

**Comparative studies on
the morphometry and
physiology of European
populations of the lagoon
specialist *Cerastoderma
glaucum* (*Bivalvia*)***

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Abstract

Seasonal changes in the morphometric and physiological parameters of the cockle *Cerastoderma glaucum* (*Bivalvia*) from the Baltic Sea (GD), the North Sea (LV), and the Mediterranean Sea (BL) were investigated. The cockles from GD were much smaller than those from other populations due to osmotic stress. The female to male ratios did not differ significantly from 1:1. The northern populations

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(GD, LV) had a monocyclic reproductive pattern, whereas the southern population (BL) seemed to reproduce throughout the year. Seasonal changes in the contents of biochemical components appeared to be correlated with changes in trophic conditions and the reproductive cycle. Protein content was the highest in spring for all the populations. The highest lipid contents and lowest carbohydrate contents were noted in GD and BL in spring, while no marked differences were noted among seasons in LV (probably because the data from both sexes were pooled). Respiration rates in GD were the highest among the populations, which could have been due to osmotic stress. High metabolic rates expressed by high respiration rates in GD and LV in spring and autumn could have resulted from gamete development (in spring) and phytoplankton blooms (in spring and autumn).

1. Introduction

Suspension-feeding bivalves are often key species in estuarine and coastal habitats (Gili & Coma 1998). Changes in their growth rates, abundance, or distribution can have cascading effects on both benthic and pelagic ecosystems (Newell 2004). Therefore, bivalve preferences and environmental condition limits need to be studied to predict the consequences of environmental perturbations, such as global warming (Hughes 2000) or eutrophication (Cloern 2001).

The lagoon cockle, *Cerastoderma glaucum* (Lamellibranchia: Cardiidae), is a bivalve that inhabits seas across Europe from the Caspian to the Baltic (Brock 1979). It tolerates temperatures from 0°C to over 45°C (Zaouali 1974), and salinities from 5 to at least 45 PSU (Rygg 1970). The distribution of *C. glaucum* is fragmented, as it is usually restricted to isolated or semi-isolated, shallow, non-tidal biotopes, like brackish lagoons (Russell 1972). These habitats are often fragile, highly unpredictable, and more frequently subjected to short-term variations in temperature, salinity and pH than are marine habitats (Bamber et al. 1992). Restricted gene flow among these water basins can lead to local selection and adaptation to different environmental conditions as well as to genetic drift within populations (Pearson 2003). In the present study, the adaptations to local conditions in *C. glaucum* were investigated by comparing some morphometric and physiological parameters among three European populations.

2. Material and methods

Samples were collected from the Gulf of Gdańsk-GD (Baltic Sea, Poland; sampling by dragging from a depth of 5 metres performed 5 times between October 2005 and September 2006), Lake Veere-LV (North Sea, the Netherlands; sampling by hand from a depth of about 1 metre performed 4 times between November 2006 and August 2007), and the Berre La-

goon-BL (Mediterranean Sea, France; sampling by hand from a depth of about 1 metre performed 4 times between February 2007 and November 2007) (Figure 1). During each sampling event, water temperature and salinity were also measured.

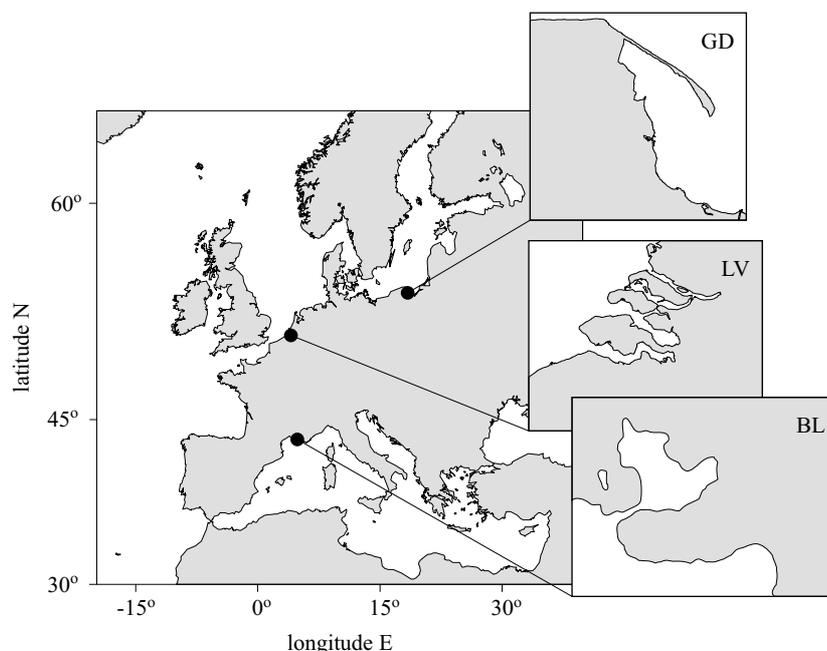


Figure 1. Sampling locations: Gulf of Gdańsk, Baltic Sea, Poland (GD) (54°40'N, 18°30'E); Lake Veere, North Sea, the Netherlands (LV) (51°35'N, 3°38'E); Berre Lagoon, Mediterranean Sea, France (BL) (43°24'N, 5°08'E)

Shell length was measured with slide callipers to the nearest 0.01 mm. Soft tissues were frozen at -80°C and freeze-dried for 72 h. The shells were dried at 55°C . The morphometric condition index (CI), which is the soft tissue dry weight per shell volume calculated from $(\text{length})^3$, was determined (Beukema & De Bruin 1977). Sex and gonad development stage were analysed under a microscope and classified according to a 5-stage scale: 1 – initiation of gametogenesis; 2 – development; 3 – ripe stage; 4 – spawning; 5 – post-spawning (Wołowicz 1987). Gonadic indices (GI) were calculated as follows: $\text{GI} = \sum (\text{number of individuals at each gonad maturity stage} \times \text{numerical value of the stage}) / \text{total number of individuals in the sample}$ (Chipperfield 1953). The numerical values of the maturity stages were the same as the stage numbers (from 1 to 4) except for the post-spawning stage, which had a numerical value of 0, not 5. Dry soft tissues were homogenised with a planetary micro mill (Fritsch

Pulverisette 7). Protein (Lowry et al. 1951), lipid (Bligh & Dyer 1959, Marsh & Weinstein 1966), carbohydrate and glycogen (Dubois et al. 1956) contents were determined. These parameters were determined for 30 individuals per season per site.

Oxygen consumption was measured every season for 45 to 120 minutes at 4, 10, 17 and 24°C in temperature-controlled respiration chambers with a volume of 0.3 dm³ on 5–10 (LV and BL) or about 20 (GD – due to the smaller, average size) individuals per chamber. The individuals were purged overnight in filtered water from the sampling site and at the ambient temperature of the site in order to prevent any disturbance in oxygen consumption due to (pseudo)faeces. The decrease in oxygen tension was measured with YSI 5331 oxygen probes (Clark type polarographic electrodes). The measurements were performed in three replicates (3 respiration chambers) and in one control chamber without animals. After the experiment, the animals were frozen at –80°C and freeze-dried for 72 h to the soft tissue dry weight. Respiration rates were calculated.

Statistical analyses were performed using STATISTICA v. 8. The χ^2 test was applied to test the significance of differences in the sex ratio. The normality of the data distribution was checked using the Shapiro-Wilk test (significance level 5%). The statistical significance of differences in morphometric parameters among seasons and sites was verified using Kruskal-Wallis non-parametric ANOVA.

3. Results

In each season, the water temperature in BL was higher than at other sampling sites. GD differed from the other sites because of its much lower water salinity (Table 1), and the individuals from GD were generally much smaller than those from LV or BL (Figure 2). Based on the assumption that the values of morphometric parameters do not change a lot year on year, as our results were similar to those obtained by Wołowicz (1991), the measurements from different seasons are arranged from winter to autumn to

Table 1. Temperatures T [°C] and salinities S [PSU] measured at each sampling site each season

Site	GD		LV		BL	
	T	S	T	S	T	S
winter	2.0	7.3	3.0	23.1	15.0	19.5
spring	12.0	6.0	15.0	27.3	20.0	22.9
summer	23.9	6.2	19.0	28.5	28.0	25.2
autumn	14.1	7.0	10.0	28.5	22.0	22.0

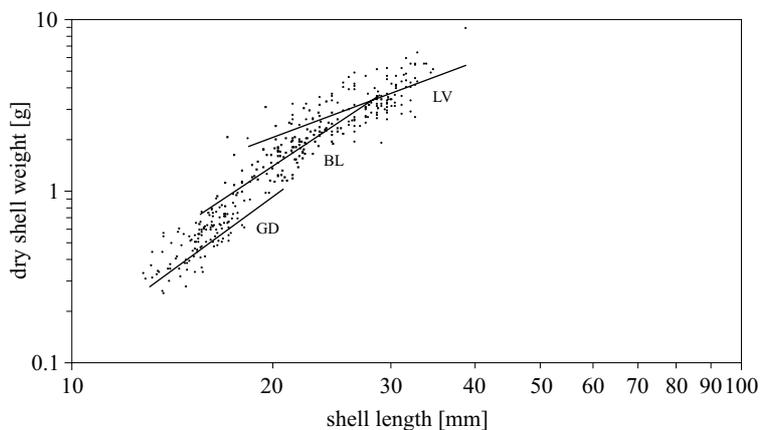


Figure 2. Dry shell weights [g] plotted against shell lengths [mm] on a logarithmic scale; GD: $y = 0.00021x^{2.85317}$ ($R^2 = 0.64458$), LV: $y = 0.03030x^{1.44442}$ ($R^2 = 0.37716$), BL: $y = 0.00069x^{2.58453}$ ($R^2 = 0.67520$)

facilitate comparisons among populations in the graphs. Most shell length, soft tissue dry weight and shell dry weight data did not have normal distributions. However, distributions were unimodal, so averages (\pm SD) instead of medians were calculated. Differences in soft tissue dry weight and in shell length were significant among sites ($p < 0.001$) but were non-significant among seasons within sites ($p > 0.001$). The mean shell lengths of cockles used to investigate condition and biochemical composition were 15.83 mm (SD = 1.46) for GD, 27.80 mm (SD = 3.26) for LV, and 20.95 mm (SD = 2.47) for BL. Differences in condition index were significant among sites ($p < 0.001$) and among seasons within sites ($p < 0.001$; at BL – $p < 0.01$) (Figure 3). The average female to male ratios were 1:0.74 for GD, 1:1.22 for LV and BL, neither of which differed significantly from 1:1 ($p > 0.05$). Most of the differences in sex ratios among seasons and sites were non-significant ($p > 0.05$). In GD and LV only one summer spawning period was observed, whereas in BL the differences in gonadic indices among seasons were less marked, and it was hard to identify a distinct spawning season (Figure 4). Protein contents were between 37.5% and 77.4%, lipid contents were between 5.7% and 13.6%, and the protein content was the highest in spring for all the populations (Figure 5a). In GD and BL, the lipid content was the highest in spring (Figure 5b). Carbohydrate contents were between 4.1% and 16.1%, and glycogen contents were between 2.8% and 13.3%. Glycogen comprised from about half to all of the carbohydrate content. Carbohydrate and glycogen contents in GD and BL were the lowest in spring (Figures 5c–d). In LV, the differences in lipid, carbohydrate, and glycogen contents among seasons were much less pronounced than

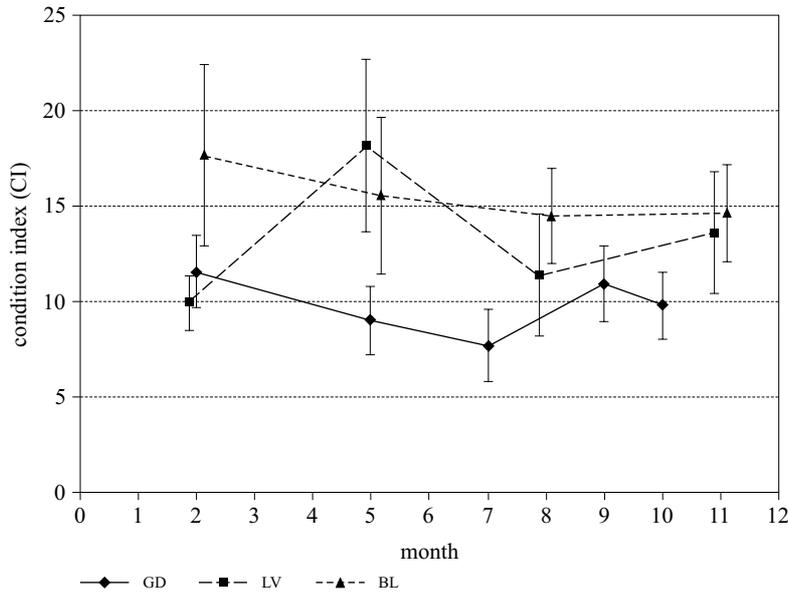


Figure 3. Seasonal changes in condition index (CI), expressed as the soft tissue dry weight per shell volume calculated from $(\text{length})^3$ (Beukema & De Bruin 1977)

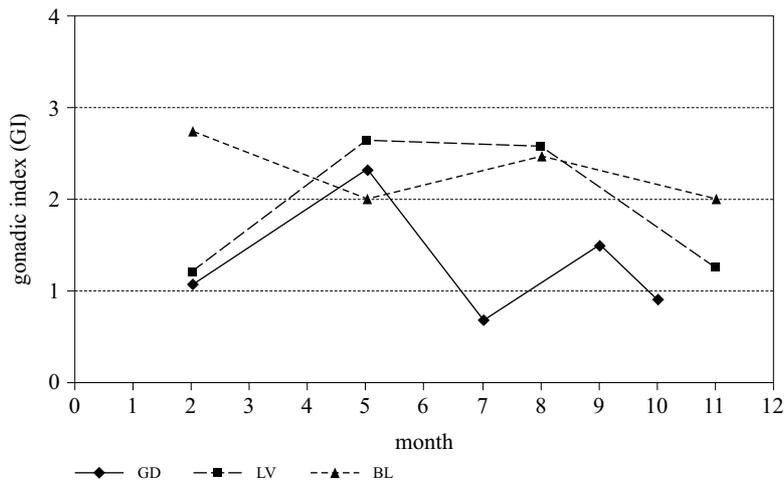


Figure 4. Seasonal changes in gonadic index; $GI = \sum (\text{number of individuals at each gonad maturity stage} \times \text{numeric value of the stage}) / \text{total number of individuals in the sample}$ (Chipperfield 1953). When $GI = 0$, all the gonads have already spawned and they are empty, and when $GI = 4$ all the gonads are spawning

in the other populations (Figures 5b–d). The sum of protein, lipid, and carbohydrate contents in the soft dry tissue of *Cerastoderma glaucum* was

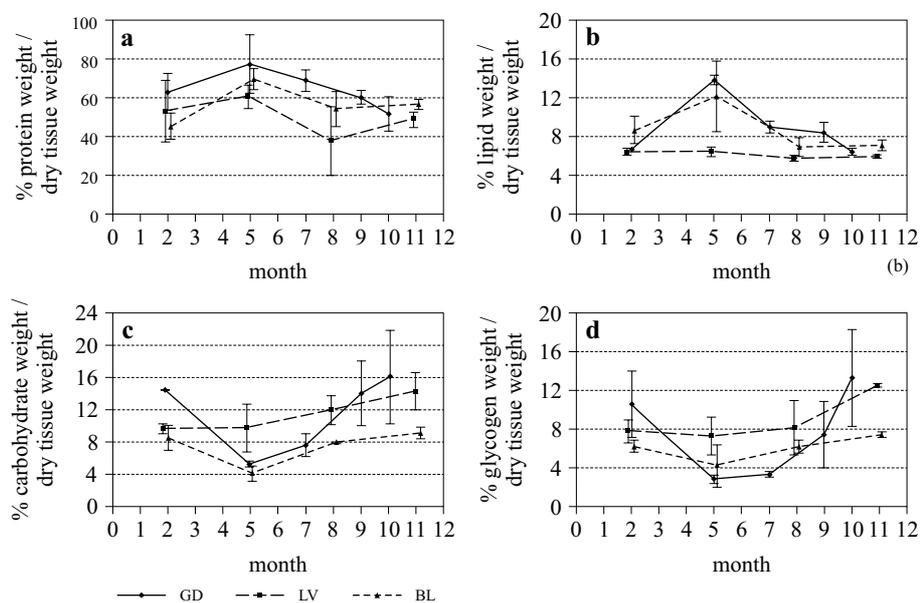


Figure 5. Seasonal changes in biochemical component contents: (a) protein, (b) lipid, (c) carbohydrate, (d) glycogen

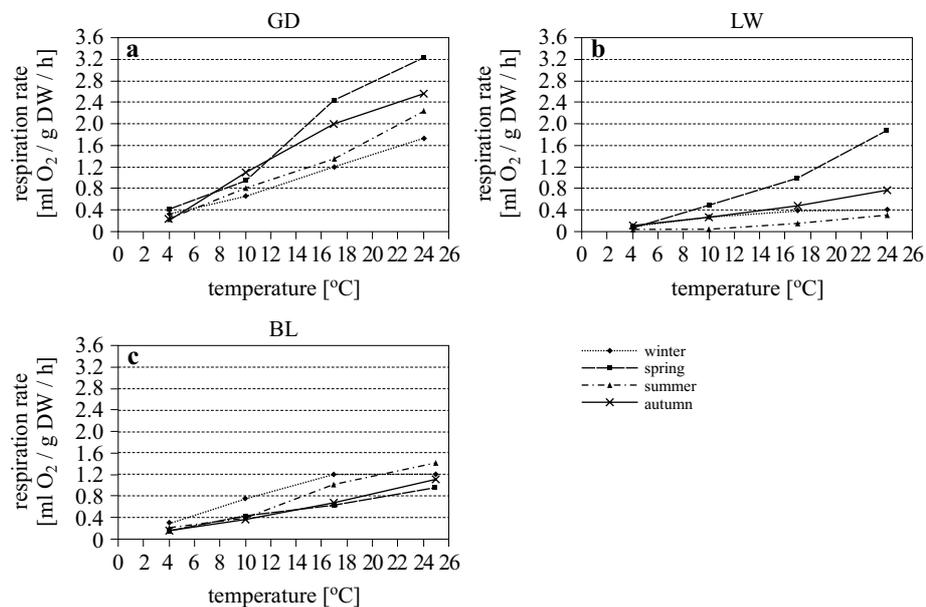


Figure 6. Seasonal changes in the respiration rate at different water temperatures. Measurements were averaged among three replicates: (a) Gulf of Gdańsk (GD), (b) Lake Veere (LV), (c) Berre Lagoon (BL)

from 55.1% to 96.3%. Respiration rates were the lowest at 4°C. In GD and LV, they were the highest in spring and autumn. In GD, the respiration rates were higher than in the other populations, while in BL, most of the winter and summer respiration rates were higher than spring and autumn rates at the same temperatures (Figure 6).

4. Discussion

4.1. Environmental conditions

The temperatures of the northern locations (GD and LV) are similar (IMGW 2009, RIKZ & RIZA 2009), whereas BL has high water temperatures and intense evaporation in summer, which raises the salinity (Stora et al. 1995, Gouze et al. 2005). The low salinity of around 5–7 PSU (Nowacki 1993) makes GD different from the other sampling locations. In LV, the salinity varies from around 22 to 30 PSU, and in spring it increases because North Sea water is let in through the dam (Nienhuis 1992, RIKZ & RIZA 2009). In BL, there was an excessive freshwater inflow in 1966, resulting in a salinity decrease to below 10 PSU, but since 1997 the salinity has increased to around 20–25 PSU (Stora et al. 1995, Gouze et al. 2005). The salinity at all the sampling sites can be considered low in comparison to the average ocean salinity of around 35 PSU (Pickard & Emery 1990).

As *Cerastoderma glaucum* very rarely occurs in tidal areas, it is less subject to sudden changes of food supply than intertidal bivalves like *Cerastoderma edule*, which often experiences food shortages due to aerial exposure (Honkoop & Van der Meer 1998). Sarà (2007) indicated that in Mediterranean ponds the dominant organic source in the diet of *C. glaucum* was the detritus derived from the seagrass *Cymodocea nodosa*, the macroalga *Ulva lactuca*, and the sand microflora. However, it was observed that the sudden removal of nearly all mussels and cockles from the ecosystem led to increased diatom concentrations (Beukema & Cadée 1996), which indicates they are the main food of *C. glaucum* (Wołowicz 1991). Diatoms are an important component of the phytoplankton in GD (Pliński 1995, Wasmund et al. 1998), LV (Nienhuis 1992), and BL (Lelong & Riva 1976). In northern sampling locations, phytoplankton blooms take place in spring, with chlorophyll *a* concentrations reaching around 8–10 $\mu\text{g dm}^{-3}$ in GD (IMGW 2009) and around 25–55 $\mu\text{g dm}^{-3}$ in LV (RIKZ & RIZA 2009). There are also smaller blooms in autumn (Pliński 1995, RIKZ & RIZA 2009). Before 1997 in BL, phytoplankton blooms occurred in winter and spring, and chlorophyll *a* concentrations sometimes reached 300–400 $\mu\text{g dm}^{-3}$. Since then, however, chlorophyll *a* concentrations have decreased distinctly and now rarely exceed 20 $\mu\text{g dm}^{-3}$. There is no longer any spring bloom

and phytoplankton populations are much more stable, which has led to a decrease in the quantity of sestonic matter and diminishing eutrophication (Gouze et al. 2005). This has resulted in a reduction in the periods of anoxia in BL; these are common in lagoons and, together with elevated water temperatures, they can give rise to large-scale summer mortality events in benthic communities (Allen et al. 1995, Stora et al. 1995).

4.2. Morphometric parameters and condition indices

In addition to *C. glaucum*, there is another cockle species, *C. edule*, that inhabits European seas. There are areas where the two species occur sympatrically (Brock 1987), and distinguishing between these two species based on morphological traits is very difficult (Machado & Costa 1994). However, in the current study there is no risk of confusion between the two species as genetic studies based on mitochondrial DNA and microsatellites were also performed on the studied populations, proving that they consisted only of *C. glaucum* (Tarnowska et al. – submitted).

The cockles from GD were by far the smallest specimens collected at the sampling sites (Figure 2). This was because of the low average salinity in the Baltic Sea, which affects active intracellular transport, feeding rate and nutritive absorption, respiration, excretion, and, particularly, osmoregulation. Organisms under osmotic stress have to expend additional energy to maintain their haemolymph osmolality above that of the environment (Schmidt-Nielsen 1990). Consequently, less energy is expended for shell growth. In the Baltic Sea, a tendency for shell length to decrease in parallel with a drop in salinity was reported in *Macoma balthica* (Wenne & Klusek 1985). Environmental salinity and temperature influence shell size and shape (Eisma 1965), as well as its composition (aragonite and calcite proportions) (Kennedy et al. 2008). The physiological parameters depend on body size and age (Najdek & Sapunar 1987, Navarro et al. 1989, Yukihiro et al. 1998, Sukhotin et al. 2003). The average shell lengths and dry tissue weights of cockles differed among the studied populations, which makes interpopulational comparisons less reliable. On the other hand, shell sizes at which cockles reach maturity and also their maximum body sizes differ among populations. Therefore, it was not possible to sample animals of the similar size. However, differences in shell lengths and dry tissue weights among seasons and within sites were non-significant, so it is plausible that comparisons within populations are not affected by this factor.

The condition index depends mainly on bivalve growth, metabolism and gonad development stage (Lucas & Beninger 1985, Smaal & Stralen 1990, Hummel et al. 2000b). For northern populations of European bivalves with

a monocyclic reproduction pattern, the highest values of condition index were reported in spring, before spawning (*C. glaucum*, Wołowicz 1991, *M. balthica*, Hummel et al. 2000b, *Mytilus trossulus*, Wołowicz et al. 2006). The seasonal changes of condition index that we found in northern populations (GD, LV) did not fully reflect this pattern. In GD, CI decreased between spring and summer because of spawning. The subsequent increase between summer and autumn may have been caused by favourable trophic conditions resulting from autumn phytoplankton blooms (Pliński 1995). In LV, CI increased between winter and spring because of gonad development and phytoplankton blooms; surprisingly, this was not the case in GD. In LV, CI was low in summer, although, according to gonad development stage analysis, the spawning stage (stage IV) prevailed, so a high condition index was expected. The reason for this could have been that gonad development stages and condition indices were determined on different individuals. It is possible that the individuals used for CI measurements had already spawned. In winter, the CI for LV was low, which was not the case for GD. Studies on *C. edule*, *Mytilus edulis*, and *M. balthica* proved that in bivalves from temperate latitudes (like GD and LV) body mass (and condition index) declines in winter (Honkoop & Beukema 1997). In BL, differences in condition index among seasons were not distinct, as the cockles spawn throughout the year. Bivalve condition can be influenced by parasites, which were not found in this study, but since only a small piece of gonad tissue was scanned, their presence cannot be excluded. *C. glaucum*, as well as *C. edule*, are host species for the metacercariae of parasites from the genus *Meiogymnophallus* (Digenea: Gymnophallidae) (Bowers et al. 1996). Condition index has also been reported to decrease with increasing age and size (Wenne & Styczyńska-Jurewicz 1985, Bawazir 2000).

4.3. Reproduction

Differences in the *C. glaucum* sex ratio among seasons were mostly non-significant. In some molluscs, like *Chlamys islandica* (Brokordt & Guderley 2004) or *M. trossulus* (Wołowicz et al. 2006), increased female mortality after spawning was reported owing to the high cost of gonad maturation and spawning. In other species, like *Choromytilus meridionalis* (Griffiths 1977) or *Perna perna* (Lasiak & Dye 1989), the male:female sex ratios reportedly did not differ significantly from 1:1. The northern populations of *C. glaucum* (GD, LV) have a monocyclic reproductive cycle with the initialisation of gametogenesis in September/October and spawning between May and July. LV seemed to reproduce later than GD. Even populations experiencing similar thermal regimes (like GD and LV) can exhibit temporal discrepancies in the reproductive cycle as a result of

variations in food availability (Newell et al. 1982, Navarro et al. 1989). In the southern population (BL), spawning cockles were present throughout the year, because higher water temperatures result in prolonged spawning in comparison to that in boreal areas (Pieters 1980). Ivell (1979) found that Mediterranean populations of *C. glaucum* spawn up to three times a year. The current seasonal sampling was definitely not frequent enough to allow precise statements to be made concerning the BL population, which spawns a few times a year. Thus, more detailed studies with monthly sampling are needed, like Bachelet's (1980) study on a *M. balthica* population from the south-west of France. As for the northern populations, the current data indicating a monocyclic reproductive cycle is in accordance with previous research on the *C. glaucum* populations of northern Europe, where sampling was carried out more often (e.g. Wołowicz 1991, Brock & Wołowicz 1994). The timing of *C. glaucum* spawning depends on the water temperature; it starts at 15–17°C, so the more northerly the locality inhabited by a population, the later reproduction begins (Kingston 1974, Ivell 1979, Wołowicz 1991, Brock & Wołowicz 1994). Temperature and food availability have been proven to be critical for spawning in *M. balthica*, *C. edule*, *M. edulis* (Honkoop & Van der Meer 1998), and also *C. glaucum* (Kingston 1974).

4.4. Biochemical composition

Energy input in excess of metabolic requirements can be utilised for somatic growth and/or gamete production. Energy allocation to reproduction differs with age and size, as young bivalves grow rapidly and convert little or no energy into reproduction (Kautsky 1982). Changes in biochemical composition were shown to be correlated with the reproductive cycle in (adult) bivalves, as in, for example, Pelecypoda (Sastry 1979), *M. edulis* (Pazikowska & Szaniawska 1988), *Pecten maximus* (Pazos et al. 1997), or *P. perna* (Bawazir 2000). Bayne (1976) divided bivalves into two groups. In 'conservative' species, like *M. trossulus* (Bawazir 2000), gametogenesis occurs in autumn-winter at the expense of nutrient stores accumulated during the previous summer, which results in an inverse relationship between the levels of biochemical components (mainly carbohydrates) and reproductive condition. In 'opportunistic' species, like *P. perna* (Bawazir 2000), *Ostrea edulis* (Ruiz et al. 1992) or *C. glaucum*, winter is a period of sexual 'rest', and gametogenesis starts in spring, when sufficient food is available to fuel biosynthesis. Therefore, gonad development and the accumulation of energy reserves overlap temporally.

Trophic conditions also determine seasonal changes in the contents of biochemical components. Unfavourable trophic conditions first induce the

catabolisation of carbohydrates, then of lipids, and, finally, of structural proteins (Beninger & Lucas 1984). Wołowicz (1991) suggested that in southern populations of *C. glaucum* periods of unfavourable conditions are short, so they result in carbohydrate catabolism, whereas in northern populations long periods of unfavourable environmental conditions lead to lipid decomposition.

The protein and lipid contents in the tissue of *C. glaucum* reported by Wołowicz (1991) were the highest in spring in the northern populations, whereas the differences among seasons in the southern populations were small. These contents increase in female tissues before spawning and then decrease after spawning, since proteins and lipids are the main components of oocytes (Gabbott 1975, Pieters et al. 1979, Houlihan 1991). This trend was visible in GD. Proteins are synthesised during gametogenesis, while lipids are partially moved from somatic tissues to the gonads (Holland 1978, Barber & Blake 1981). In LV, differences among seasons, especially in lipid content, were not distinct. There was no spring increase in lipid content despite gamete development. This may have been due to the pooling of the sexes for the biochemical composition analyses, since no clear relationship between lipid levels and reproduction should be expected in males (Navarro et al. 1989). Although there is no clear spawning season in BL, protein and lipid contents decreased between spring and summer, which could have been due to unfavourable trophic conditions, as lipids also serve as an energy reserve during periods of nutritional stress (Beukema & De Bruin 1977, Beninger & Lucas 1984). In many bivalves, lipids are stored mainly in the gonads (e.g. *M. edulis*, Zandee et al. 1980, *M. balthica*, Wenne & Styczyńska-Jurewicz 1987). Lipids can also be stored in the digestive glands as surplus energy to be transferred to the gonads when needed (*Chlamys opercularis*, Taylor & Venn 1979).

The lowest carbohydrate and glycogen contents were noted in GD in spring, because glycogen is used for gonad development. In females, it is converted into lipids in the oocytes. The increase in the carbohydrate content of northern populations (GD, LV) between summer and autumn seems to be correlated with phytoplankton blooms (Wasmund et al. 1998). While in BL the differences among the seasons in carbohydrate content are small, they could be due to changes in trophic conditions (Wołowicz 1991). In LV, the seasonal differences are less marked, which could also be influenced by the fact that the data from both sexes were pooled and were not divided into age groups (Newell & Bayne 1980, Navarro et al. 1989, Wołowicz et al. 2006).

The protein, lipid, and carbohydrate contents did not add up to 100% (55.1%–96.3%), because the other components were ash, nucleic acids and

free amino acids, which comprised around 7–12% of the dry weight (Pieters et al. 1980), with the remaining water comprising 2–3% of the dry weight (Beukema & De Bruin 1979). In the *P. perna* and *M. trossulus* bivalves, the protein, lipid, and carbohydrate contents made up c. 60–75% (Bawazir 2000).

4.5. Respiration

Oxygen consumption reflects the metabolic activity of an organism and is proportional to its instantaneous ATP demand. The synthesised ATP is utilised in various processes, including ion pump activity, muscular activity, neural activity, growth, gametogenesis and catabolite excretion (Bayne & Newell 1983, Clarke 1991). Metabolic activity is influenced by ambient temperature (Clarke 1991). Reduced oxygen uptake can indicate stress and reduced feeding activity (Akberali & Trueman 1985, Riisgård et al. 2003). Some molluscs are able to use anaerobic pathways as an energy source when they are exposed to stress (Liu et al. 1990, Oeschger 1990), which can bias conclusions on energy metabolism based on respiration rate measurements. It was found that oxygen consumption increases with bivalve size according to the power law, $R = aW^b$, where R is oxygen uptake, W is the body weight, a is the intercept, and b is the slope. Metabolic rates rise more slowly than body size, because $b < 1$ (Dame 1996). Therefore, because of significant differences in dry tissue weights among populations ($p < 0.001$), the current results could serve better for comparisons within populations among seasons than among populations.

Apart from GD, where respiration rates were higher than in other populations, oxygen uptake rates were within the same range as those reported for *C. glaucum* (Wilson & Elkaim 1997) and other bivalves (McMahon & Wilson 1981, Wilson & Davis 1984, Wilson 1990, Wilson & Elkaim 1991, Hummel et al. 2000b). The exceptionally high respiration rates in GD cockles, which, to our knowledge, have not been reported before in Baltic Sea invertebrates, could be due to elevated metabolic levels because of the energetic costs of osmotic adjustment to low water salinity (Engel et al. 1975, Newell 1979). In spring, the metabolic levels and oxygen consumption of GD and LV were high, and the cockles were sensitive to temperature increase as they needed additional energy for gonad development. The respiration rate can increase by about 30–80% in reproducing cockles (*C. edule*) (Iglesias & Navarro 1991), and by more than 50% in mussels (*M. edulis*) (De Vooys 1976). Metabolic rates decreased in both GD and LV in summer, by which time many individuals had probably already spawned. The autumn metabolic rate was high as well in GD and LV, because of phytoplankton blooms and increased feeding activity

(Wołowicz 1991). In winter, respiration rates were low. The metabolic rate of another cockle species, *C. edule* from England, measured as the rate of oxygen consumption, was lowest in winter (December to March; Newell & Bayne 1980). Respiration rates in the BL population, which experiences high temperatures during summer, were higher in winter than in summer (except at 24°C). This was also noted for *C. glaucum* from the southwest coast of France (Arcachon) and was interpreted as metabolic down-regulation aimed at saving energy (Wilson & Elkaim 1997); this also occurs in some marine ectotherms at high water temperatures during summer (Calow 1975, Jansen et al. 2007). On the other hand, the respiration rate in BL at 24°C (which is close to the ambient summer temperature in this lagoon) was the highest in summer, so the current data do not demonstrate metabolic down-regulation in *C. glaucum*.

4.6. Conclusions and perspectives

C. glaucum is a eurytopic lagoon specialist adapted to extreme environmental conditions, like the low salinity of the Baltic Sea, or the extremely high summer temperatures in Mediterranean Sea lagoons, like those of the Berre Lagoon. Changing environmental conditions in the Berre Lagoon lead to rapid fluctuations of dominant macrobenthic species and often to their extinction. However, *C. glaucum* seems to be a stable element of the communities in this lagoon (Stora et al. 1995, Stora et al. 2004), which also demonstrates the resistance of this species to extreme and unstable environmental conditions. There are substantial physiological differences among *C. glaucum* populations (Wołowicz 1987, Wołowicz 1991, Wilson & Elkaim 1997) owing to individual acclimatisation or genetically fixed adaptations (Nevo 1978, Brock & Wołowicz 1994). Lagoon isolation impedes gene flow and has been proved to facilitate both genetic drift and local adaptations (Porter et al. 2001, Pearson 2003). A high level of genetic structuring was found in the European populations of *C. glaucum* (Hummel et al. 1994, Mariani et al. 2002, Nikula & Väinölä 2003), so local adaptations were to be expected. Translocation experiments could be helpful to verify whether cockles from distant locations can survive in basins with different environmental conditions (Hummel et al. 2000a). The molecular background of physiological responses and adaptation mechanisms in *C. glaucum* could be better understood by studying, for example, heat shock proteins (HSP), whose expression is increased when the cells are exposed to high temperatures or other stress factors (Lyons et al. 2003). As far as morphometric and physiological analyses are concerned, seasonal sampling appears to be insufficient for understanding the physiological performance of *C. glaucum* under different

environmental conditions since there are probably also some short-term variations in these parameters. Therefore, monthly sampling would be advisable in a subsequent study.

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