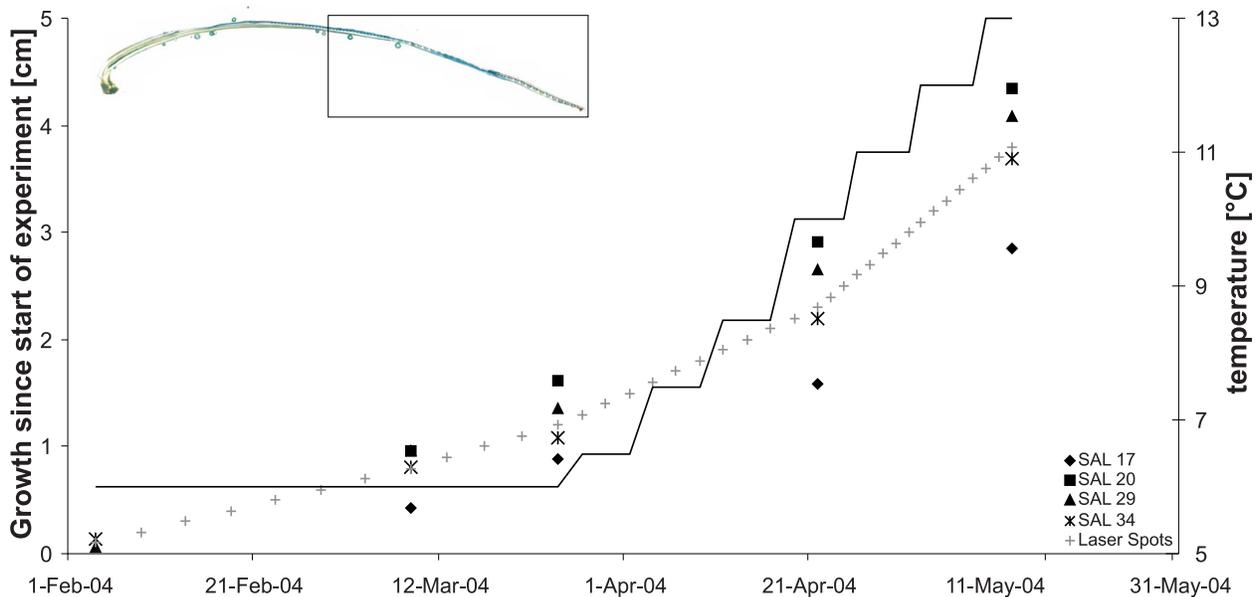
	Salinity 17	Salinity 20	Salinity 29	Salinity 34
<i>Mg/Ca (mmol/mol)</i>				
mean	6.2	8.0	7.7	7.8
variance	1.6	3.0	2.5	0.5
<i>Sr/Ca (mmol/mol)</i>				
mean	1.379	1.55	1.54	1.47
variance	0.001	0.01	0.02	0.01

<sup>a</sup>Grouped with respect to the treatment applied.

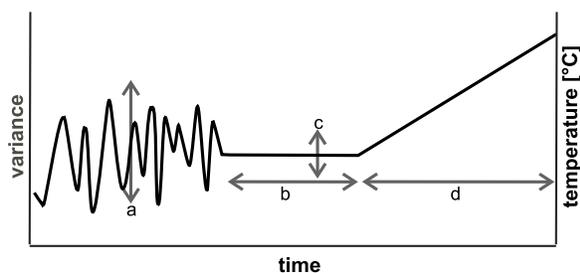
and 13 May). At the end of the experiment, the size range was 11–14 mm.

## 2.2. Sample Preparation

[8] At the end of the treatment phase, mussels were sacrificed by freezing (−18°C) and their soft body removed. From each salinity treatment the shell of one individual (randomly selected among the survivors of the 20 pseudo replicates per experimental unit) was embedded in a two component epoxy resin (Buehler, EPO-THIN, Low Viscosity Epoxy Resin). When the resin had hardened, shells were repeatedly cut along the axis of maximum length using a microtome saw (Leica SP 1600) producing 200 μm thick sections.



**Figure 1.** Growth of mussels during the experiment. Length was measured at five dates. Distance between laser spots was 100 μm and their location was calculated by the known points of growth. Line shows temperatures during experimental phase [*Kossak*, 2006].



**Figure 2.** Scheme of values used for calculations of the relative contribution of individual differences (a), physiological variability (b), salinity (c–a) and temperature (d–b) to the overall variance of elemental ratios. Horizontal arrows display variances within one shell; vertical arrows display variances between the four shells.

These sections were mounted onto glass slides with thermal wax (Crystalbond 509 Amber, Aremco Products Inc.).

### 2.3. Analytical Methods

[9] Ca, Sr and Mg profiles were measured in the calcite layer of the shell using laser ablation–inductively coupled plasma–mass spectrometry (LA-ICP-MS) along the axis with spot size of 35  $\mu\text{m}$  and a distance between spots of 100  $\mu\text{m}$  (with Thermo Sci. AXIOM multicollector–inductively coupled plasma–mass spectrometry (MC-ICP-MS); New Wave Res. UP193 solid state; parameters shown in Table 1) [Fietzke *et al.*, 2008]. Repeated measurements of silicate glass SRM NIST610 were used to normalize the data applying the reference values of Pearce *et al.* [1997]. Subsequently, Mg/Ca and Sr/Ca ratios were calculated. Reproducibility of the elemental ratios was typically found to be better than 3% (RSD). Knowing the growth rates in the different periods of the treatment, the position of the laser spots made it possible to relate measured elemental ratios to the temperature at any given point in time (Figure 1). Since the entire length of the shell was sampled, we obtained elemental ratios from the three subsequent phases Kiel Fjord (means and variances are shown in Table 2), culture room with constant 6°C and salinity treatment and, finally, with increasing temperature and salinity treatment.

[10] The relative contributions of biotic factors to the elemental ratios (Mg/Ca and Sr/Ca) were quantified (Figure 2) by (1) the mean variance among mean elemental ratios in parts of the shells of all 4 individuals grown in situ where we

assumed environmental conditions to be identical for all individuals,

$$s_{\text{ind}}^2 = \sum_{i=1}^n (\bar{x}_i - \bar{X})^2 / (n - 1), \quad (1)$$

(“individual differences,” where  $n$  is the number of individuals: 4,  $\bar{x}_i$  is the average elemental ratio of the individual  $i$ , and  $\bar{X}$  is the average elemental ratio of all 4 individuals) and (2) the mean variance of elemental ratios of the 4 single individuals over different points in time during the phase of constant abiotic conditions,

$$s_{\text{phys}}^2 = \sum_{i=1}^n \left( \sum_{j=1}^n (x_{ij} - \bar{x}_i)^2 / (n - 1) \right) / n, \quad (2)$$

(the 6°C phase, “physiological variability,” where  $n$  is the number of measurements within one individual  $i$  and  $x_{ij}$  is the elemental ratio of the measure  $j$ ). The influence of abiotic factors was calculated (1) by subtracting the value of the individual differences from the mean variance among the individuals cultured at different salinities during 6°C phase (“salinity”),

$$s_{\text{sal}}^2 = s_{\text{ind}}^2(6^\circ\text{C-phase}) - s_{\text{ind}}^2, \quad (3)$$

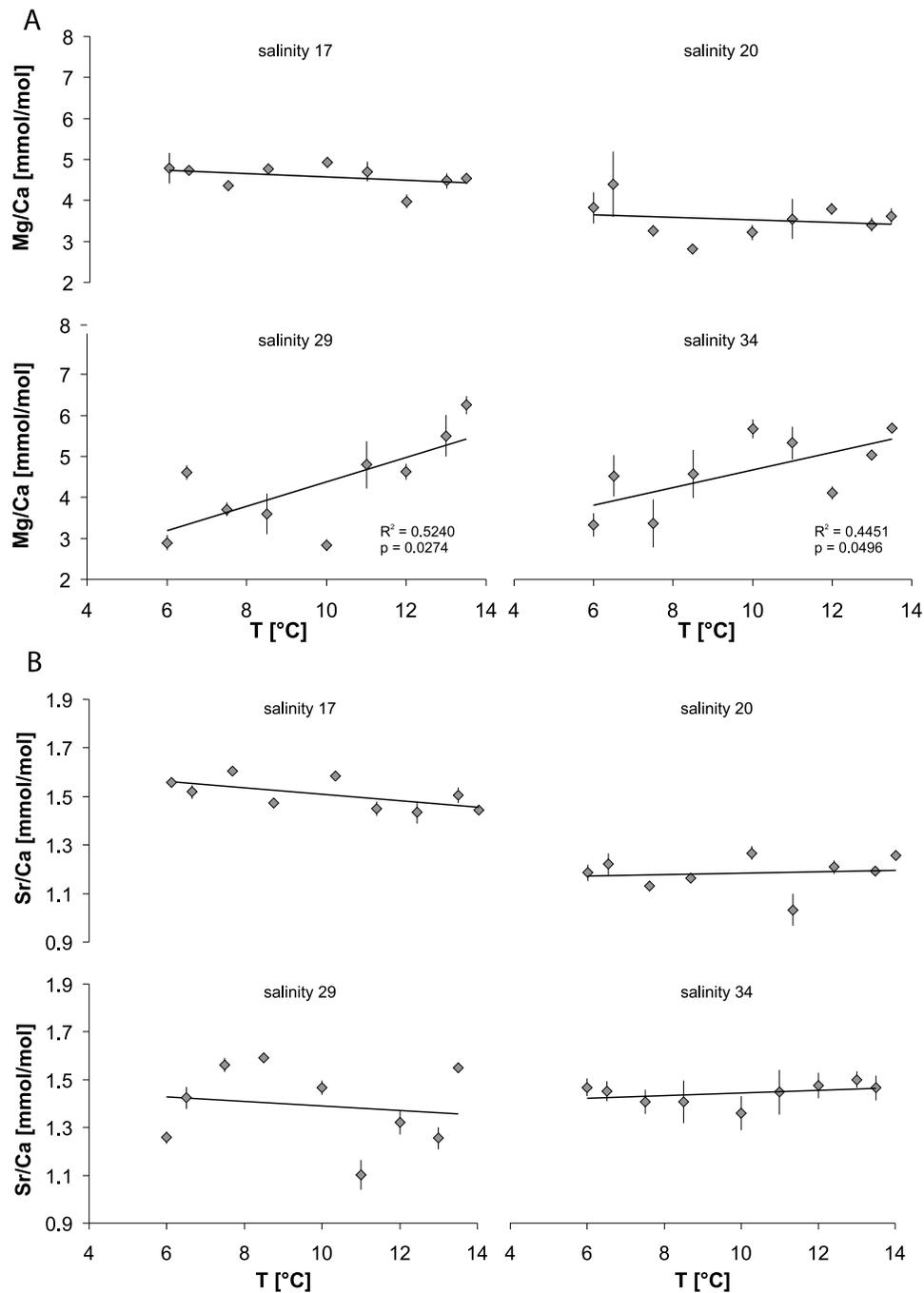
and (2) by subtracting the physiological variability from the average variance over the time while temperature increased (t↑-phase, “temperature”),

$$s_t^2 = s_{\text{phys}}^2(\text{t}\uparrow\text{-phase}) - s_{\text{phys}}^2. \quad (4)$$

To reveal possible significant differences between contributions of different factors (physiological variability, individual differences, temperature, salinity) to the overall variance, we performed multiple  $F$  tests. To reduce the probability of type 1 errors, the significance level ( $\alpha$ ) was Bonferroni-corrected.

### 3. Results and Discussion

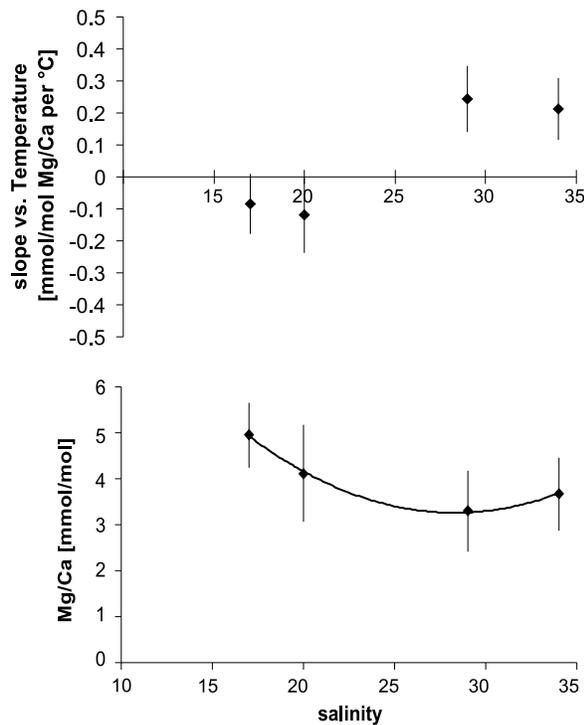
[11] Klein *et al.* [1996a] reported that skeletal Mg/Ca ratios of *Mytilus trossulus* grown in the field provide an accurate measure of temperature and that weekly sea surface temperature may be estimated with an apparent accuracy of approximately  $\pm 1.5^\circ\text{C}$ . In the shells of *M. edulis* individuals cultured at high salinities (29, 34), we also observed Mg/Ca ratios in the calcite layer to be positively related to temperature (Figures 3a and 4). However,



**Figure 3.** (a) Mg/Ca and (b) Sr/Ca ratios of the different salinity treatments in comparison to temperature. Each data point represents the median of all laser spots in the considered part of shell grown of a given temperature period. Errors are given as SE.

this pattern was not found in shells of individuals cultured at lower salinities (17, 20). *Wanamaker et al.* [2008] found a more robust Mg/Ca temperature relationship at salinity 23 and 28 than at higher salinity (32) in their study on Mg/Ca and Sr/Ca ratios in the calcite of juvenile *Mytilus edulis*. They concluded that Mg/Ca and Sr/Ca ratios in juvenile *M. edulis* calcite may possibly be used for

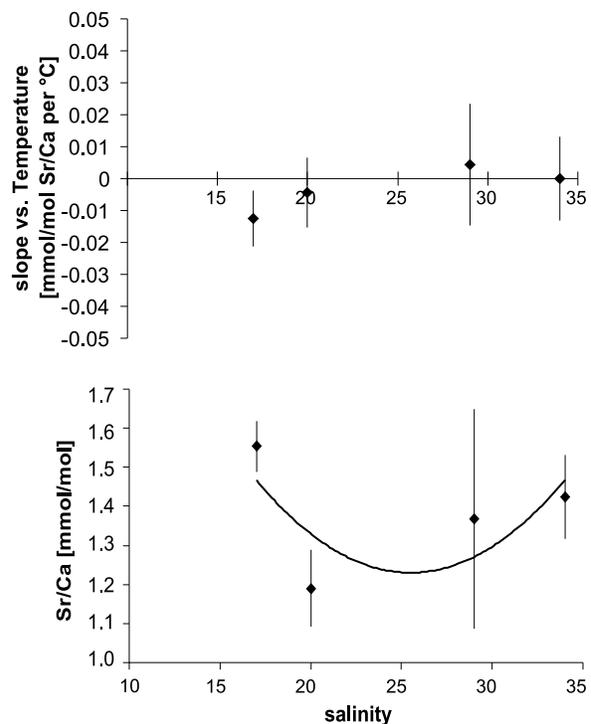
reconstruction of water temperatures from an upper estuarine setting. For mean values of the investigated salinity range (23–32), *Wanamaker et al.* [2008] observed an increase of 6%/°C for Mg/Ca and 1%/°C for Sr/Ca, respectively. The results of Mg/Ca are nearly similar to the results of the overlapping salinity range of this study (29, 34) where a temperature relation of 6.5%/°C was



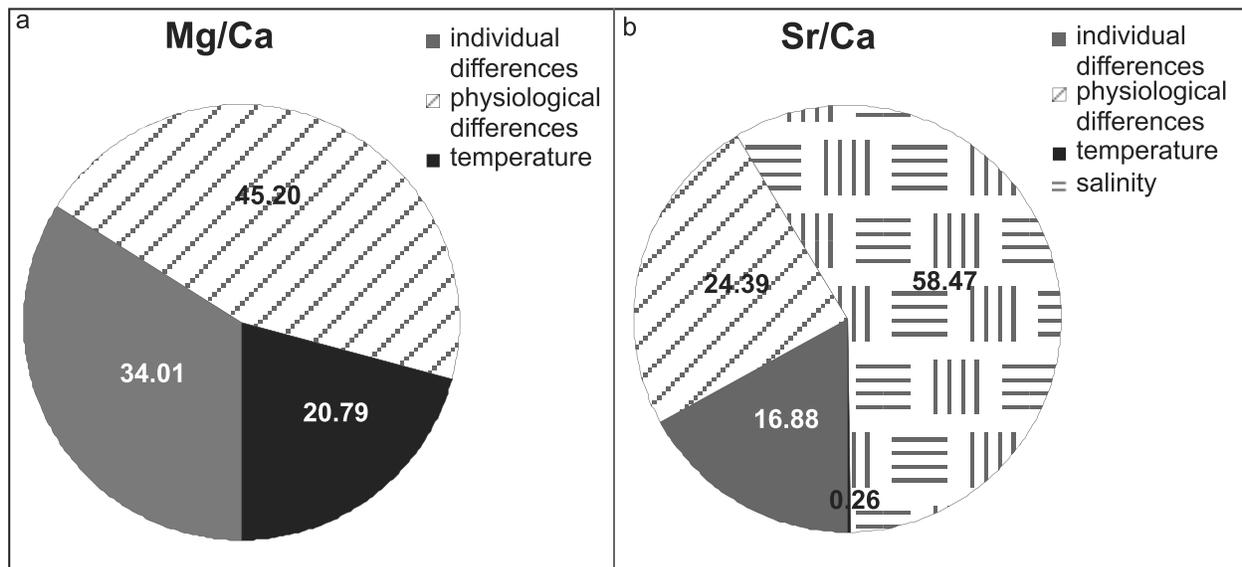
**Figure 4.** Temperature effects on (top) Mg/Ca ratios and (bottom) influence of salinity during constant temperature treatment (6°C). Errors in Figure 4 (top) are given as confidence interval. A nonoverlap between CI bars among each other or with the zero line indicates significant differences. In Figure 4 (bottom), means of one individual per treatment is shown with a typical measurement error (2SD).

found. The different findings for Sr/Ca may be a result of adaptation and/or physiology as our animals originated from a low salinity habitat (~18) the ones cultured by *Wanamaker et al.* [2008] came from a salinity of ~31. Furthermore, we investigated a smaller temperature range of 6°C–14°C in contrast to 7°C–19.3°C. Our results partly correspond with previous findings where Mg/Ca ratios of different taxa are also reported to be influenced by salinity. *Dodd* [1965] showed that the Mg concentration in the outer prismatic layer of *M. edulis* increases markedly with decreasing salinity and that it shows a weak positive correlation with temperature. Further, studies on foraminifera demonstrate that variations in temperature and salinity are reflected in the magnesium content of foraminifera calcite [e.g., *Nürnberg et al.*, 1996]. Their experiments reveal that pronounced salinity changes (>10) at constant temperature significantly affect the Mg concentrations. *Nürnberg et al.* [1996] therefore suggested that Mg may serve as a paleoproxy for past surface water temperatures, as long as salinity variations

and post depositional alterations like carbonate dissolution can be shown to be small or absent. Our results likewise show that temperature interacts with other factors influencing Mg/Ca ratios in the shell of *M. edulis*. Strikingly, individual differences among mussels (34.0%) living under similar environmental conditions and temporal variability within individuals in constant environmental conditions (45.2%) contribute a substantially higher proportion to the overall variance of the Mg/Ca ratio than temperature does (20.8%) (Figure 6a). As the influence of the physiological state of the bivalves on Mg/Ca incorporation into bivalve shells is likely to vary with environmental fluctuations as well as growth and reproductive cycles, food availability, fouling or infection rates, our findings may explain the absence of a consistent Mg/Ca-temperature relationship over the year in *M. edulis* calcite observed by *Vander Putten et al.* [2000]. Additionally, as variances of Mg/Ca ratios among individuals decreased after placing the mussels into different salinity treatments relative to variability of Mg/Ca in shell parts grown in nature



**Figure 5.** Temperature effects on (top) Sr/Ca ratios and (bottom) influence of salinity during constant temperature treatment (6°C). Errors in Figure 5 (top) are given as confidence interval. A nonoverlap between CI bars among each other or with the zero line indicates significant differences. In Figure 5 (bottom), means of one individual per treatment is shown with a typical measurement error (2SD).



**Figure 6.** Influence of individual differences, physiological state, salinity, and temperature on (a) Mg/Ca and (b) Sr/Ca ratios in the prismatic layer of *M. edulis* shells. Salinity contribution on Mg/Ca was not detectable.

indicates that a putative salinity effect on Mg/Ca is smaller than interindividual differences in a fluctuating natural environment. Consequently, no influence of salinity on the Mg/Ca ratio which was strong enough to emerge from the biological background “noise” could be detected. While Mg/Ca tended to be highest in the two low salinity treatments individuals’ shells (SAL 17 and 20, Figure 4), partly corroborating Dodd’s [1965] results a reliable Mg/Ca-salinity effect was not apparent.

[12] Sr/Ca ratios in *M. edulis* shells were not significantly affected by temperature (Figures 3b, 5, and 6b). The temperature contribution to the overall variance (0.3%) was significantly smaller than the contribution of physiological state (24.4%), individual differences (16.9%) and salinity (58.5%) (*F* test,  $p < 0.0001$ ). Therefore, we cannot corroborate findings of Dodd [1965] who found that the strontium concentration in *M. edulis* calcite correlates positively with temperature. Instead, we found the salinity treatment to have the highest impact on Sr/Ca (58.5%, Figure 6b). We observed the highest Sr/Ca value in the shell grown at the lowest salinity (SAL 17). However, no significant Sr/Ca-salinity relationship was detected (Figure 5).

#### 4. Conclusion

[13] We observed relations between Mg/Ca ratios and temperature in two of the measured *Mytilus edulis* shells. Still, biological control (physiological state and individual differences) has a dominant

influence (~79% contribution to overall variance on Mg/Ca and ~41% contribution on Sr/Ca) on the elemental ratios in *M. edulis* shells. This can be taken as a likely reason for the large discrepancies in the discussions whether carbonates of bivalve shells can be used as proxy archives. It appears that mussel carbonate can only be used as a proxy archive if the combination of environmental conditions and the major contribution of biology are considered. Therefore, the data stress the importance of replicating at the biological level, i.e., measure several animals from the same location and time, even though this drastically increases the measuring effort.

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