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ORIGINAL PAPER

Low salinity is associated with reduced size and altered shell thickness and shape in the lagoon cockle, *Cerastoderma glaucum*, in the Baltic Sea

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Abstract

Calcifying bivalves account for >80% of the total macrozoobenthic biomass in the southern Baltic Sea. Salinity declines from around 30 in the western Kattegat to 7 in the central Baltic Proper providing a natural gradient along which to investigate the impact of lowering salinity on shelled organisms. Low salinity conditions constrain biomineralisation with limited calcification substrates and periods of aragonite undersaturation. For species with wholly aragonitic shells like the cockle, *Cerastoderma glaucum*, shell maintenance and production can be challenging. While studies have investigated the corrosive effects of ocean acidification on calcifying organisms, few have considered the long-term consequences of low salinity. This study investigated the shell characteristics of *C. glaucum* sampled in 2016 and 2024–25 along the southern Baltic salinity gradient to examine variations in shell thickness, shape and condition. Comparisons were made with populations sampled from coastal lagoons in 2024–25 (UK and France) where seasonal salinity fluctuations are significant (<20 to >40). This comparative study revealed Baltic populations of *C. glaucum* exposed to salinities of <10 to produce shells that are up to 85.2% thicker than populations in more variable environments. However, their size is limited to lengths of 20 mm, around 58% of the usual length achieved by individuals in salinities of >10. Integral to survival, the shell offers protection from predation and adverse ambient conditions. Ocean freshening poses significant threats to biomineralisation and understanding the response of calcifying species to low salinity is fundamental for assessing their adaptive capacity to future projections of declining salinity.

Keywords Biomineralisation · Dissolution · Mollusc · Periostracum · Calcite · Brackish

Introduction

As one of the world's largest brackish water basins, the Baltic Sea offers a unique and natural laboratory for the examination of a salinity gradient. The Baltic Sea has been brackish for around 7000 years and stabilised at its current mean salinity of 7.4 approximately 2000 years ago (Meier et al. 2022). The semi-enclosed, nontidal basin has a limited exchange of seawater with the North Sea through the Danish Straits, and dominant freshwater input from river runoff and precipitation (Kniebusch et al. 2019; Stockmayer and Lehmann 2023). Across the 100 km transitional zone from the Kattegat to the central Baltic Proper, salinity drops rapidly from around 30 to 7, and reaches 2–4 in the northern Gulf of Bothnia (Schneider and Müller 2017; Szymczycha et al. 2019). The estuarine-like properties of the Baltic Sea contribute significantly to its biological diversity, supporting low species richness, and being characterised by euryhaline, opportunistic species (Leppäkoski et al. 2002; Zettler et al. 2007). The Baltic taxa also include Arctic relicts from the last glaciation period that became permanent residents after the connection with the White Sea was lost (Vuorinen 2018). Other species have invaded over its short evolutionary

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history from the adjacent North Sea and coastal freshwater habitats, but many niches remain available for colonisation (Jansson and Jansson 2002; Bonsdorff 2006).

Brackish conditions are energetically demanding and require significant osmotic regulation, which have detrimental effects on reproduction, growth and survival (Smyth and Elliott 2016; Peteiro et al. 2018; Park et al. 2020; Domínguez et al. 2020; Vázquez et al. 2021; Röthig et al. 2023; Barrett et al. 2025). A simultaneous and gradual decrease in the biodiversity of marine species is observed along the Baltic salinity transition as conditions reach beyond species environmental tolerance limits, while the taxonomic diversity of freshwater species increases (Zettler et al. 2007, 2014; Ojaveer et al. 2010). Species richness is estimated to be 3.7 times lower in the low salinity Baltic Proper than in the more saline waters of the Kattegat (Ojaveer et al. 2010). The euryhaline fauna and flora exploit their ability to tolerate the challenging conditions, often producing large populations (Smyth and Elliott 2016). Molluscs occupy a large proportion of the total species diversity, with high numbers of marine and freshwater bivalves and gastropods (Bonsdorff 2006; Zettler et al. 2007, 2014; Gogina et al. 2016). Bivalves alone account for over 80% of the total macrozoobenthic biomass in the southern Baltic (Warzocha 1995; Kube et al. 1996), and provide key ecological functions as important food sources for molluscivorous invertebrates and fish, and nutrient cycling (Westerbom et al. 2002; Järv et al. 2011; Nurkse et al. 2016; Vaughn and Hoellein 2018). *Macoma balthica* (Baltic clam), *Mya arenaria* (soft-shell clam) and *Cerastoderma glaucum* (lagoon cockle) have wide spatial distributions across Europe and are dominant in the bivalve community of the Baltic Sea (Warzocha 1995; Darr et al. 2014; Gogina et al. 2016; Schade et al. 2016).

The cockle, *C. glaucum*, is a filter-feeding bivalve with a distribution from Norway to North Africa. It has an habitual preference for sheltered, nontidal coastal lagoons, and is commonly referred to as the 'lagoon cockle' (Boyden and Russell 1972; Malham et al. 2012). It is the congener of *Cerastoderma edule*, the widely exploited edible cockle found in the shallow subtidal and intertidally on European coastlines (Malham et al. 2012). The ribbed shell of *C. glaucum* is made wholly of aragonite, which is protected by an insoluble organic coating known as the periostracum on the external shell surface (Taylor and Kennedy 1969). *C. glaucum* can tolerate salinities ranging from around 5 to more than 70 (Boyden and Russell 1972; Barnes 1980) and its success in the Baltic Sea is unsurprising given the parallels with lagoon environments. Coastal lagoons are hydromorphically similar and brackish in nature, with limited seawater input through narrow channels or percolation across a natural barrier, and significant freshwater sources from terrestrial runoff and precipitation (Barnes 1980). High nutrient loads from rivers drive high levels of primary productivity (Szymczycha et al. 2019), but limited water exchange and high residence times of the water masses make these environments vulnerable to eutrophication and concomitant anoxia (Barnes 1991; Szymczycha et al. 2019; Meier et al. 2022). An interesting distinction between the two environments, however, are the salinity dynamics. Characteristically shallow (less than 2 m in depth), isolated and of small size (Bamber et al. 1993), coastal lagoons can experience significant seasonal fluctuations in salinity. Hot, dry summers promote hypersaline conditions through evaporation, while wet, stormy winters drive down the salinity with acute freshwater input (Barnes 1980; Kennish and Paerl 2010). Coastal lagoons in the UK commonly record winter salinities of less than 20 versus summer salinities of more than 35–40. Although small but significant decadal variability in salinity has been observed in regions of the Baltic (Meier et al. 2022; Stockmayer and Lehmann 2023), overall changes have been minimal. For example, long-term freshening in the northern Baltic Sea has led to a decline in salinity ranging from 0.31 to 1.14 (Kankaanpää et al. 2023).

Through natural selection and prolonged exposure, organisms like those inhabiting coastal environments have adapted to endure the physiological constraints imposed by low and variable salinity conditions through euryhalinity (Lockwood 1976; Wrange et al. 2014; Kijewska et al. 2016; Knöbel et al. 2021; Zhou et al. 2023). Marine calcifiers that biomineralise an external skeleton, like bivalves, face additional stressors for shell building and maintenance. Depleted levels of calcium [Ca^{2+}] and bicarbonate [HCO_3^-] ions constrain shell construction, while calcium carbonate is undersaturated which increases the dissolution of unprotected shells once they are formed (Thomsen et al. 2018; Sanders et al. 2018, 2021). Offering protection to the soft-bodied dweller from predators and unfavourable ambient conditions, biomineralised skeletons are vital to survival. Shell-building organisms have shown the potential to induce compensatory mechanisms, such as altering their microstructural composition (Araujo et al. 2014; Telesca et al. 2019), increasing shell or periostracum thickness (Harper 1997), or modifying biomechanical properties (Telesca et al. 2024), to resist the corrosive conditions of ocean acidification and low salinity.

Anthropogenic climate change introduces uncertainty to the future functioning of coastal and marginal marine ecosystems. Global temperatures continue to rise, and the duration of heatwaves is increasing, with significant impacts on Earth's systems. End-of-century predictions project the sea surface temperatures of the Baltic to increase by 1.2 °C under the low-emission scenario (RCP 2.6) and by 3.3 °C under the high-emission scenario (Zalewska et al. 2024). Warmer air holds significantly more moisture (7% increase for every 1 °C of warming), leading to more frequent and intense precipitation and storm events (Semmler and Jacob 2004; Trenberth 2011; Liu et al. 2020). Oceans receive 80% of global rainfall, contributing substantially to decreasing sea surface salinities in precipitation-dominant temperate, polar and tropical regions (Durack et al. 2012). By 2100, the salinity of the Baltic Sea is predicted to decrease by an average of 0.6 (Lehmann et al. 2022). Already at the lower threshold for most euryhaline species, a reduction in salinity is likely to significantly impact species ranges and survival (Westerbom et al. 2018).

Environmental stressors can strongly influence the phenotypic traits of biomineralised shells. Temperature has been identified as a primary driver of shell shape (Telesca et al. 2018; Mayk et al. 2022a), while ocean acidification and low salinity have been shown to drive compensatory increases in shell thickness (Cross et al. 2019; Mayk et al. 2022b; Telesca et al. 2024). Other stressors, including food availability, eutrophication and predation, also significantly influence the shell traits of marine calcifiers (Smolarz and Bradtke 2011; Telesca et al. 2018; Johnson 2020; Morán et al. 2022; Mayk et al. 2022b). Environmental heterogeneity is a key driver of significant spatial variation in shell morphology. This comparative study examines the shell characteristics of *C. glaucum* across salinity regimes to determine whether: (i) *C. glaucum* exhibits any compensatory macro- or microstructural responses to low salinity; (ii) shell dissolution is greater under sustained low salinity conditions; and (iii) salinity is associated with variations in shell geometric morphology. Improving our understanding of the long-term effects of low salinity exposure may help when predicting the effects of future ocean freshening on biomineralising marine invertebrates.

Materials and methods

Sites and the collection of specimens

Adult *C. glaucum* specimens ranging approximately from 1 to 3 years of age were collected from six sites along the southern coastline of the Baltic Sea, covering approximately 550 km and a salinity gradient ranging from around 15 in Odense Fjord (55°27’07.5"N 10°29’44.4"E) to less than 7 in the Gulf of Gdańsk (Ujście Wisły: 54°22’09.2"N 18°57’01.2"E), and five coastal lagoons, including one hypersaline lagoon located in the south of France and four UK lagoons of variable salinity regimes (Fig. 1; Table 1). Baltic specimens were collected in the years of 2016 and 2024/2025 by dredging on cruises carried out by the Department of Oceanography at the University of Gdańsk (r/v Oceanograf) and the Institute of Oceanology of the Polish Academy of Sciences (r/v Oceania). Water was collected with a Go-Flo Niskin water sampler (5 dm^3) to measure salinity onboard using a Multi-Parameter Portable Meter WTW MULTI 3620 IDS SET C equipped with a WTW TetraCon® 925 Conductivity Cell. A total of 607 specimens were stored frozen, then processed by removing the soft tissue and drying at 55 °C. A total of 245 specimens were collected from coastal lagoons in the UK and France during 2024 and 2025 by hand picking individuals off the substratum surface or sieving. Salinity and temperature were recorded on the day of collection using a handheld salinity tester accurate to ± 1.0 (HI-98319, Hanna Instruments).

Variations in shell characteristics were examined among three different systems. Group 1 included specimens collected in 2024/5 from Mechelinki – Rewa, Gulf of Gdańsk (MECH), Redłowo station, Gulf of Gdańsk (GDA) and the Southern Middle Bank (SMB) to examine variations on a small spatial scale within the Baltic Proper with a minimal salinity range of 6.0–8.0. Group 2 collections were made in 2016 and examined a transect along the southern Baltic from Odense Fjord (ODE), Denmark to the mouth of the Vistula River (UJW), Poland, across a salinity gradient (15.0–3.0). Group 3 compared *C. glaucum* from the Baltic Proper (Group 1) with specimens from coastal lagoons in the UK and France collected in 2024/5. Although UJW is in the Baltic Proper it was not included in Group 1 to avoid confounding environmental noise because of different collection years (2016 vs. 2024/5). Lagoons were selected to capture a representative spectrum of these dynamic systems and are outlined in Table 1.

Shell size and condition

Length (L), width (W) and height (H) of articulated valves were measured using digital callipers to 0.1 mm precision and each right valve weighed using digital scales to an accuracy of 0.001 g. Due to the ribbed ornament of *C. glaucum* and the difficulties this presents for measuring shell thickness accurately, a shell thickness index was calculated using the equation outlined by Freeman and Byers (2006):

$$\mathit{Shell\ thickness\ index} = 1000 \times \ \mathit{dry\ shell\ weight} \div \left[L \times \left(H^2 \times W^2\right)^{0.5} \times \frac{\pi}{2}\right]$$

Shell thickness index was used as a proxy for absolute shell thickness in all statistical analyses, where a high shell thickness index indicates a thicker shell and a low shell thickness index indicates a thinner shell. This method has been considered to be a suitable measure of shell thickness in several classes of bivalve species (Fitzer et al. 2015; Mele et al. 2023; Babarro et al. 2023).

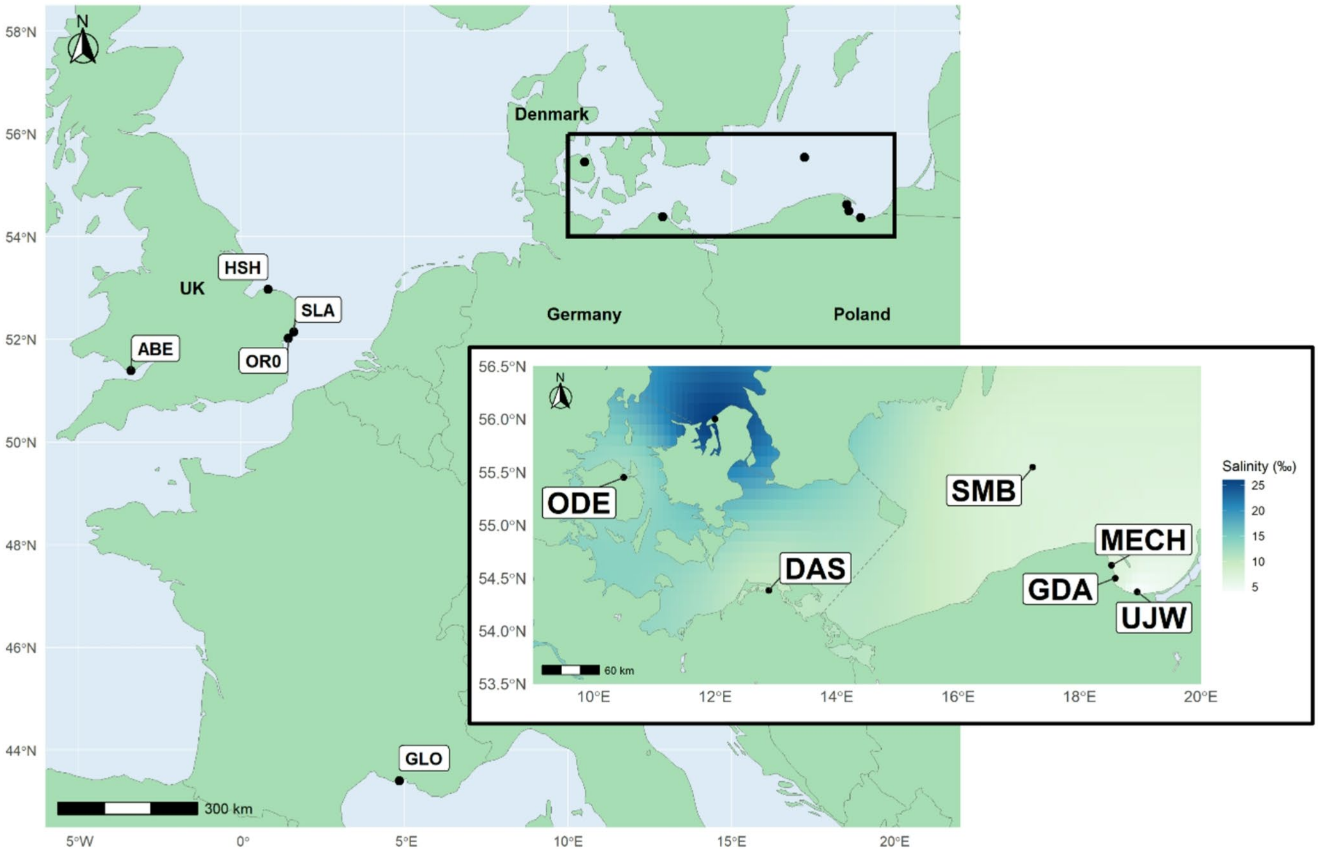

Fig. 1 Map showing sites sampled for *Cerastoderma glaucum*. Insert of the southern Baltic Sea with sea surface salinity gradient. Specimens were collected from across the Baltic Sea salinity gradient (DAS, Darß-Zingst-Bodden Chain; GDA, Redłowo station; MECH, Mechelinki – Rewa; ODE, Odense Fjord; SMB, Southern Middle Bank; and UJW, Ujście Wisły, mouth of the Vistula) and coastal lagoons with variable salinities (ABE, Aberthaw lagoon; GLO, Bassin du Gloria; HSH, Holkham Salts Hole; OR0, Shingle Street lagoon 0; and SLA, Slaughden). See Table 1 for full details

Structural characterisation

Examination of dissolution extent

Scanning electron microscopy (SEM) was carried out on a Zeiss EVO HD15 at the Sainsbury Laboratory, University of Cambridge, UK, to examine the external and internal surfaces of shells collected from MECH in 2024. Single valves of specimens that were alive ($n = 2$) and deceased ($n = 2$) on collection were selected to compare both the in vivo and postmortem condition of the periostracum and extent of mineral dissolution. Shell valves were fragmented, ultrasonicated, mounted on aluminium stubs and gold coated. SEM micrographs were collected of all fragment surfaces for analysis. Shell surfaces of *C. glaucum* collected from two variable but generally low salinity UK coastal lagoon systems (ABE and SLA) were also imaged to compare dissolution extent between shells exposed to salinities consistently less than 10 and those exposed to variable hyposaline conditions.

Organic content analysis

Thermogravimetric analysis (TGA) was used to estimate the weight proportion (wt%) of the organic matrix within the crossed-lamellar part of the microstructure. Four specimens from MECH were selected for analysis. Periostracum was removed by sanding, and fragments of shell were taken from along the ventral margin (outside of the pallial line) using a Dremel MultiPro® 395 rotary tool with a 3.2 mm drill bit. Shell fragments were ground using a pestle and mortar, and 10 mg samples were tested using a thermal analyser (Discovery SDT650, TA Instruments) at the Department of Material Sciences and Metallurgy, University of Cambridge, UK, following the procedure outlined in Telesca et al. (2019). The wt% of organic content was estimated by calculating the proportion of weight loss between 150 °C and 550 °C. The organic content of MECH was compared to the previously measured average organic content of *C. glaucum* from eight coastal lagoons using the same methods.

Table 1 Summary of sample sites

Site	Location	Year (*n*)	Depth (m)	Latitude	Longitude	Collection salinity	Salinity variability
Group 1: Baltic Proper							
GDA	Redłowo station, Gulf of Gdańsk, Poland	2025 (107)	10	54.49853	18.58417	7.5	6.0–8.0
MECH	Mechelinki – Rewa, Gulf of Gdańsk, Poland	2024 (302)	9	54.62061	18.52738	6.8	
SMB	Southern Middle Bank, Baltic Sea	2025 (37)	37	55.54828	17.22831	7.6	
Group 2: southern Baltic gradient							
DAS	Darß-Zingst-Bodden Chain, Germany	2016 (60)	2.3	54.38333	12.88333	8.8	3.4–9.0
MECH	Mechelinki – Rewa, Gulf of Gdańsk, Poland	2016 (34)	9	54.62061	18.52738	7.7	6.0–8.0
ODE	Odense Fjord, Funen, Denmark	2016 (55)	2	55.45208	10.49566	8.4	10.0–15.0
UJW	Ujście Wisły, mouth of the Vistula River, Gdańsk, Poland[a]	2016 (12)	14	54.36922	18.95033	7.3	3.0–8.0
Group 3: constant[b] vs. varied salinity							
ABE	Aberthaw lagoon, Wales, UK	2024 (43)	0.25	51.385278	-3.384361	14.6	11.0–15.0
GLO	Bassin du Gloria, Marseille, France	2024 (16)	0.25	43.40247	4.831639	63.4	>35.0 to >60
HSH	Holkham Salts Hole, Norfolk, UK	2024 (54)	0.5	52.96972	0.8075	21.9	17.9–24.3
OR0	Shingle Street lagoon 0, Suffolk, UK	2023 (58)	0.5	52.01724	1.436592	31.8	25.1–39.2
SLA	Slaughden, Suffolk, UK	2024 (148)	0.5	52.14408	1.598667	15.3	7.3–25.4

[a] Since the exact depth and geographic coordinates of the specimens collected from UJW are unknown, we used average depth and coordinates taken from Google Maps at the mouth of the Vistula River; [b] Group 1 reflects sites of constant salinity in analyses. Collection salinity is the salinity recorded on the day specimens were collected. Seasonal salinity variability for Group 1 was obtained from the European Union-Copernicus Marine Service (2018). For Group 2, data sources were Schumann et al. (2023) for DAS, Riisgård et al. (2008) for ODE, and the European Union-Copernicus Marine Service (2018) for MECH and UJW. For Group 3, salinity data at UK lagoons were collected intermittently throughout the year for this project, and variability at GLO was obtained from the European Union-Copernicus Marine Service (2018)

Periostracum thickness

The thickness of the periostracum on the shell surface of five specimens each from MECH, SLA and ABE was measured from scanning electron micrographs to the nearest 0.1 µm using ImageJ software (Schneider et al. 2012).

Morphology

A Fourier shape analysis was used to assess variations in shell shape across the three groups (Group 1 [GDA, MECH, SMB], $n=65$; Group 2 [DAS, MECH, ODE, UJW], $n=76$; Group 3 [ABE, GDA, GLO, HSH, MECH, OR0, SLA, SMB], $n=201$). Images of individual right valves were made using a flatbed scanner (Konica Minolta bizhub c451i) and processed in GIMP (GNU Image Manipulation Program, https://gimp.org). Images were grey-scaled, and a threshold was applied to create well-defined outline boundaries of the shell shape. Two-dimensional outline contours of these boundaries, traced clockwise, were obtained using the imager package on R (Barthelme et al. 2025). Fourier coefficients were computed and manipulated using the suite of programmes, Hangle, Hmatch and Hcurve, developed by Crampton and Haines (1996). The digitised xy-coordinates were used as input data into Hangle to obtain 15 Fourier coefficients (harmonics) derived from the contours. During this process, outlines were smoothed to reduce "noise" and standardised for size to ensure the shape results were not dominated by size differences (Crampton and Maxwell 2000). Hmatch was used to standardise starting positions across populations using the umbo and determined by the highest xy-coordinate. The normalised Fourier coefficients were then extracted and used as variables to quantify the geometric morphology of specimens. Hcurve was used to inversely transform Fourier coefficients and generate a series of xy-coordinates and tangent angles. This allowed the reconstruction of synthetic outlines, which were useful for establishing an average population shape and to decipher shape variations within the morphometric space of principal component analyses (PCAs).

Multivariate analysis of shell shape

Using methods outlined in Telesca et al. (2018); Mayk et al. (2022a), a PCA was performed using the matrix of Fourier coefficients to examine shape variation among individual specimens and populations from different salinity regimes. Calculated principal components (PCs) were considered to represent new shape variables. Synthetic outlines were reconstructed to determine shape change along PCs. PCs 1 and 2 accounted for almost 50% of shape variation across populations. These were used as response variables in generalised additive mixed models (GAMMs) to investigate the relationships between shape and environmental drivers.

Environmental data

Temperature (°C) and rainfall (mm) records were obtained from the Centre for Environmental Data Analysis (Met Office 2006) for UK locations, and from online sources for Montpellier, France and Sopot, Poland (www.extreme-weatherwatch.com and www.weatherspark.com, respectively). To ensure comparability across stations, monthly means were calculated for the months of March to October to capture the seasonal growth period of *C. glaucum* between the years of 2023 and 2025. Although data were acquired from different sources, the use of monthly means minimises differences in temporal resolution and reduces potential site-specific variability. Water salinity and depth (m) were recorded at each location on the day of collection.

Statistical analysis

Data exploration was carried out following the protocol described in Zuur et al. (2010). Cleveland dotplots were used to visualise outliers, and assumptions of normality were assessed by examining the distribution of variables in histograms. Shell thickness index was transformed using a log transformation to improve normality. Linear regression models were used to explore differences in the relationship between length and shell thickness index by comparing intercepts and slopes. Length was centred by subtracting the mean length from each value to allow for a more meaningful interpretation of the intercept by examining the probability of shell thickness at the average length versus 0. The level of significance was set at $p < 0.05$.

GAMMs were applied using the mgcv package in R studio (Wood 2011) to assess relationships between shape PCs and environmental factors to account for the random effects introduced by collection site and any nonlinear relationships. Shell length was also included to account for allometric relationships between shape and size.

Results

Shell thickness and shape

Group 1: Baltic Proper (sites GDA, MECH and SMB; see Fig. 1 *and* Table 1 *for full details).*

C. glaucum collected from SMB and GDA exhibited significantly higher intercepts than specimens collected from MECH (linear regression: MECH: $\beta = -0.58$, 95% CI -0.59 to -0.56; SMB: $\beta = -0.05$, 95% CI -0.11 to -0.02; GDA: $\beta = -0.49$, 95% CI -0.53 to -0.44; $p < 0.001$; adjusted $R^2 = 0.75$; Fig. 2a). At a shell length of 15 mm, shells from SMB were 70.0% thicker and shells from GDA were 9.4% thicker than those from MECH (Fig. 2b). Shell length was restricted to approximately 20 mm across all sites but specimens at GDA were significantly larger than MECH (Dunn's test: $p < 0.001$; Fig. 2c), despite growth lines from both locations suggesting ages ranging between 1 and 3 years (Fig. 2).

PCA analysis revealed significant shape differences among collection sites (multivariate analysis of variance [MANOVA]: $n = 68$, Wilk's $\lambda = 0.12$, approx. $F_{2,65} = 59.04$, $p < 0.001$). Univariate analysis of variance revealed significant differences in PC1 (analysis of variance [ANOVA]: $n = 68$, $F_{2,65} = 93.10$, $p < 0.001$) and PC2 (ANOVA: $n = 68$, $F_{2,65} = 5.82$, $p < 0.01$). Post hoc pairwise comparisons identified significant differences between both MECH and GDA, and SMB (PC1 Tukey's test: $p < 0.001$; PC2 Tukey's test: $p < 0.05$) (Table S1). SMB showed strong morphological differentiation with no regions of overlap with MECH or GDA within the morphospace. *C. glaucum* collected from SMB were shorter in height, but greater in length than those collected from MECH or GDA (Fig. 3).

Group 2: southern Baltic gradient (sites DAS, MECH, ODE and UJW; see Fig. 1 *and* Table 1 *for full details).*

Significant differences were observed in shell thickness across the southern Baltic gradient. *C. glaucum* specimens collected from DAS (linear regression: $\beta = -0.45$, 95% CI -0.67 to -0.24; $p = 0.001$; adjusted $R^2 = 0.68$) and MECH (linear regression: $\beta = -0.49$, 95% CI -0.71 to -0.27; $p = 0.015$; adjusted $R^2 = 0.68$) had significantly higher intercepts than shells collected from UJW (linear regression: $\beta = -0.64$, 95% CI -0.74 to -0.54; $p = 0.001$; adjusted $R^2 = 0.68$) and ODE (linear regression: $\beta = -0.63$, 95% CI -0.85 to -0.41; $p = 0.001$; adjusted $R^2 = 0.68$). At a shell length of 15 mm, *C. glaucum* were significantly thicker at DAS by 20.5% compared to specimens from UJW. Specimens from

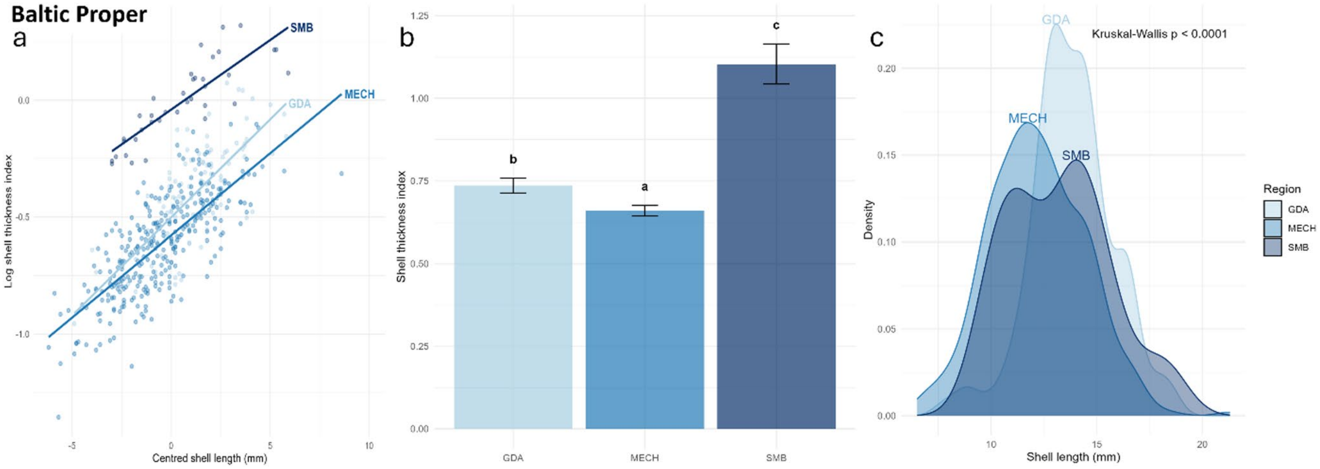

Fig. 2 Group 1: Baltic Proper shell parameters. (**a**) Linear regression analysis revealed significant relationships between shell length and shell thickness, with *C. glaucum* collected from GDA and SMB exhibiting significantly higher intercepts than specimens collected from MECH. (**b**) Shell thickness differences at a shell length of 15 mm supported these findings. Different letters indicate significant differences between groups ($p<0.05$) and error bars represent 95% confidence intervals. (**c**) Shell length distributions at each site revealed shell lengths restricted to approximately 20 mm. GDA, Redłowo station; MECH, Mechelinki–Rewa; SMB, Southern Middle Bank

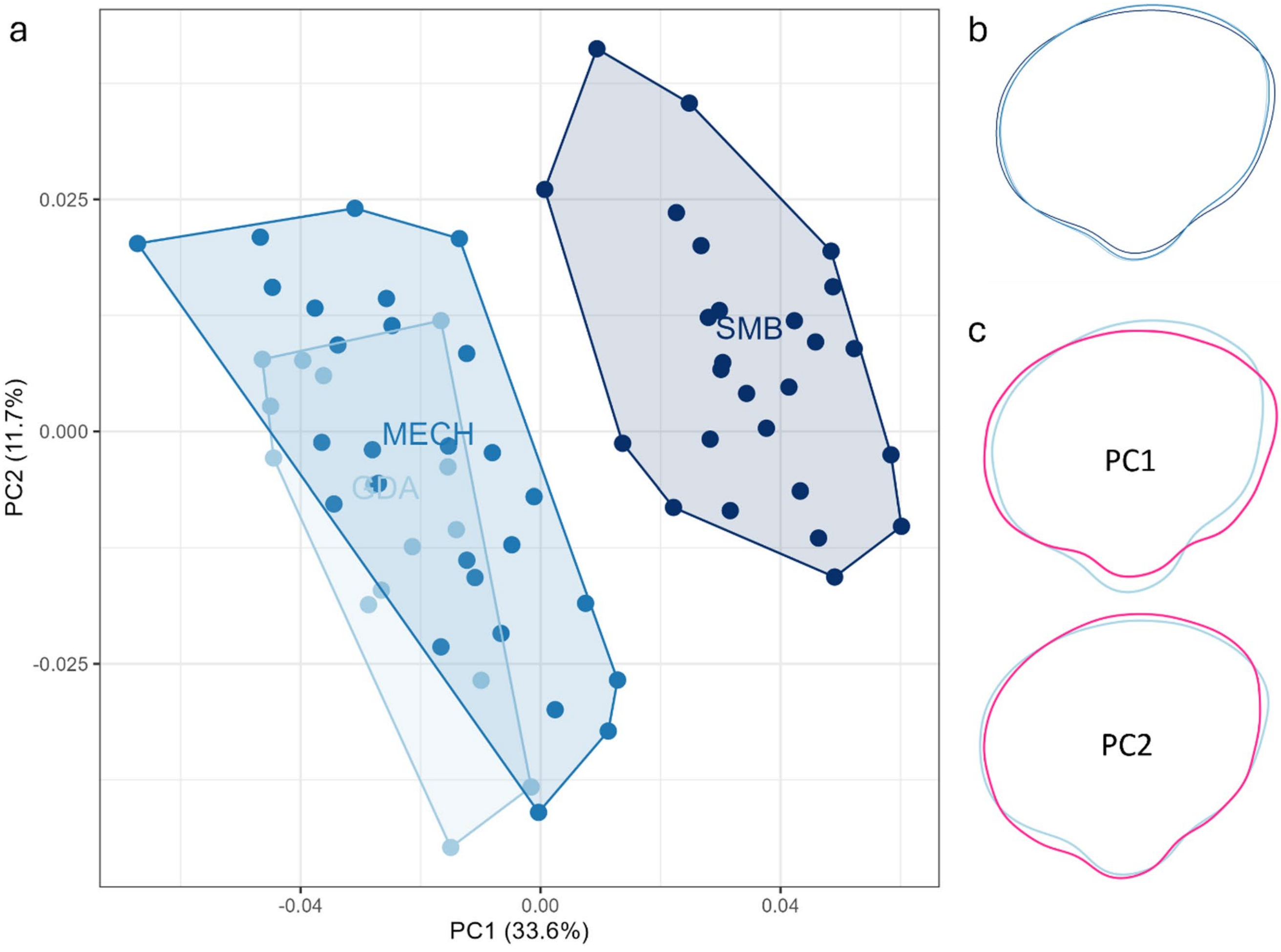

Fig. 3 Group 1: Baltic Proper shape variations. (**a**) Principal component analysis plot showing shape variation across sites. (**b**) Average shape outlines of *C. glaucum* across sites. (**c**) Outlines defining: blue, -2 standard deviations (SD); and pink, +2SD. GDA, Redłowo station; MECH, Mechelinki – Rewa; PC, principal component; SMB, Southern Middle Bank

MECH were 15.8% thicker than those from UJW, although this was not statistically significant (Fig. 4b). No significant difference in thickness was observed between specimens from UJW and ODE (Fig. 4a, b). At DAS, MECH and UJW, 99.9% of specimens had shell lengths less than 20 mm, whereas at ODE a smaller proportion (74.6%) measured below this threshold, with a maximum recorded length of 27.2 mm (Fig. 4c).

Shape changed significantly across the southern Baltic gradient (MANOVA: $n = 80$, Wilk's $\lambda = 0.68$, approx. $F_{3,76} = 5.40$, $p < 0.001$). Univariate analysis of variance revealed no significant differences in PC1 but significant differences in PC2 (ANOVA: $n = 80$, $F_{3,76} = 8.39$, $p < 0.001$). Post hoc pairwise comparisons identified significant differences in PC2 values between MECH and DAS (Tukey's test: $p < 0.001$), and UJW and DAS (Tukey's test: $p = 0.023$) (Table S2). No significant differences were observed between MECH and UJW (Tukey's test). *C. glaucum* from ODE occupied a broad region of the morphospace, indicating substantial within-site shape variation and shared shape characteristics with other sites, resulting in no significant differences (Tukey's test: $p > 0.05$). Cockles collected from MECH, UJW and DAS formed more distinct clusters, but also exhibited areas of overlap and shared shape characteristics (Fig. 5).

Group 3: Constant versus varying salinity (sites ABE, GLO, HSH, OR0, SLA, GDA, MECH and SMB; *see* Fig. 1 *and* Table 1 *for full details).*

C. glaucum collected from the Gulf of Gdańsk and the nearby Southern Middle Bank (Group 1: MECH, GDA and SMB) had significantly higher intercepts than cockles collected from coastal lagoons (linear regression: Baltic: $\beta = -0.22$, 95% CI -0.26 to -0.20; Lagoons: $\beta = -0.79$, 95% CI -0.86 to -0.71; $p < 0.001$; adjusted $R^2 = 0.72$). A significantly steeper slope also revealed a greater increase in shell thickness with length at these sites (Baltic [GDA, MECH, SMB]: $\beta = 0.081$, 95% CI 0.073–0.089; UK [ABE, GLO, HSH, OR0, SLA]: $\beta = 0.065$, 95% CI 0.049–0.081) (Fig. 6a). *C. glaucum* collected from around the Gulf of Gdańsk were on average 58.0%, 71.1% and 85.2% thicker at 10 mm, 15 mm and 20 mm, respectively (Fig. 6b) than populations in coastal lagoons. Although significantly thicker, length was significantly reduced (Kruskal–Wallis: $\chi^2 = 361.64$; $p < 0.001$) and appeared to be limited to approximately 20 mm with 99.8% of Baltic specimens measuring below this threshold versus 50.8% from coastal lagoons, where maximum lengths of 48.4 mm, 33.3 mm, 32.2 mm and 36.8 mm were recorded at ABE, HSH, OR0 and SLA, respectively (Fig. 6c).

There were significant differences in shape between sites (MANOVA: $n = 209$, Wilk's $\lambda = 0.11$, approx. $F_{7,201} = 58.29$, $p < 0.001$). Univariate analysis of variance revealed significant differences in PC1 (ANOVA: $n = 209$, $F_{7,201} = 82.53$, $p < 0.001$) and PC2 (ANOVA: $n = 209$, $F_{7,201} = 35.52$, $p < 0.01$). Post hoc pairwise comparisons showed that MECH and GDA formed distinct clusters, with almost no overlap with the other collection sites, exhibiting shells shorter in length, with a lifted posterior and less pronounced umbonal region (Table S3). Of interest, SMB overlapped considerably with SLA and ABE, indicating shared shape characteristics (Fig. 7). By contrast, HSH, GLO and OR0 were characterised by negative PC1 values, which relate to a more distinct umbo region, increased height and elongation of the posterior (Fig. 7).

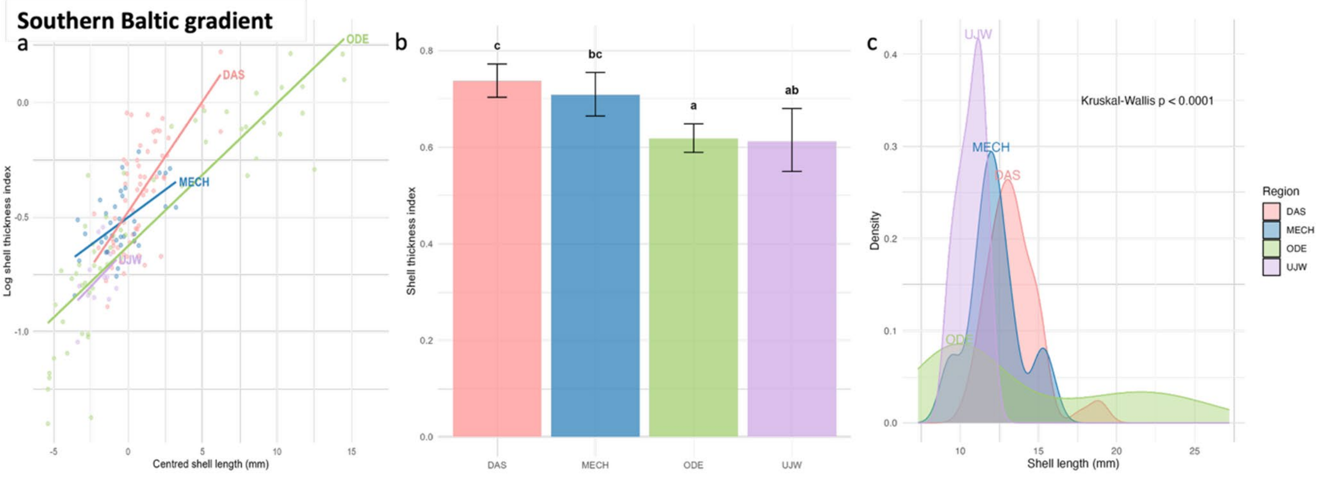

Fig. 4 Group 2: southern Baltic gradient shell parameters. (**a**) Linear regression analysis revealed significant relationships between shell length and shell thickness, with *C. glaucum* collected from DAS and MECH exhibiting significantly higher intercepts than specimens collected from ODE and UJW. (**b**) Shell thickness differences at a length of 15 mm. Different letters indicate significant differences between groups ($p < 0.05$) and error bars represent 95% confidence intervals. (**c**) Shell length distributions at each site reveal sizes restricted to approximately 20 mm at DAS, MECH and UJW, while specimens from ODE reached a maximum recorded length of 27.2 mm. DAS, Darß-Zingst-Bodden Chain; MECH, Mechelinki – Rewa; ODE, Odense Fjord; UJW, Ujście Wisły, mouth of the Vistula River

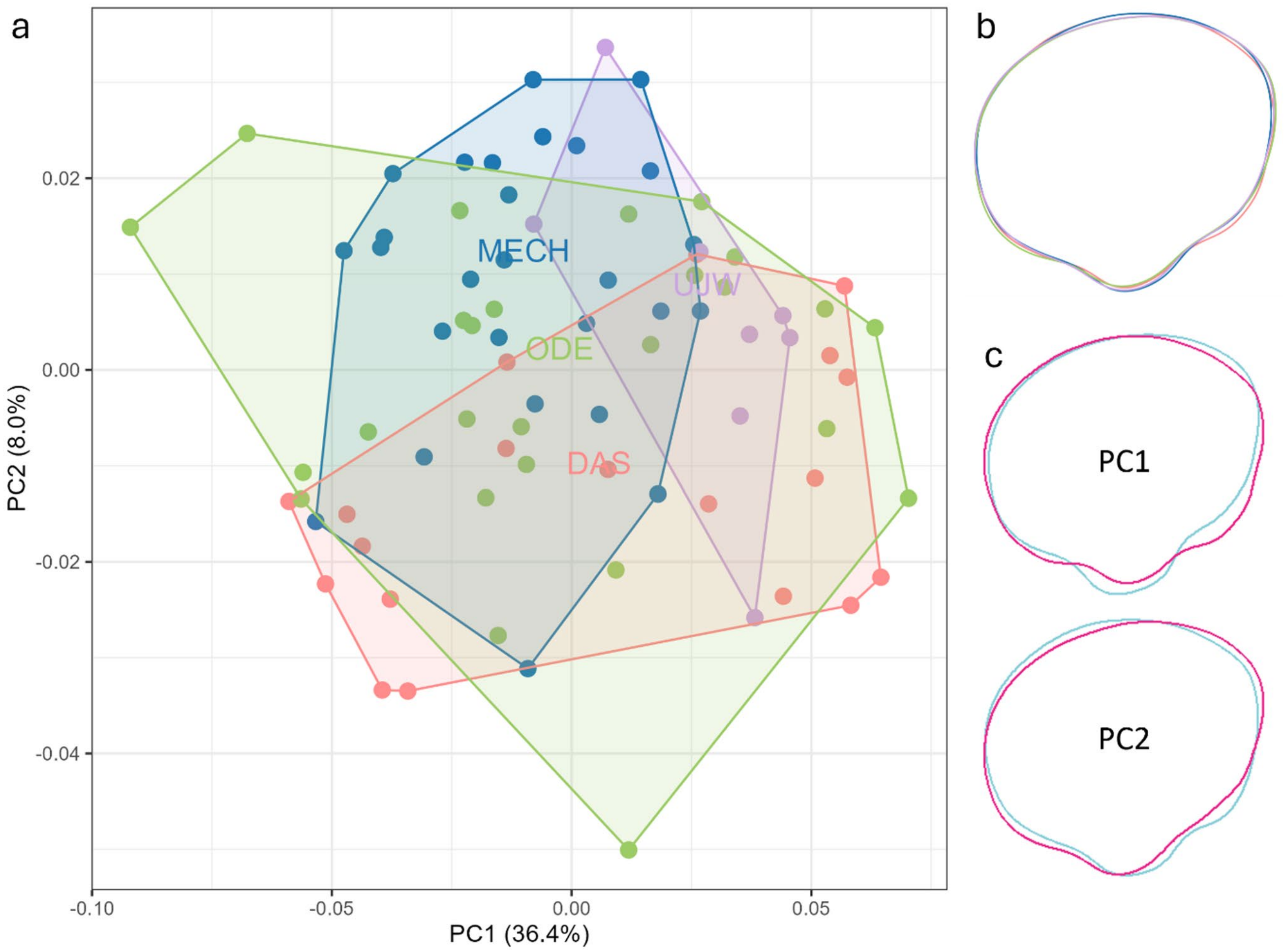

Fig. 5 Group 2: southern Baltic gradient shape variations. (**a**) Principal component analysis plot showing shape variation across sites. (**b**) Average shape outlines of *C. glaucum* across sites. (**c**) Outlines defining: blue, -2 standard deviations (SD); and pink, +2SD. DAS, Darß-Zingst-Bodden Chain; MECH, Mechelinki – Rewa; ODE, Odense Fjord; PC, principal component; UJW, Ujście Wisły, mouth of the Vistula River

GAMMs revealed significant relationships between shell shape and environmental factors (Fig. 8; Table S4). Significant nonlinear relationships were observed between shape PC1 and salinity (GAMM: edf = 1.97; F = 49.84; $p < 0.001$), seasonal rain (GAMM: edf = 1.98; F = 21.9; $p < 0.001$) and depth (GAMM: edf = 1.98; F = 34.28; $p < 0.001$). There was no significant influence of salinity on variations in shape PC2, but there were significant linear relationships with seasonal rain (GAM: edf = 1.00; F = 5.74; $p = 0.017$) and depth (GAM: edf = 1.00; F = 21.04; $p < 0.001$). Shell length showed significant nonlinear relationships with shape PC1 (GAM: edf = 1.94; F = 14.8; $p < 0.001$) and shape PC2 (GAM: edf = 1.69; F = 15.90; $p < 0.001$), indicating significant allometric growth. Variation among collection sites was significant (GAM: edf = 2.18; F = 3.21; $p < 0.01$), and together with environmental drivers and shell length explained 73.5% of the observed variation in shell shape.

Extent of dissolution

External surfaces

Extensive dissolution was observed on MECH specimens collected in vivo, particularly in the umbonal region, which was compromised structurally (Fig. 9a). The shell of *C. glaucum* comprises a very thin outer composite prismatic layer with a substantial thickness of crossed-lamellar microstructure below (the shell inside the pallial line is complex crossed-lamellar). Although a proportion of periostracum was remaining in patches on shell surfaces (particularly close to the ventral edge), it was visibly peeling away and interspersed with patches of exposed calcareous shell (Fig. 9b–d). Where the periostracum had been lost, there was marked evidence of progressive loss of the calcareous shell material, revealed by rough textures and extensive pitting, with some detail of the composite prism margins and first-order

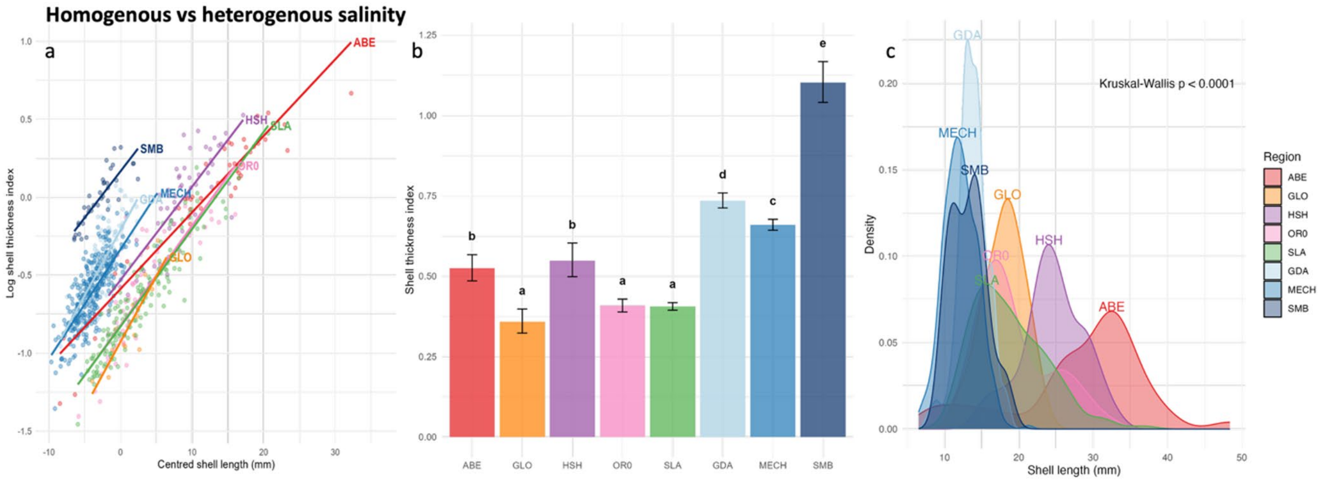

Fig. 6 Group 3: Shell parameters in *C. glaucum* collected from constant and varying salinity regimes. (**a**) Linear regression analysis revealed significant relationships between shell length and shell thickness, with *C. glaucum* from the Baltic Proper exhibiting significantly higher intercepts than those collected from coastal lagoons. (**b**) Shell thickness differences at a shell length of 15 mm. Different letters indicate significant differences between groups ($p < 0.05$) and error bars represent 95% confidence intervals. (**c**) Shell length distributions at each site reveal the approximate restriction in the length of cockles from the Baltic Proper to approximately 20 mm. ABE, Aberthaw; GDA, Redłowo station; GLO, Bassin du Gloria; HSH, Holkham Salts Hole; MECH, Mechelinki – Rewa; OR0, Shingle Street lagoon 0; SLA, Slaughden; SMB, Southern Middle Bank

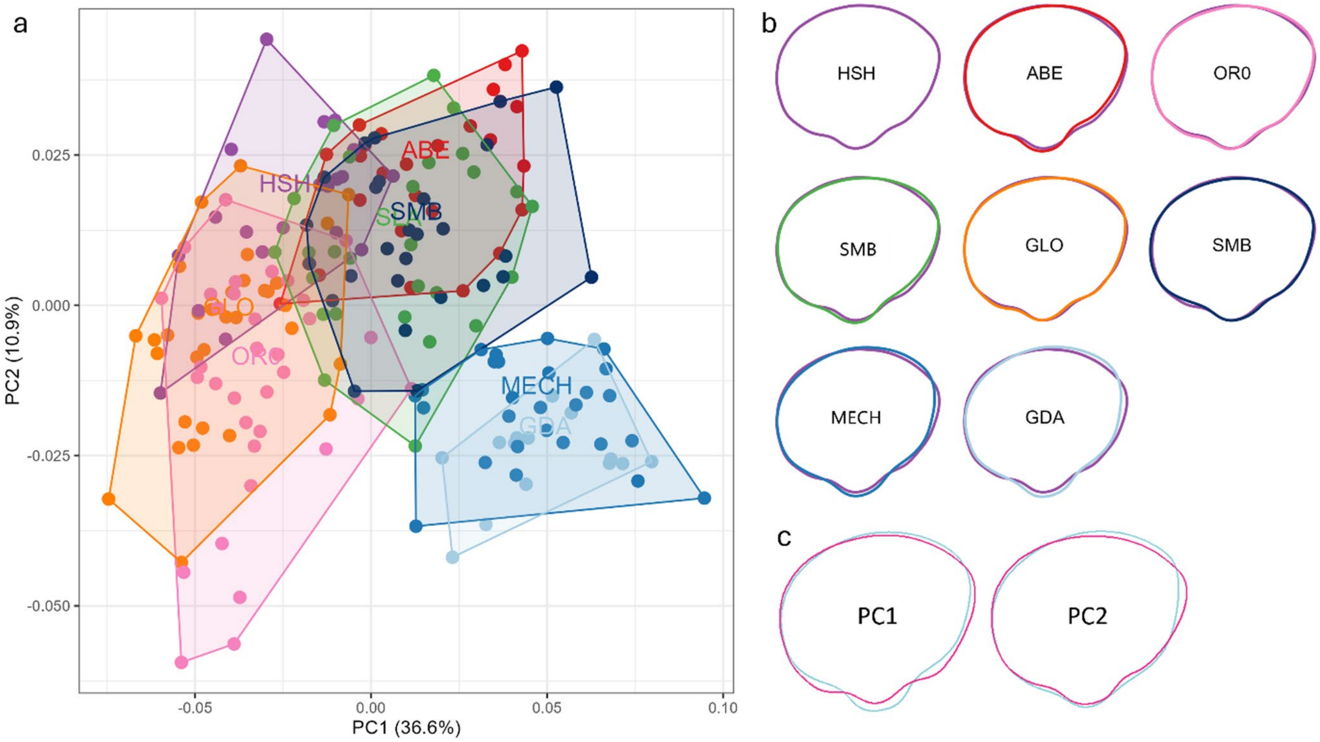

Fig. 7 Group 3: Shape variations in *C. glaucum* collected from constant and varying salinity regimes. (**a**) Principal component analysis plot showing shape variation across sites. (**b**) Average shape outlines of *C. glaucum* across sites compared to the relatively stable coastal lagoon, Holkham Salts Hole (HSH). (**c**) Outlines defining: blue, -2 standard deviations (SD); and pink, +2SD. ABE, Aberthaw; GDA, Redłowo station; GLO, Bassin du Gloria; HSH, Holkham Salts Hole; MECH, Mechelinki – Rewa; OR0, Shingle Street lagoon 0; PC, principal component; SLA, Slaughden; SMB, Southern Middle Bank

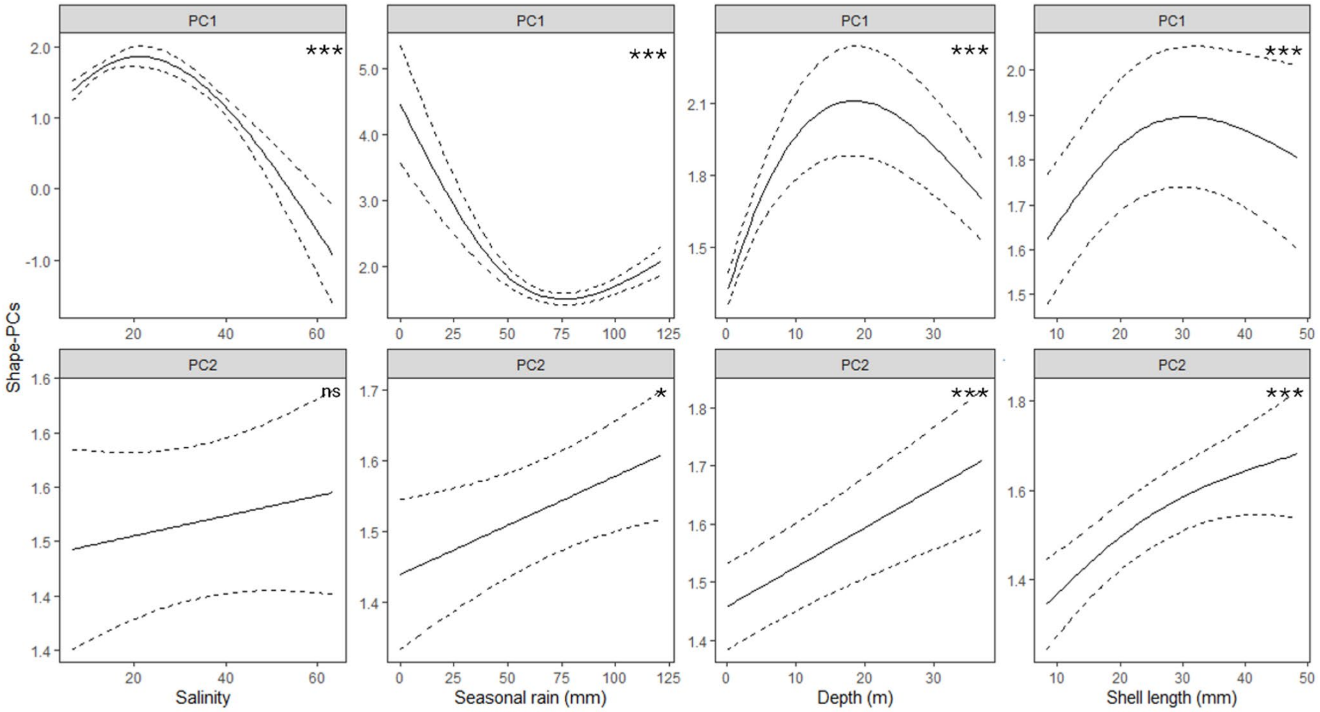

Fig. 8 Group 3: Relationships between environmental factors and shape PCs. Generalised additive models used to interpret the influence of salinity, seasonal rain, depth and shell length on the shape PCs extracted from *C. glaucum* collected from constant and varying salinity regimes. ns = not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. PC, principal component

lamels of the crossed-lamellar structure visible (Fig. 9b–d). Specimens from coastal lagoons had better preservation of the periostracum, but where this had been lost, dissolution was significant, with similar exposure of the outer composite prismatic and crossed-lamellar microstructures, but less evident pitting (Fig. 10). Patches of damage by endolithic borers were also observed, which had encouraged dissolution deeper into the mineral layers (Fig. 10d). Postmortem dissolution of Baltic specimens was substantial (see Fig. S1 in the supplementary information).

Internal surfaces

Almost no dissolution was observed on the internal surfaces of the specimen fragments collected in vivo, with only very sparse patches of abrasion (Fig. 11a). Postmortem dissolution was pronounced with large craters exposing underlying mineral layers and damage by shell-boring organisms (Fig. 11b).

Organic content

C. glaucum collected from the consistently low salinity MECH had a mean organic wt% of 1.83 ± 0.5 ($n = 4$), which was not significantly different to the average mean organic wt% of *C. glaucum* specimens ($n = 57$) collected from eight coastal lagoon environments with variable salinity regimes (Table S5; 2.16 ± 0.4 wt%, $n = 57$; Dunn's test: $p > 0.05$).

Periostracum thickness

Specimens from MECH had an average periostracum thickness of 1.11 ± 0.55 µm ($n = 5$), significantly thicker than specimens from SLA (Tukey's test: $p < 0.01$), which had periostraca measuring 0.94 ± 0.38 µm ($n = 5$). Specimens from ABE had an average periostracum thickness of 1.07 ± 0.33 µm ($n = 5$), which was not significantly different to specimens from MECH or SLA (Fig. 12).

A summary of the shell characteristics from each site can be found in Table 2.

Discussion

Significant spatial variations in shell thickness, size and shape were revealed in *C. glaucum* collected across salinity regimes. Our findings generally support the initial hypotheses: (i) Baltic populations of *C. glaucum* exhibit macrostructural adaptations to compensate for sustained salinities below 10 by producing significantly thicker shells compared to populations inhabiting more variable salinity environments; (ii) extent of dissolution is significant under

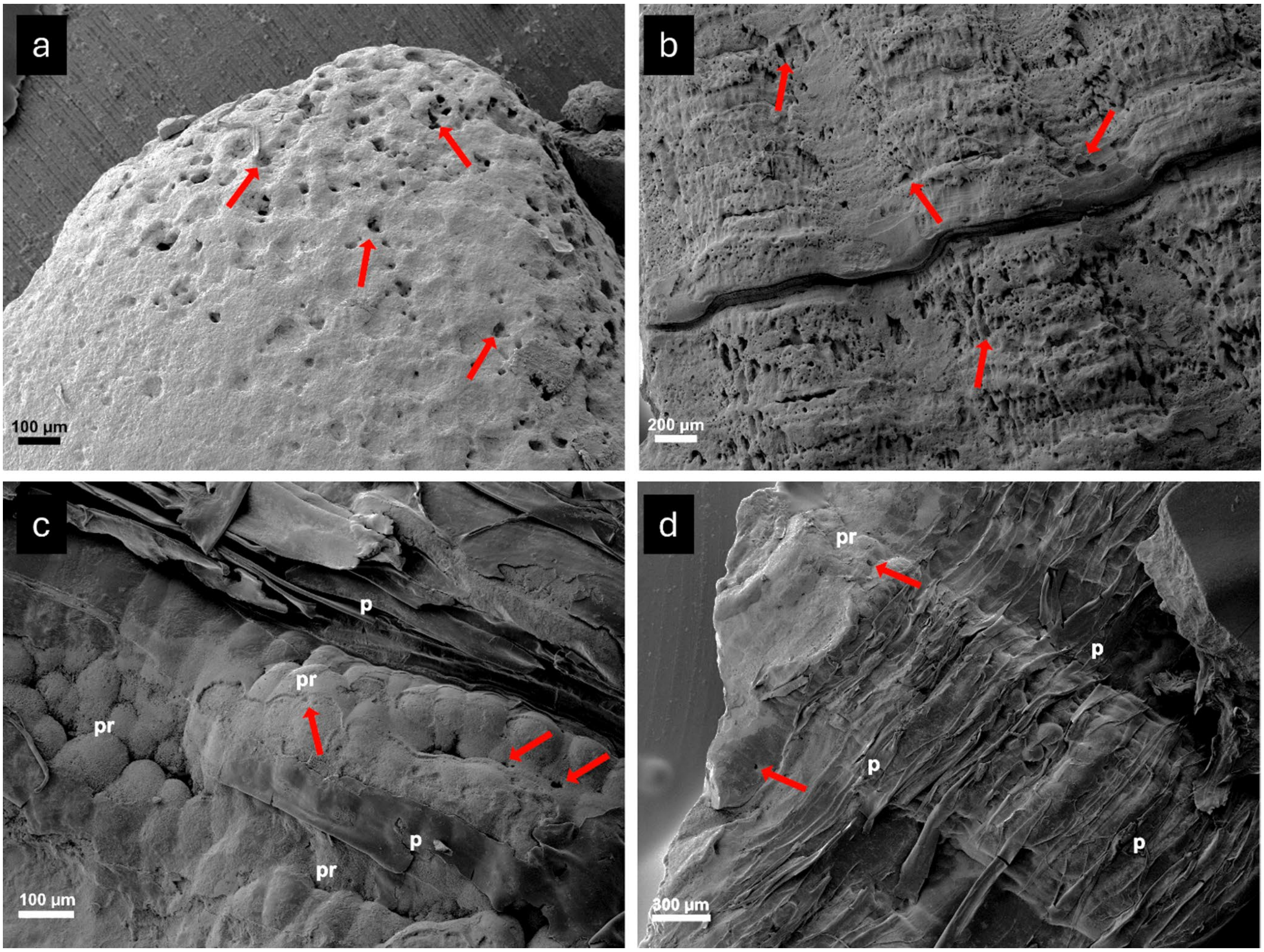

Fig. 9 Scanning electron micrographs of the surface of a specimen collected alive from Mechelinki – Rewa [MECH]. (**a**) Total absence of periostracum at the umbo, which has led to significant dissolution and deterioration of the mineral layer; (**b–d**) patches of intact periostracum protecting the external surface but interspersed with exposed calcareous shell showing progressive shell dissolution of outer prismatic and crossed-lamellar layers. Pitting of individual crystals and structural damage demonstrate the extent of dissolution (arrows). Letter labels represent: p, periostracum and pr, outer composite prismatic

constant low salinities, resulting in substantial structural damage and sparse regions of intact periostracum; and (iii) salinity is associated with significant changes in shape, revealing rounder more globular-shaped shells with a less pronounced umbo in salinities sustained below 10. Other factors, including depth, seasonal rain and age, also significantly influenced shape.

Variations in shell thickness

Group 1: Baltic Proper

Local variations in shell thickness were significant within the Baltic Proper. Major Baltic inflows are strong barotropic influxes of dense, oceanic salinity, oxygen-rich waters from the North Sea through the Danish Straits (Löptien et al. 2025). The Southern Middle Bank [SMB] north of the Słupsk Furrow is an important region for major Baltic inflows, providing the only pathway for saline waters to reach the central and northern Baltic (Rak et al. 2020). The oxygen-rich waters mix vertically (Bulczak et al. 2016; Krek et al. 2021) and subhalocline salinity increases locally from approximately 10 to 13 (Witek et al. 2003). Simultaneous displacement of the halocline upwards also allows saline water to reach shallower flanks of the basin (Zhurbas et al. 2011; Bielecka et al. 2024). Already well adapted to the low salinity conditions (~ 7), episodic increases in salinity to 10–13 during major Baltic inflows, combined with associated increases in oxygen availability, may enable the production of the even thicker shells (70% thicker) observed at a depth of 37 m at SMB.

Differences between *C. glaucum* shells collected from MECH and GDA in the Gulf of Gdańsk were significant but more subtle, with shells from GDA found to be 9.4% thicker.

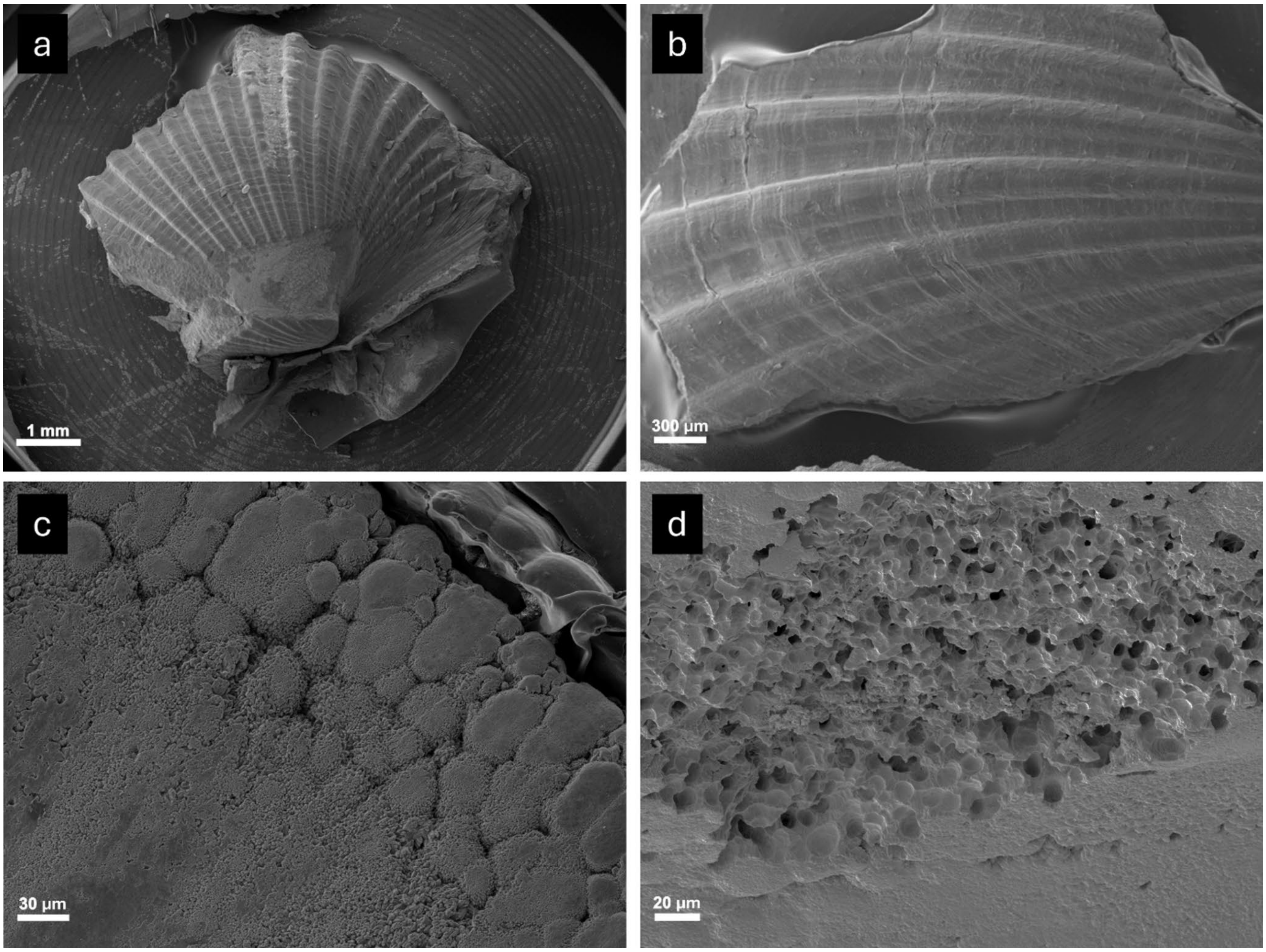

Fig. 10 Scanning electron micrographs of specimens collected alive from (**a**) Aberthaw [ABE] and (**b**, **c**, **d**) Slaughden [SLA]. (**a**, **b**) Periostracum is largely intact across the shell surfaces, but where it is compromised, significant dissolution is evident, exposing (**c**) the calcareous microstructure. (**d**) Dissolution deeper into the mineral layers exacerbated by endolithic boring damage

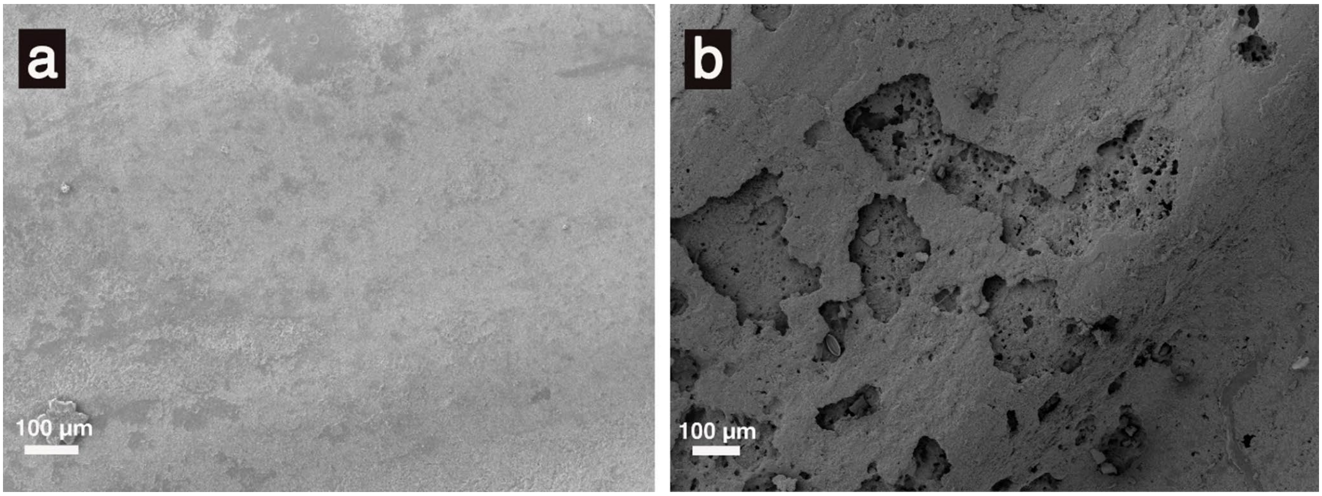

Fig. 11 Condition of internal surfaces (**a**) in vivo and (**b**) postmortem of specimens collected from Mechelinki – Rewa [MECH]

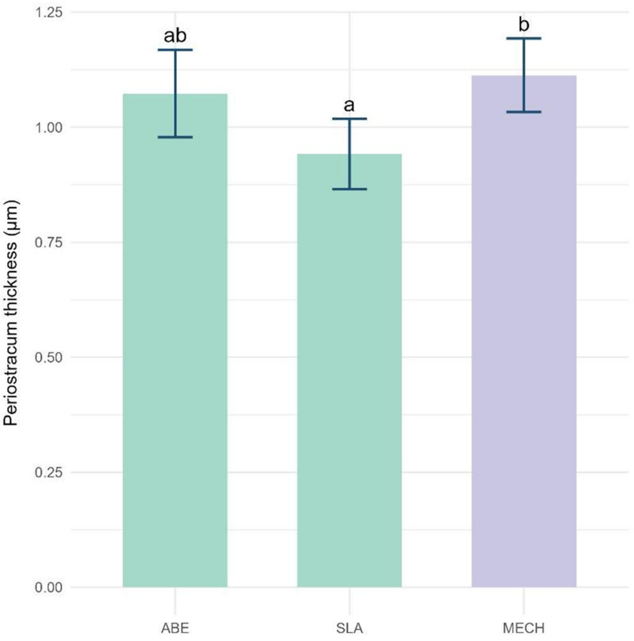

Fig. 12 Periostracum thickness. Specimens from MECH had significantly thicker periostracum compared to specimens from SLA, a UK lagoon where the salinity is variable ranging between 7 and 25 across seasons. No significant difference was revealed with specimens from ABE, a lagoon with low and variable salinity (11–15), suggesting a progression in the thickening of the periostracum with salinity decreases. Different letters indicate significant differences between groups ($p<0.05$) and error bars represent 95% confidence intervals. ABE, Aberthaw; MECH, Mechelinki – Rewa; SLA, Slaughden

Anthropogenic nutrient loading is a chronic problem in the Baltic Sea, contributing to its status as one of the largest hypoxic regions in the world (Meier et al. 2006). The Vistula River in the Gulf of Gdańsk is the second largest river draining into the Baltic Sea and accounts for large percentages of the land-based discharges of total nitrogen (25%) and phosphorus (35%) (Räike 2025). Energy demands for calcification and organic production may be ameliorated by the high productivity of the Baltic waters (Szymczycha et al. 2019). However, Puck Bay where MECH is situated is one of the most heavily polluted areas within the already contaminated gulf (Zima 2019). Although the bay supports a high level of biodiversity and large populations of *C. glaucum* (Piesik et al. 2009; Janas and Kendzierska 2014; Polak-Juszczak and Szlider-Richert 2024), a substantial proportion of abnormalities have been observed in bivalve larvae (Lasota et al. 2018). These abnormalities have been linked to the adverse impact of local sewage inflows from a treatment plant in synergy with other abiotic conditions, i.e. temperature and salinity (Lasota et al. 2018). The high levels of pollution are likely a primary driver of the thinner shells observed at MECH compared to the population from GDA. The thicker shells observed from SMB may also benefit from their distance to the Gulf, being a site where the accumulation of pollutants is much lower (Piesik et al. 2009).

Group 2: southern Baltic gradient

The salinity gradient across the approximate 550 km transect of the study area in the southern Baltic is associated with significant changes in the shell thickness of *C. glaucum*, in addition to nuanced shape changes. Specimens from the most easterly site, MECH, were collected from the heavily polluted Puck Bay (mean depth of 9 m) found within the Gulf of Gdańsk where salinity is low and ranges from 6 to 8. Moving west, specimens were collected from the shallow (mean depth of 2.3 m), well-mixed, oxygenated estuarine lagoon system known as the Darβ-Zingst Bodden chain in the German southern Baltic (Nausch and Schlungbaum 1991; Schumann et al. 2023). Within this system, DAS specimens were collected in the eutrophic Grabow Bodden, the outermost and first basin to receive a direct inflow of saline Baltic water (Paar et al. 2021). Sea surface salinity in the year of collection (2016) ranged between 5.7 in January and 9.6 in September (European Union-Copernicus Marine Service 2018). Although summer salinities are slightly higher than those in MECH, they remain below 10 and drop to less than 6 in the winter. These intervals of lower salinity are likely accompanied with even lower calcium carbonate saturation levels and periods of more intense dissolution (Sanders et al. 2018, 2021). Sustained oxygen levels above 60% (Schumann et al. 2023) and high concentrations of chlorophyll *a*, an important food source for the bivalves (Paar et al. 2021), may augment the capacity to biomineralise shells that are 4.1% thicker in DAS compared to MECH to compensate for the periods of further reduced salinity. DAS specimens exhibited lengths restricted to approximately 20 mm, a response that has been observed previously at salinities of less than 10, as a result of living at the edge of their tolerance limits (Jansson and Jansson 2002; Landes et al. 2015; Sanders et al. 2018).

ODE is a shallow (less than 0.8 m) eutrophic Danish fjord that supports a large biomass of *C. glaucum* (Riisgård et al. 2007). Salinity typically ranges from 10 in the winter to 15 in the summer (Riisgård et al. 2008). While size may reflect differences in several factors, including age, growth rate, food supply, oxygen etc., the lengths of more than 20 mm observed in ODE specimens where salinities reach beyond the salinity threshold of 10 is congruent with a study from Kiel Bay where *C. glaucum* reached sizes of up to 50 mm at a salinity of 12, compared to the smaller specimens found on the Polish coast (Obolewski et al. 2007). Shell thickness in ODE specimens, however, is reduced by 12.7% compared to MECH. The slightly higher salinities and likely improved

Table 2 Summary table of measured parameters

Site	*n*	Salinity range	Mean shell thickness index at 15 mm (95% CI)	Length range (mm)	Organic content, wt% (SD) [*n*][a]	Periostracum, μm (SD) [*n*]
Group 1						
GDA	107	6.0–8.0	0.72 (0.71, 0.74)	7.8–18.5	–	–
MECH	302	6.0–8.0	0.66 (0.65, 0.68)	6.5–21.3	1.83 (0.51) [4]	1.11 (0.55) [5]
SMB	37	6.0–8.0	1.13 (1.08, 1.18)	9.7–18.6	–	–
Group 2						
DAS	60	3.4–9.0	0.74 (0.70, 0.77)	10.4–18.9	–	–
MECH	34	6.0–8.0	0.71 (0.66, 0.75)	9.1–15.9	–	–
ODE	55	10.0–15.0	0.62 (0.59, 0.65)	7.3–27.2	–	–
UJW	12	3.0–8.0	0.61 (0.55, 0.68)	9.3–11.9	–	–
Group 3						
ABE	43	11.0–15.0	0.52 (0.49, 0.57)	7.7–48.4	–	1.07 (0.33) [5]
GDA	107	6.0–8.0	0.74 (0.71, 0.76)	7.8–18.5	–	–
GLO	16	> 35.0 to > 60.0	0.36 (0.32, 0.40)	12.2–22.6	–	–
HSH	54	17.9–24.3	0.55 (0.50, 0.60)	14.5–33.3	–	–
MECH	302	6.0–8.0	0.66 (0.64, 0.68)	6.5–21.3	1.83 (0.51) [4]	1.11 (0.55) [5]
OR0	58	25.1–39.2	0.41 (0.39, 0.43)	10.3–32.2	–	–
SLA	148	7.3–25.4	0.41 (0.39, 0.42)	10.2–36.8	–	0.94 (0.38) [5]
SMB	37	6.0–8.0	1.10 (1.04, 1.17)	9.7–18.6	–	–

[a] The mean organic content of specimens from MECH were compared to the mean organic content of *C. glaucum* from variable coastal lagoon systems (2.16 ± 0.38 wt%; *n* = 57). ABE, Aberthaw; CI, confidence interval; GDA, Redłowo station; GLO, Bassin du Gloria; HSH, Holkham Salts Hole; MECH, Mechelinki – Rewa; OR0, Shingle Street lagoon 0; SD, standard deviation; SLA, Slaughden; SMB, Southern Middle Bank; wt%, weight proportion

calcium carbonate saturation levels may enable the reallocation of energy for growth as the extent of dissolution and the requirement for thicker shells is diminished.

Specimens from UJW were collected at the mouth of the heavily polluted Vistula River, which drains much of the Polish territory and flows directly into the Gulf of Gdańsk (Miernik et al. 2023). At this transitional zone where freshwater meets saline, organisms experience higher levels of osmotic stress (Wielgat-Rychert et al. 2013). Salinity is variable and influenced by climatic factors, i.e. precipitation and temperature, and human interventions (Kubiak-Wójcicka 2020; Bogdanowicz et al. 2021). In the year of collection (2016), sea surface salinity fluctuated from approximately 3 to 8 (European Union-Copernicus Marine Service, 2018). Although salinity is higher and more stable (7.1–7.6) in the near-bottom zone inhabited by *C. glaucum* (Sokolowski et al. 2001), aragonite undersaturation prevails between March and November within the Vistula River plume (Stokowski et al. 2021). Specimens from UJW had 13.7% thinner shells than those collected from MECH, likely a consequence of the multistressor impacts of pollution and the undersaturation of aragonite.

Group 3: constant versus varying salinity

C. glaucum populations in the Baltic Proper produce shells that are up to 85.2% thicker than those of individuals inhabiting coastal lagoons. Limited concentrations of the necessary substrates (Ca^{2+} and $HCO^{-}{}_{3}$) and the undersaturation of aragonite ($\Omega_{arag} < 1$) should make biogenic calcification challenging (Thomsen et al. 2018; Sanders et al. 2018). Sanders et al. (2018) calculated that total shell production, including the $CaCO_3$ and organic components, can demand up to 67% of assimilated energy at salinities of less than 10. This energetic cost is considered to be the most important limiting factor for growth, surpassing the energy demands for osmoregulation (Sanders et al. 2018). Dwarfism in blue mussels (Riisgård et al. 2014) and the reduced growth of *M. arenaria* (Filippenko and Naumenko 2014) in the Baltic Sea have been reported and the restricted size of Baltic *C. glaucum* to lengths of less than 20 mm is in agreement. By contrast, in coastal lagoons where salinity is more variable and exposure to salinities less than 10 is limited, *C. glaucum* is capable of reaching much greater lengths of up to almost 50 mm.

Shell thickening has been observed across several species of mollusc in adaptive response to factors including predator threat (Boulding 1984; Brookes and Rochette 2007; Telesca et al. 2019; Mayk et al. 2022b), ocean acidification (Coleman et al. 2014; Marshall and Tsikouras 2024) and temperature (Graus 1974; Doyle et al. 2010; Telesca et al. 2019). Predation pressure on benthic communities within the Baltic is relatively low (Kautsky 1981). It is dominated by fish, *Platichthys flesus* (marine flounder), *Rutilus rutilus* (freshwater roach) and *Neogobius melanostomus* (round goby), in addition to *Crangon crangon* (brown shrimp), *Saduria entomon* (benthic isopod), and the invasive species, *Rhithropanopeus harrisii* (North American mud crab) and *Orconectes limosus* (spiny-cheek crayfish), all of which have been recorded to prey on *C. glaucum* (Obolewski et al. 2007; Nurkse et al. 2016, 2018; Westerbom et al. 2018; Henseler et al. 2020). Baltic *M. balthica* also produce significantly thicker shells than populations in the adjacent North Sea; traits identified as improving resistance to predation by Baltic *C. crangon* and *S. entomon* (Ejdung et al. 2009). However, despite facing threats from similar predators, the same increase in shell thickness is not observed in Baltic mytilid mussels, which produce thinner and more fragile shells than their North Sea relatives where predation by the common shore crab, *Carcinus maenas*, and sea star, *Asterias rubens*, is predominant (Reimer and Harms-Ringdahl 2001; Arivalagan et al. 2020).

Variation in shell thickness among *C. glaucum*, *M. balthica* and *Mytilus* spp. may instead be driven by their mineralogic properties. *C. glaucum* and *M. balthica* have wholly aragonitic shell compositions, while *Mytilus* species fabricate bimineralic shells with an outer calcite layer (Checa et al. 2014). The calcium carbonate saturation state in the Baltic Sea shows large seasonal variations because of low salinity and temperatures (Tyrrell et al. 2008). Between November and March, aragonite is undersaturated ($\Omega_{arag} < 1$), exacerbating dissolution, while calcite stays close to the saturation threshold ($\Omega_{calcite} \geq 1$) (Tyrrell et al. 2008). This is advantageous for calcite polymorphs and likely reduces dissolution rates. Since inorganic calcite is also 35% less soluble than inorganic aragonite (Mucci 1983), and significantly more resistant to dissolution in lower salinities (King et al. 2026), *Mytilus* species likely do not need to produce thicker and energetically more costly shells. By contrast, there may be a cost benefit for vulnerable aragonite polymorphic species to produce thicker more robust shells as an adaptation to counteract the significant levels of dissolution. Indeed, in vivo shell dissolution of *C. glaucum* was extensive. Furthermore, the proportion of organics within the shell can significantly affect the costs of shell production. Despite only making up small proportions of the shell by weight (~0.1–5.0 wt%) the organics account for disproportionate amounts of the metabolic costs (Palmer 1983, 1992). The organic matrix accounts for approximately 22% of the energy budget for shells containing 1.5 wt% organic matrix, and almost 50% for shells containing 5.0 wt% organic matrix (Palmer 1983, 1992). The organic-rich nacre (3.1 wt%) in *Mytilus* spp. will be significantly more costly to produce than that of the crossed-lamellar in *C. glaucum* (2.2 wt%). It therefore may not be energetically viable for organic-rich *Mytilus* spp. to become thicker as a defence against dissolution, compared to organic-poor crossed-lamellar heterodont groups like *C. glaucum* and *M. balthica*.

Coastal lagoons are ephemeral features of dynamic coastal systems, with lifespans of considerably less than 1000 years (Barnes 1980). This is substantially shorter than the recorded subfossil age of *C. glaucum* in the Baltic dating back 7000 years (Nikula and Väinölä 2003). Populations of *C. glaucum* are present across continuous regions of the Baltic Sea, unlike their sporadic and isolated distribution across the Atlantic and North Sea coastlines where they experience frequent extinctions (Sromek et al. 2019). These deviations in habitat have led to significant genetic differences. Evolutionary exposure to a low and constant salinity has driven populations within the Baltic Sea to naturally select and adapt to the demanding conditions, producing a highly distinct population with reduced genetic diversity (Geburzi et al. 2022). By contrast, *C. glaucum* inhabiting coastal lagoons have adapted to thrive in the unpredictable dynamic conditions, exhibiting high levels of local adaptation and plasticity, and significant genetic variation (Tarnowska et al. 2009; Sromek et al. 2019). Exposure to salinities of less than 10 is transient, or unprecedented, in most coastal lagoons and reduces periods of significant shell dissolution, eliminating the need for thicker shells with higher energetic costs. The increased osmoregulatory demands needed to cope with fluctuating salinities are also likely to require increased proportions of energy. Variations in shell thickness have been observed with changing salinity in the Sea of Azov (Mirzoeva and Demchenko 2022) and even cockles inhabiting the relatively stable lagoon Holkham Salt's Hole, Norfolk, UK (HSH; seasonal salinity fluctuations between 18 and 26; Hunt 1971) have significantly thinner shells than those found in the Baltic, probably because the extent of dissolution is lower. The thinner shells may also be explained by the limited threat of predation to only fish (*Gasterosteus aculeatus* and *Potamoschistus microps*), one crustacean (*Palaemonetes varians*) and the occasional aquatic bird (McArthur 1998).

Variations in shape

Bivalve species show high spatial and temporal morphological plasticity with many studies showing shape change driven by environmental factors, including temperature (Peyer et al. 2010), predation (Neo and Todd 2011), hydrodynamics (Zieritz and Aldridge 2009; Hornbach et al. 2010; Vekhova 2013), pH (Fitzer et al. 2015; Telesca et al. 2019) and salinity (Telesca et al. 2018). Our results corroborate these findings by revealing the environment to be a significant driver of shell shape in *C. glaucum* (Fig. 8), which as a taxon shows strong local and spatial ecophenotypic variations (Fig. 7). Salinities consistently less than 10 appear to influence a distinct shift in morphology with shells that are more globular in shape, a trait that has also been observed in Baltic *M. balthica* (Ejdung et al. 2009). By contrast, *C. glaucum* in more variable environments exhibit broader morphological diversity, displaying shared shape characteristics across populations. Similar variations in morphology have also been recognised in mussels found in Baltic coastal lagoons, which has been linked to seasonal food availability (Telesca et al. 2018). In this study, GAMMs revealed the influence of multiple predictors on shell shape and the persistence of site-specific variation. Shape PC1 was driven by significant interactions among salinity, seasonal rain, depth and shell length. The nonlinear relationships reflect a complexity in the influence of the environmental factors on driving shape patterns in shape PC1 defined predominantly by changes in shell height and the prominence of the umbo. Meanwhile, shape PC2, linked to posterior elongation, shows direct linear relationships with increasing shell size, depth and rainfall. Elongation is commonly seen with increasing ontogeny (Ubukata 2003; Signorelli et al. 2013), while the relationships with increasing depth and rainfall remain undetermined.

Dissolution across salinity regimes

Function of the periostracum The periostracum is the first part of the shell to form and continues to serve as a template for the crystallisation of the calcium carbonate layers (Harper 1997). Its second important function, as the outermost layer, is to shield the underlying calcareous minerals from the ambient environment (Harper 1997). When intact, it achieves this well, with some species evolving thicker periostraca to enhance protection against dissolution in fresh and acidic environments (Taylor and Kennedy 1969; Harper 1997; Tunnicliffe et al. 2009). In addition to producing thicker shells, Baltic *C. glaucum* also appears to produce a thicker periostracal layer than specimens where salinity fluctuations are variable (i.e. 7–25 at SLA), likely as further compensation for the corrosive low and stable salinity conditions. The periostracum thickness was not significantly different to specimens from ABE, but since this lagoon has a low and variable salinity (11–15), may indicate a progression in the thickening of the periostracum with declining salinity. Atlantic *Mytilus edulis* already possess a significantly thicker periostracum (approximately 20 to 50 µm) than *C. glaucum* (Dunachie 1963), but Baltic individuals of both species exhibit periostracal thickening (Telesca et al. 2019). This protection is, however, compromised when the periostracum is lost by factors such as abrasion or decay (Peck et al. 2016), or deteriorates with age and increasing exposure. Intact periostracum was sparse on the 2-year-old MECH specimen, revealing large proportions of the mineral layer (Fig. 9), enabling widespread dissolution, of which the umbo region is especially susceptible. Extensive damage to the periostracum under a low salinity of 16 has also been recorded in *Mercenaria mercenaria* (hard-shell clam) in the western Atlantic, deterioration which was exacerbated by ocean acidification (Dickinson et al. 2013).

Function of the organic matrix

The role of the organic matrix is ambiguous. Shrouding the individual calcium carbonate crystals, it may have a protective role in helping to retard dissolution. Some bivalves enrich their biogenic shells with an increased proportion of organics to retard dissolution in unfavourable conditions, such as low salinity and pH (Lagos et al. 2021; Telesca et al. 2024). However, other studies show that the organic matrix may in fact encourage dissolution by serving as a microbial substratum, resulting in the interruption of the microstructural scaffold and individual crystals, increasing surface exposure and accelerating dissolution (Glover and Kidwell 1993; Peck et al. 2015; Chadwick et al. 2019). *C. glaucum* has an organic-poor microstructure (2.2 ± 0.4 wt%) and Taylor and Kennedy (1969) report only thin, 30-nm thick membranes between laths in the crossed-lamellar structure. The high energetic costs and structural limitations of the crossed-lamellar microstructure to incorporate increased amounts of organics may explain the lack of significant differences in organic content between specimens from low salinity MECH and those from variable coastal lagoons (Palmer 1983, 1992). However, broader sampling across a greater range of environmental conditions is needed to make more informed conclusions about potential microstructural adaptations.

Future outlook in the Baltic Sea

C. glaucum appears to have evolved significantly thicker shells and a distinct morphology to impede dissolution in the sustained critically corrosive low salinity conditions of the Baltic Sea. The contrasting responses observed in *M. balthica* and *Mytilus* spp. are interesting, and given the similar predation threats, suggests that microstructural characteristics drive contrasting responses to low salinity. These findings highlight some important insights into species-specific variation in low salinity biomineralisation. The absence of strong predators likely plays an auxiliary role, particularly the reduction of shell thickness observed in *Mytilus* spp.

Continued destabilisation of the climate may jeopardise the future of Baltic *C. glaucum*, and other benthic invertebrates, particularly if salinity declines further because of predicted increases in precipitation and river runoff (Kniebusch et al. 2019). The horohalinicum defines the critical salinity at 5–7 where species richness is minimal and the transition from freshwater to marine species abundance is marked (Kinne 1971). By end of century, the horohalinicum is predicted to retreat significantly southwards, with salinity declining to below 5 in the northern basins, 5–6 in the Baltic Proper and below 7 in its western reaches through to the Kattegat (Vuorinen et al. 2015). Salinity reductions will exacerbate the corrosive conditions and compromise shell integrity. Shifts in salinity will also be accompanied by significant temperature increases of approximately 2 °C (Meier et al. 2012), which is also encouraging the intrusion of non-indigenous opportunistic species from waters of warmer climates (Hinrichsen et al. 2022). The redistribution of species is reshaping the Baltic ecosystem, with significant consequences on food webs and predator–prey interactions (Westerbom et al. 2018; Serandour et al. 2024).

Conclusions

We revealed that *C. glaucum* in the Baltic Proper, where salinity is consistently maintained at less than 10, appear to exhibit shells that are up to 85.2% thicker than species in higher salinity environments, but to the detriment of shell size, with lengths limited to approximately 20 mm. Although true causality is not established in this study, the thickening observed likely compensates for the high levels of dissolution because of aragonite undersaturation, and is accompanied by a thicker protective periostracum. A morphological shift to a more globular shape also decreases the overall surface area and exposure to the corrosive sea water. Nevertheless, *C. glaucum* populations in locations with less favourable conditions, e.g. MECH and UJW, show that there are limitations to the species ability to effectively produce thicker shells and highlights the multistressor influence of environmental conditions. Continued anthropogenic activities are likely to persist in inducing additional stress on marine organisms including periods of low oxygen (Meier et al. 2012; Carstensen et al. 2014), though positive action is being taken to reduce eutrophication and pollution levels through strategies such as the Baltic Sea Action Plan (Svendsen and Gustafsson 2022). Low total alkalinity also increases the vulnerability of the Baltic Sea to ocean acidification (Havenhand 2012), which will further intensify dissolution risk. These multifactorial challenges and the low levels of genetic variation may limit the capacity of *C. glaucum* to adapt to the rapidly changing environment.

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Data availability The datasets generated during and analysed in the current study are available in the GitHub repository https://github.com/bethanyfrancesking/C.-glaucum-in-the-Baltic-Sea.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval This work did not require ethical approval from a human subject or animal welfare committee.

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