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Baseline

Biogeographic vulnerability to ocean acidification and warming in a marine bivalve

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ABSTRACT

Anthropogenic CO_2 emissions are rapidly changing seawater temperature, pH and carbonate chemistry. This study compares the embryonic development under high pCO_2 conditions across the south-north distribution range of the marine clam *Limecola balthica* in NW Europe. The combined effects of elevated temperature and reduced pH on hatching success and size varied strongly between the three studied populations, with the Gulf of Finland population appearing most endangered under the conditions predicted to occur by 2100. These results demonstrate that the assessment of marine faunal population persistence to future climatic conditions needs to consider the interactive effects of co-occurring physico-chemical alterations in seawater within the local context that determines population fitness, adaptation potential and the system resilience to environmental change.

Anthropogenic carbon dioxide emissions are rapidly changing seawater pH and carbonate chemistry at global scales with vast repercussions on marine biodiversity and ecosystem functioning (Dupont and Portner, 2013). Meta-analysis (Kroeker et al., 2013) revealed that the early life stages of mollusks are particularly vulnerable to ocean acidification. Disruption of physiological processes and altered mineral kinetics associated with low carbonate saturation states and low pH in high pCO_2 waters hinder the ability to normally develop shells during the pelagic larval development phase and increase dissolution mortality during the early settlement phase (Waldbusser et al., 2015a; Waldbusser et al., 2015b). Hence exposure of early life stages of mollusks to ocean acidification may represent a bottleneck for their populations. Yet, evidence exist that the magnitude of acidification effects on marine biota might strongly depend on the local environmental context such as temperature and food availability (Kroeker et al., 2013; Thomsen et al., 2013), as well as on the potential for local adaptation (Calosi et al., 2017). In this study we compared the embryonic development under combined conditions of seawater pH and temperature predicted for 2100 (IPCC, 2014) between different clades of the benthic tellinid bivalve *Limecola* (*Macoma) balthica* that occur across the coastal south-north range of the species in northwestern Europe.

Previous work on *L. balthica* demonstrated the presence of at least three divergent mitochondrial clades in northwestern Europe (Saunier et al., 2014), from which adult organisms were sampled in this experiment (Table 1): a Baltic lineage, and a southern and northern Atlantic lineage that are separated by the French Finistère peninsula. The low saline water at the subtidal sampling location in the Gulf of Finland (6 PSU) had lower buffering capacity to change in seawater carbonate chemistry (total alkalinity = 1.47 $\mu mol \cdot kg^{-1}$ ± 0.03 SD; Gran titration (Dickson et al., 2007), n = 6 per location) as compared to the two intertidal sampling locations along the NE Atlantic coast (Gulf of Biscay and southern North Sea TA = 2.35 $\mu mol \cdot kg^{-1}$ ± 0.02 SD and 2.48 $\mu mol \cdot kg^{-1}$ ± 0.04 SD, respectively). The experiments were performed in February 2014 (northern Atlantic lineage; SST = 5.7 °C), March 2014 (southern Atlantic lineage; SST = 10.6 °C) and May 2014 (Baltic lineage; SST = 6.5 °C). About 120 adults of each population were induced to spawn in 0.2 µm filtered seawater from the study area following the procedures described in (Van Colen et al., 2009). Spawning success and egg production per female varied among populations with the highest reproductive output for the southern North Sea population (Table 1). After 3 h of gamete fertilization under ambient seawater pH (Bay of Biscay, southern North Sea, Gulf of Finland: 8.14, 7.89, 8.04 respectively) and a temperature of 15 °C, embryos were transferred to 5 replicate 58 mL vials containing 0.2 µm filtered seawater that was conditioned to different carbonate chemistry (Table 2) and temperature, i.e. 15 °C and 18 °C. The 15 °C treatment represents

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Table 1
Characteristics of the sampling location and parental properties of the studied populations. Condition index is determined as shell-free dry weight·shell dry weight^{-1} in mg g^{-1} from 15 individuals per population. Mud content is taken from (Du et al., 2017)* and (Van Colen et al., 2010)** and calculated from 4 replicate samples collected at Storfjärden. Error bars denote standard deviations.

Sampling location			
Region	Gulf of Biscay	Southern North Sea	Gulf of Finland
Sampling site	Aytré	Schelde, Paulina	Storfjärden
Coordinate	46.13 N, 1.13 W	51.34 N, 3.72E	59.84 N, 22.44E
Mud content (% < 63 μm)	37.33*	30.9**	92.2
Parental properties			
Mitochondrial lineage	Southern NE Atlantic	Northern NE Atlantic	Baltic
Condition index	118.60 ± 6.75	108.78 ± 7.62	112.94 ± 6.87
Spawning success (%)	4.3	31.4	7.6
Egg production·spawning female^{-1}	22,222	13,615	3051

Table 2
Average pH (NBS scale), partial pressure of CO_2 (pCO_2 in μatm), carbonate ion concentration (CO_3^{2-} in μmol·kg^{-1}) and saturation state of the water regarding calcite ($\Omega_{calcite}$) during the 72 h incubations (salinity Bay of Biscay, southern North Sea, Gulf of Finland: 32, 31, 6 PSU respectively).

Population	15 °C				18 °C			
	pH	pCO_2	CO_3^{2-}	Ω_c	pH	pCO_2	CO_3^{2-}	Ω_c
Bay of Biscay	8.09	365.8	168.6	4.1	8.07	440.3	162.3	4.0
	8.02	443.5	146.8	3.6	7.99	548.0	138.3	3.4
	7.92	576.9	120.3	2.9	7.88	721.8	111.8	2.7
	7.82	769.1	95.6	2.3	7.79	932.0	90.9	2.2
	7.73	956.4	79.7	1.9	7.70	1165.7	75.3	1.8
	7.61	1314.5	60.5	1.5	7.60	1522.5	59.7	1.5
Southern North Sea	7.80	848.2	95.7	2.3	7.79	996.7	93.4	2.3
	7.70	1099.3	76.9	1.9	7.68	1303.7	74.4	1.8
	7.62	1350.3	64.3	1.6	7.59	1666.6	59.9	1.5
	7.51	1836.3	48.8	1.2	7.48	2179.9	47.0	1.2
	7.45	2103.1	43.1	1.1	7.43	2477.7	41.8	1.0
	7.35	2716.5	34.0	0.8	7.34	3066.0	34.4	0.8
Baltic Sea	7.87	680.5	23.9	0.7	7.84	805.1	23.1	0.7
	7.78	849.8	19.4	0.6	7.73	1056.3	17.9	0.5
	7.67	1122.5	14.9	0.4	7.63	1367.3	14.0	0.4
	7.58	1410.0	12.0	0.3	7.56	1629.5	11.8	0.3
	7.52	1632.8	10.4	0.3	7.49	1905.3	10.1	0.3
	7.44	1969.6	8.6	0.2	7.41	2300.1	8.4	0.2

the seawater temperature during the temporal pelagic occurrence of the larvae in the three regions (Gilbert, 1978) and the latter temperature reflects a 3 °C increase by 2100 according to IPCC RCP 8.5 (current emission trajectory) model prediction (IPCC, 2014). Seawater carbonate chemistry was manipulated through bubbling with pure CO_2 decreasing pH in a stepwise fashion of ~0.1 pH units down to ~0.5 pH units below ambient conditions covering the variability in predicted pH conditions by 2100 according to IPPC models (IPCC, 2014) and the even more acidic conditions expected to occur in coastal regions (Wootton et al., 2008; Provoost et al., 2010). Density of embryos was 10 mL^{-1} for the Gulf of Finland population and 15 mL^{-1} for the two other populations. Embryonic development was stopped after 72 h by adding 1 mL of a neutralized 4% formaldehyde–tap water solution to the culture. Hatching occurs within the first three days of development [personal observations] and hatching success was defined accordingly as the proportion of embryos that developed a D-shaped shell after 72 h. During the incubations respiration caused pH to decrease (Δ pH Bay of Biscay: −0.06 ± 0.02SD (15 °C), −0.14 ± 0.01SD (18 °C); Δ pH southern North Sea: −0.17 ± 0.05SD (15 °C), −0.22 ± 0.07SD (18 °C); Δ pH Gulf of Finland −0.25 ± 0.08 SD (15 °C), −0.31 ± 0.09 (18 °C)). pH values reported in this study were therefore calculated as the average of the pH at the start and end of incubation. All parameters of the carbonate chemistry were determined from pH_{NBS}, TA_{NBS}, temperature and salinity using CO_2SYS (Pelletier et al., 2007).

The regional difference in ambient pH and the variable pH change during the incubation resulted in a gradient of tested pH conditions (Fig. 1, Table 2). Simple linear regression models were used to determine the influence of pH on hatching success and median size of embryos. Extreme outliers were excluded from the analysis to achieve normality of residuals (casewise plot of residuals ± 3 sigma; Statistica 5.5). Subsequently, the effects of pH and temperature were analyzed through a series of regression slope comparisons. First, a homogeneity of slopes model was calculated to analyze whether the pH (i.e. continuous predictor) and temperature (i.e. categorical predictor) interacted in influencing hatching success and size. Subsequently a separate slopes model was applied when both predictors interacted, while analysis of covariance (ANCOVA) was applied when both predictors did not interact in affecting hatching success and size (Statistica 5.5).

Hatching success under control conditions (15 °C and ambient pH) varied significantly across populations with a higher number of developed D-shaped shelled larvae in the Bay of Biscay population (70 ± 3 SE %) as compared to the southern North Sea (22 ± 3 SE %) and Gulf of Finland population (39 ± 2 SE %) (Kruskal-Wallis rank sum test: $H(2) = 11.57$, $p = 0.003$). Decreasing seawater pH significantly reduced hatching success in all populations ($p < 0.001$), but an antagonistic temperature × pH interaction effect was observed in the Bay of Biscay population (Separate slopes model: temperature × pH $F_{2, 51} = 31.586$, $p < 0.001$) whereas the pH effect on hatching success was independent of temperature in the southern North Sea and Gulf of Finland population (Fig. 1, upper panel). For the southern North Sea population a higher hatching success was observed at 18 °C as compared to 15 °C (ANCOVA: pH $F_{1, 57} = 45.66$, $p < 0.001$; temperature $F_{1, 57} = 13.85$, $p < 0.001$), whereas temperature did not affect hatching success in the Gulf of Finland population (ANCOVA: pH $F_{1, 57} = 131.86$, $p < 0.001$; temperature $F_{1, 57} = 1.24$, $p = 0.974$). The size of hatched embryos under control conditions varied significantly across populations with a larger size in the southern North Sea population (141 ± 2 SE μm) as compared to the Bay of Biscay (136 ± 0.8 SE μm) and Gulf of Finland population (122 ± 0.5 SE μm) (Kruskal-Wallis rank sum test: $H(2) = 12.02$ $p = 0.003$). Hatching size in the Bay of Biscay population did not vary significantly among pH levels for both tested temperatures (Kruskal-Wallis rank sum test: 15 °C $H(5) = 1.70$, $p = 0.889$; 18 °C $H(5) = 10.20$, $p = 0.069$). In contrast, the size of hatched embryos in the southern North Sea and Gulf of Finland population decreased significantly with decreasing pH with the smallest sizes found in calcite-