

**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

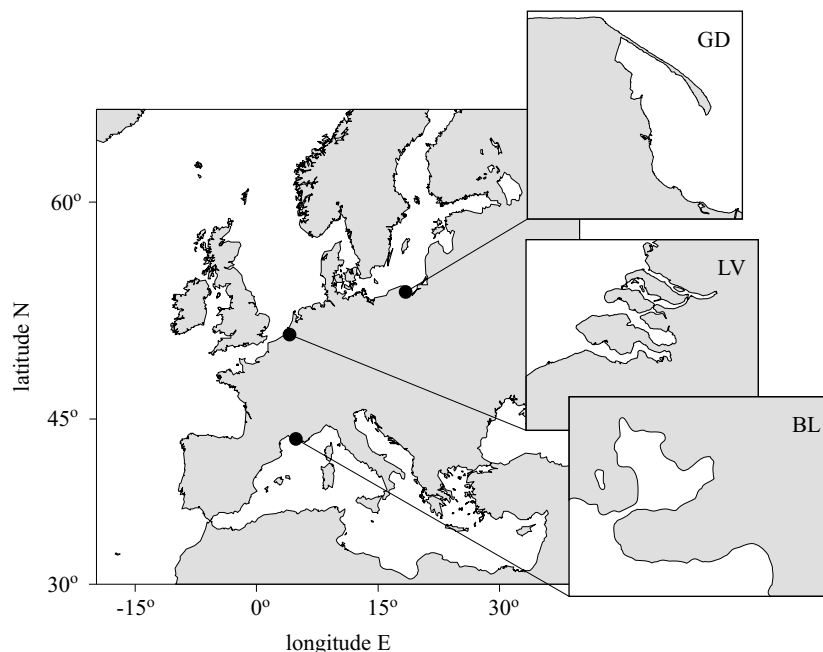
Suspension-feeding bivalves are often key species in estuarine and coastal habitats (Gili & Coma 1998). Changes in their growth rates, abundance, or distribution can have cascading effects on both benthic and pelagic ecosystems (Newell 2004). Therefore, bivalve preferences and environmental condition 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  $-80^{\circ}\text{C}$  and freeze-dried for 72 h. The shells were dried at  $55^{\circ}\text{C}$ . 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 dm<sup>3</sup> 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.

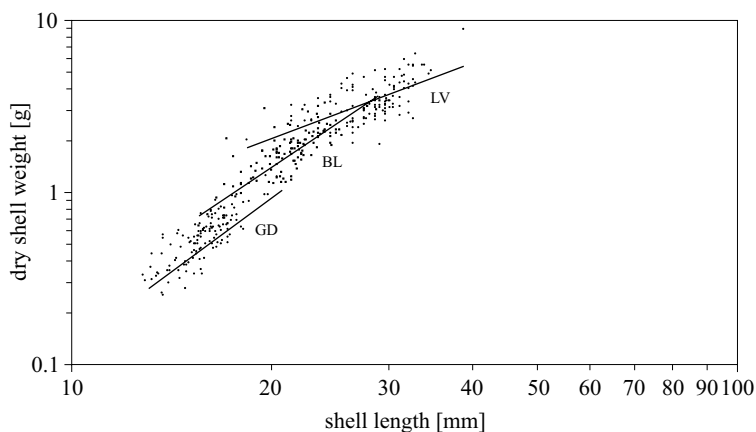
Statistical analyses were performed using STATISTICA v. 8. The  $\chi^2$  test was applied to test the significance of differences in the sex ratio. The normality of the data distribution was checked using the Shapiro-Wilk test (significance level 5%). The statistical significance of differences in morphometric 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

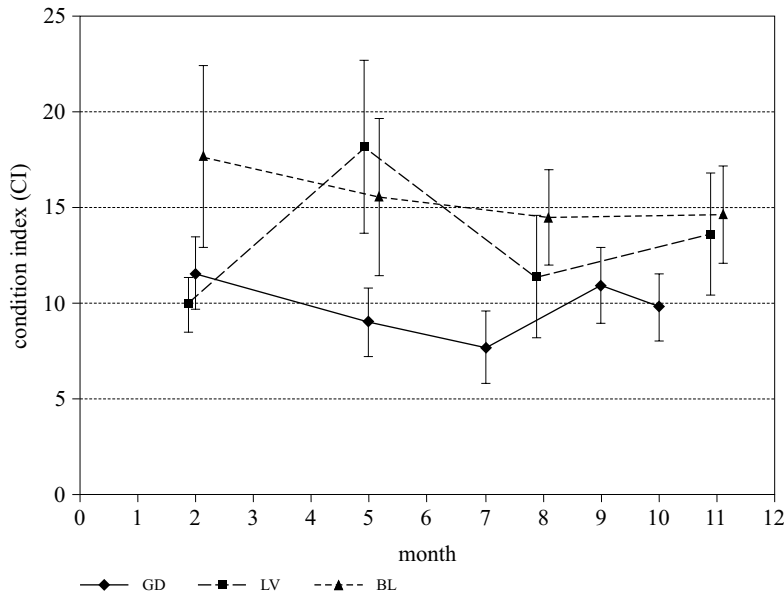
**Table 1.** Temperatures T [°C] and salinities S [PSU] measured at each sampling site each season

Site Parameters	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

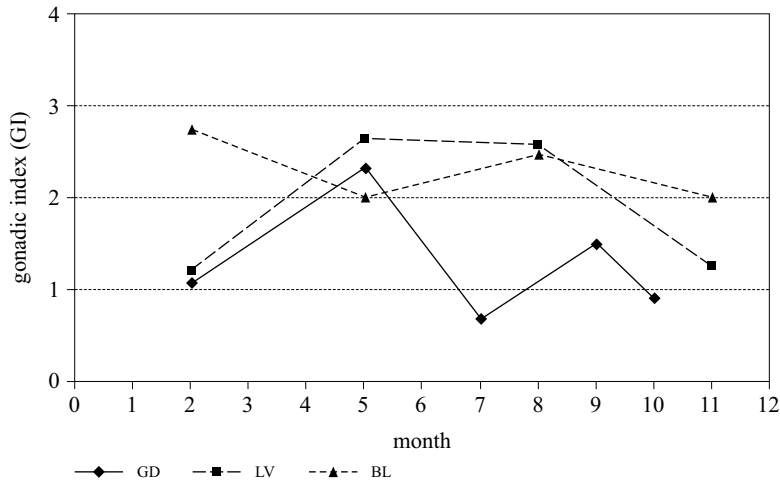


**Figure 2.** Dry shell weights [g] plotted against shell lengths [mm] on a logarithmic scale; GD:  $y = 0.00021x^{2.85317}$  ( $R^2 = 0.64458$ ), LV:  $y = 0.03030x^{1.44442}$  ( $R^2 = 0.37716$ ), BL:  $y = 0.00069x^{2.58453}$  ( $R^2 = 0.67520$ )

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

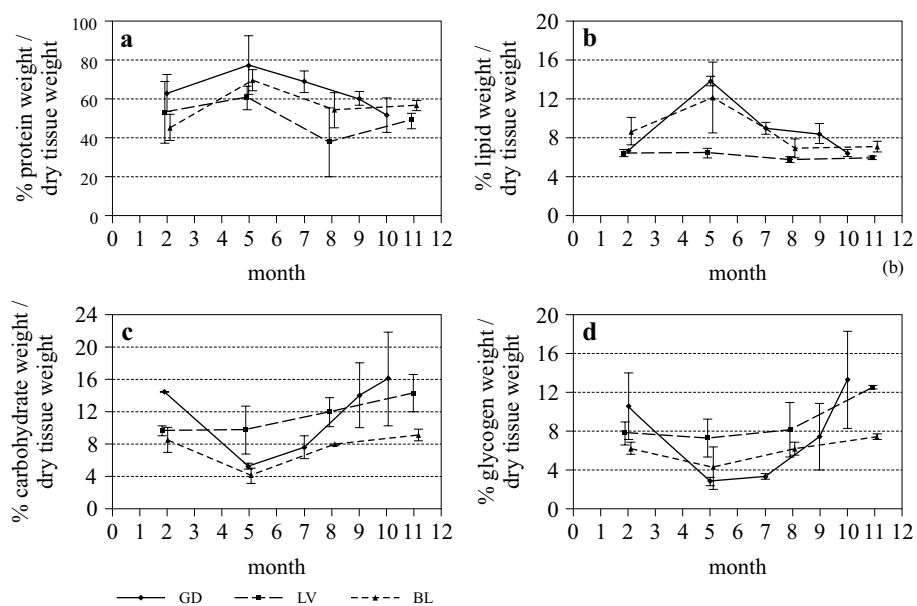


**Figure 3.** Seasonal changes in condition index (CI), expressed as the soft tissue dry weight per shell volume calculated from  $(\text{length})^3$  (Beukema & De Bruin 1977)

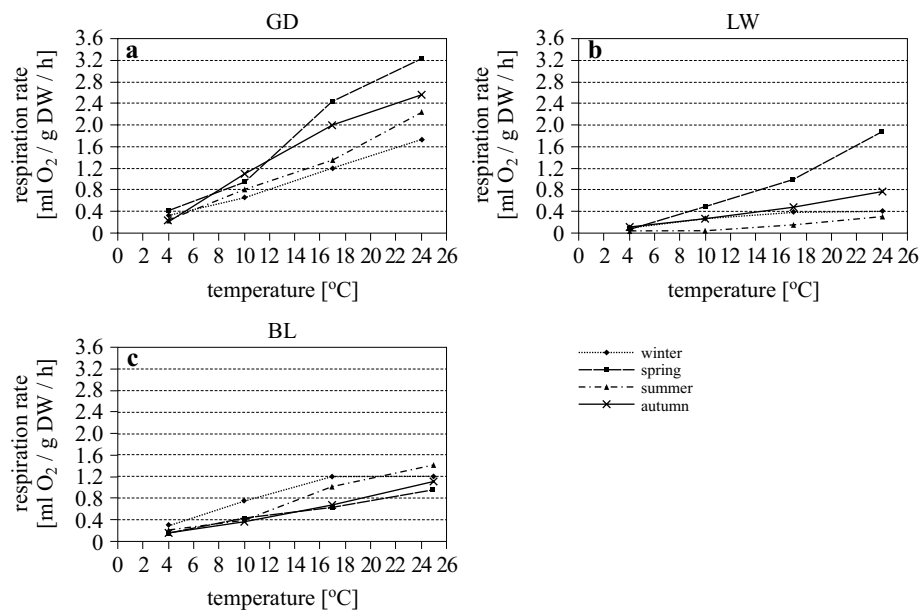


**Figure 4.** Seasonal changes in gonadic index;  $GI = \sum (\text{number of individuals at each gonad maturity stage} \times \text{numeric value of the stage}) / \text{total number of individuals in the sample}$  (Chipperfield 1953). When  $GI = 0$ , all the gonads have already spawned and they are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

- Akberali H. B., Trueman E. R., 1985, *Effects of environmental stress on marine bivalve molluscs*, Adv. Mar. Biol., 22, 101–136.
- Allen J. R., Wilkinson S. B., Hawkins S. J., 1995, *Redeveloped docks as artificial lagoons: the development of brackish-water communities and potential for conservation of lagoon species*, Aquat. Conserv., 5 (4), 299–309.
- Bachelet G., 1980, *Growth and recruitment of the tellinid bivalve Macoma balthica at the southern limit of its geographical distribution, the Gironde estuary (SW France)*, Mar. Biol., 59 (2), 105–117.
- Bamber R. N., Batten S. D., Shearer M., Bridgewater N. D., 1992, *On the ecology of brackish water lagoons in Great Britain*, Aquat. Conserv., 2 (1), 65–94.
- Barber B. J., Blake N. J., 1981, *Energy storage and utilisation in relation to gametogenesis in Argopecten irradians concentricus (Say)*, J. Exp. Mar. Biol. Ecol., 52 (2–3), 121–134.
- Bawazir A. S., 2000, *Comparative study on biology and ecology of mussels Perna perna, Linnaeus 1758, from tropical region (Gulf of Aden) and Mytilus trossulus, Gould 1850, from boreal region (Gulf of Gdańsk)*, Ph. D. thesis, Univ. Gdańsk, Gdańsk, 154 pp.
- Bayne B. L., 1976, *Aspects of reproduction in bivalve mollusks*, [in:] *Estuarine processes, Vol. 1. Uses, stresses and adaptation to the estuary*, M. Wiley (ed.), Acad. Press, London, 432–448.
- Bayne B. L., Newell R. C., 1983, *Physiological energetics of marine mollusks*, [in:] *The Mollusca. Vol. 4. Physiology. Part I*, A. S. M. Saleudin & K. M. Wilbur (eds.), Acad. Press, New York, 407–515.
- Beninger P. G., Lucas A., 1984, *Seasonal variations in condition, reproductive activity, and gross biochemical composition of two species of adult clam reared in common habitat: Tapes decussatus L. (Jeffreys) and Tapes philippinarum (Adams Reeve)*, J. Exp. Mar. Biol. Ecol., 79 (1), 19–37.

- Beukema J. J., Cadée G. C., 1996, *Consequences of the sudden removal of nearly all mussels and cockles from the Dutch Wadden Sea*, Mar. Ecol., 17 (1–3), 279–289.
- Beukema J. J., De Bruin W., 1977, *Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve Macoma balthica L. in the Dutch Wadden Sea*, Neth. J. Sea Res., 11 (1), 42–55.
- Beukema J. J., De Bruin W., 1979, *Calorific values of the soft parts of tellinid bivalve Macoma balthica (L.) as determined by two methods*, J. Exp. Mar. Biol. Ecol., 37 (1), 19–30.
- Bligh E. G., Dyer W. J., 1959, *A rapid method of total lipid extraction and purification*, Can. J. Biochem. Physiol., 37 (8), 911–917.
- Bowers E. A., Bartoli P., Russell-Pinto F., James B. L., 1996, *The metacercariae of sibling species of Meiogymnophallus, including M. rebecqui comb. nov. (Digenea: Gymnophallidae), and their effects on closely related Cerastoderma host species (Mollusca: Bivalvia)*, Parasitol. Res., 82 (6), 505–510.
- Brock V., 1979, *Habitat selection of two congeneric bivalves, Cardium edule and C. glaucum in sympatric and allopatric populations*, Mar. Biol., 54 (2), 149–156.
- Brock V., 1987, *Genetic relations between the bivalves Cardium (Cerastoderma) edule, Cardium lamarcki and Cardium glaucum, studied by means of crossed immunoelectrophoresis*, Mar. Biol., 93 (4), 489–498.
- Brock V., Wołowicz M., 1994, *Comparisons of European populations of the Cerastoderma glaucum/C. lamarcki complex based on reproductive physiology and biochemistry*, Oceanol. Acta, 17 (1), 97–103.
- Brokordt K. B., Guderley H. E., 2004, *Energetic requirements during gonad maturation and spawning in scallops: sex differences in Chlamys islandica (Muller 1776)*, J. Shellfish Res., 23 (1), 25–32.
- Calow P., 1975, *The respiratory strategies of two species of freshwater gastropods (Ancylus fluviatilis Mull. and Planorbis contortus Linn.) in relation to temperature, oxygen concentration, body size and season*, Physiol. Zool., 48 (2), 114–129.
- Chipperfield P. N. J., 1953, *Observations on the breeding and settlement of Mytilus edulis (L.) in British waters*, J. Mar. Biol. Assoc. U. K., 32 (2), 449–476.
- Clarke A., 1991, *What is cold adaptation and how should we measure it?*, Am. Zool., 31 (1), 81–92.
- Cloern J. E., 2001, *Our evolving conceptual model of coastal eutrophication problem*, Mar. Ecol.-Prog. Ser., 210, 223–253.
- Dame R. F., 1996, *Ecology of marine bivalves: an ecosystem approach*, CRC Mar. Sci. Ser., Boca Raton, 254 pp.
- De Vooy C. G. N., 1976, *The influence of temperature and time of the year on the oxygen uptake of the sea mussel Mytilus edulis*, Mar. Biol., 36 (1), 25–30.
- Dubois M., Gilles K. A., Hamilton J. K., Rebers P. A., Smith F., 1956, *Colorimetric method for determination of sugars and related substances*, Anal. Chem., 28 (3), 350–356.

- Eisma D., 1965, *Shell characteristics of Cardium edule L. as indicators of salinity*, Neth. J. Sea Res., 2 (4), 493–540.
- Engel D.W., Ferguson R.L., Eggert L.D., 1975, *Filtration rates and ATP concentrations in the excised gills of the blue crab as a function of salinity*, Comp. Biochem. Phys. A, 52 (4), 669–673.
- Gabbott P.A., 1975, *Storage cycle in marine bivalve mollusks: a hypothesis concerning the relationship between glycogen metabolism and gametogenesis*, Proc. 9th Europ. Mar. Biol. Symp., Univ. Press, Aberdeen, 191–211.
- Gili J.M., Coma R., 1998, *Benthic suspension feeders: their paramount role in littoral marine food webs*, Trends Ecol. Evol., 13 (8), 316–321.
- Gouze E., Raimbault P., Garcia N., 2005, *Ecological survey of the Berre Lagoon. Chemical analysis*, Report, GIPREB, COM, Univ. Méditerranée, France, 21 pp., (in French).
- Griffiths R.J., 1977, *Reproductive cycles in littoral populations of Choromytilus meridionalis (Kr.) and Aulacomya ater (Molina) with a quantitative assessment of gamete production in the former*, J. Exp. Mar. Biol. Ecol., 30, 53–71.
- Holland D.L., 1978, *Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates*, [in:] *Biochemical and biophysical perspectives in marine biology*, D. C. Malins & J. R. Sargent (eds.), Acad. Press, London, 85–123.
- Honkoop P.J.C., Beukema J.J., 1997, *Loss of body mass in winter in three intertidal bivalve species: an experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour*, J. Exp. Mar. Biol. Ecol., 212 (2), 277–297.
- Honkoop P.J.C., Van der Meer J., 1998, *Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea*, J. Exp. Mar. Biol. Ecol., 220 (2), 227–246.
- Houlihan D.F., 1991, *Protein turnover in ectotherms and its relationships to energetics*, [in:] *Advances in comparative and environmental physiology*, Vol. 7, R. Gilles (ed.), Springer-Verlag, Berlin, 1–43.
- Hughes L., 2000, *Biological consequences of global warming: is the signal already apparent?*, Trends Ecol. Evol., 15 (2), 56–61.
- Hummel H., Bogaards R.H., Bachelet G., Caron F., Sola J.C., Amiard-Triquet C., 2000a, *The respiratory performance and survival of the bivalve Macoma balthica (L.) at the southern limit of its distribution area: a translocation experiment*, J. Exp. Mar. Biol. Ecol., 251 (1), 85–102.
- Hummel H., Sokołowski A., Bogaards R.H., Wołowicz M., 2000b, *Ecophysiological and genetic traits of the Baltic clam Macoma balthica in the Baltic: differences between populations in the Gdańsk Bay due to acclimatization or genetic adaptation?*, Int. Rev. Hydrobiol., 85 (5–6), 621–637.
- Hummel H., Wołowicz M., Bogaards R.H., 1994, *Genetic variability and relationships for populations of Cerastoderma edule and of the C. glaucum complex*, Neth. J. Sea Res., 33 (1), 81–89.

- Iglesias J. I. P., Navarro E., 1991, *Energetics of growth and reproduction in cockles (Cerastoderma edule): seasonal and age-dependent variations*, Mar. Biol., 111 (3), 359–368.
- IMGW, 2009, *The Baltic Sea*, Inst. Meteorol. Gosp. Wod., Gdynia, (available at <http://www.imgw.pl>).
- Ivell R., 1979, *The biology and ecology of the brackish lagoon bivalve, Cerastoderma glaucum Bruguiere in Lago Lungo, Italy*, J. Mollus. Stud., 45 (3), 364–382.
- Jansen J. M., Pronker A. E., Kube S., Sokolowski A., Sola J. C., Marquiegui M. A., Scheidek D., Bonga W. S., Wołowicz M., Hummel H., 2007, *Geographic and seasonal patterns and limits on the adaptive response to temperature of European Mytilus spp. and Macoma balthica populations*, Oecologia, 154 (1), 23–34.
- Kautsky N., 1982, *Quantitative studies on the gonad cycle, fecundity, reproductive output and recruitment in a Baltic Mytilus edulis population*, Mar. Biol., 68 (2), 143–160.
- Kennedy W. J., Taylor J. D., Hall A., 2008, *Environmental and biological controls on bivalve shell mineralogy*, Biol. Rev., 44 (4), 499–530.
- Kingston P. F., 1974, *Studies on the reproductive cycles of Cardium edule and C. glaucum*, Mar. Biol., 28 (4), 317–323.
- Lasiak T., Dye A., 1989, *The ecology of the brown mussel Perna perna in Transkei, Southern Africa: Implications for the management of a traditional food resource*, Biol. Conserv., 47 (4), 245–257.
- Lelong P., Riva A., 1976, *Relations between bivalve growth and phytoplankton in lagoons and closed basins*, Haliotis, 7, 104–111, (in French).
- Liu L. L., Stickle W. B., Gnaiger E., 1990, *Normoxic and anoxic energy metabolism of the southern oyster drill Thais haemastoma during salinity acclimation. A direct calorimetric study*, Mar. Biol., 104 (2), 239–245.
- Lowry O. H., Rosebrough N. J., Farr A. L., Randall R. J., 1951, *Protein measurement with folin phenol reagent*, J. Biol. Chem., 193 (1), 265–275.
- Lucas A., Beninger P. G., 1985, *The use of physiological condition indices in marine bivalve aquaculture*, Aquaculture, 44 (3), 187–200.
- Lyons C., Dowling V., Tedengren M., Gardeström J., Hartl M. G. J., O'Brien N., Van Pelt F. N. A. M., O'Halloran J., Sheehan D., 2003, *Variability of heat shock proteins and glutathione S-transferase in gill and digestive glands of blue mussel, Mytilus edulis*, Mar. Environ. Res., 56 (5), 585–597.
- Machado M. M., Costa A. M., 1994, *Enzymatic and morphological criteria for distinguishing between Cardium edule and C. glaucum of the Portuguese coast*, Mar. Biol., 120 (4), 535–544.
- Mariani S., Ketmaier V., De Matthaeis E., 2002, *Genetic structuring and gene flow in Cerastoderma glaucum (Bivalvia: Cardiidae): evidence from allozyme variation at different geographic scales*, Mar. Biol., 140 (4), 687–697.
- Marsh J. B., Weinstein D. B., 1966, *Simple charring method for determination of lipids*, J. Lipid Res., 7 (4), 574–576.

- McMahon R. F., Wilson J. G., 1981, *Seasonal respiratory responses to temperature and hypoxia in relation to burrowing depth in three intertidal bivalves*, J. Therm. Biol., 6 (4), 267–277.
- Najdek M., Sapunar J., 1987, *Total and methyl-mercury content in bivalves, Mytilus galloprovincialis Lamarck and Ostrea edulis Linnaeus: relationship of biochemical composition and body size*, Bull. Environ. Contam. Tox., 39 (1), 56–62.
- Navarro E., Iglesias J. I. P., Larrañaga A., 1989, *Interannual variation in the reproductive cycle and biochemical composition of the cockle Cerastoderma edule from Mundaca Estuary (Biscay, North Spain)*, Mar. Biol., 101 (4), 503–511.
- Nevo E., 1978, *Genetic variation in natural populations: patterns and theory*, Theor. Popul. Biol., 13 (1), 121–177.
- Newell R. C., 1979, *Biology of intertidal animals*, Mar. Ecol. Surv. Ltd., Faversham, 781 pp.
- Newell R. I. E., 2004, *Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review*, J. Shellfish Res., 23 (1), 51–61.
- Newell R. I. E., Bayne B. L., 1980, *Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle Cardium (= Cerastoderma) edule (Bivalvia: Cardiidae)*, Mar. Biol., 56 (1), 11–19.
- Newell R. I. E., Hilbish T. J., Koehn R. K., Newell C. J., 1982, *Temporal variation in the reproductive cycle of Mytilus edulis L. (Bivalvia, Mytilidae) from localities on the east coast of the United States*, Biol. Bull., 162 (3), 299–310.
- Nienhuis P. H., 1992, *Ecology of coastal lagoons in the Netherlands (Veerse Meer and Grevelingen)*, Vie Milieu, 42 (2), 59–72.
- Nikula R., Väinölä R., 2003, *Phylogeography of Cerastoderma glaucum (Bivalvia: Cardiidae) across Europe: a major break in the Eastern Mediterranean*, Mar. Biol., 143 (2), 339–350.
- Nowacki J., 1993, *Temperature, salinity and density of water*, [in:] *Bay of Puck*, K. Korzeniowski (ed.), Wyd. UG, Gdańsk, 416–421, (in Polish).
- Oeschger R., 1990, *Long-term anaerobiosis in sublittoral marine invertebrates from the western Baltic Sea: Halicyrtus spinulosus (Priapulida), Astarte borealis and Arctica islandica (Bivalvia)*, Mar. Ecol.-Prog. Ser., 59, 133–143.
- Pazikowska G., Szaniawska A., 1988, *Variations in energy and lipid content in Mytilus edulis from the Gulf of Gdańsk*, Oceanologia, 25, 99–107.
- Pazos A. J., Román G., Acosta C. P., Abad M., Sánchez J. L., 1997, *Seasonal changes in condition and biochemical composition of the scallop Pecten maximus L. from suspended culture in the Ria de Arousa (Galicia, N.W. Spain) in relation to environmental conditions*, J. Exp. Mar. Biol. Ecol., 211 (2), 169–193.
- Pearson C., 2003, *The genetic population structure of the lagoon specialists Nematostella vectensis, Cerastoderma glaucum and Gammarus insensibilis from populations along the southern and eastern coasts of the United Kingdom*, Ph.D. thesis, Univ. Southampton, Southampton, 229 pp.

- Pickard G.L., Emery W.J., 1990, *Descriptive physical oceanography. An introduction*, 5th edn., Pergamon Press, Oxford, 320 pp.
- Pieters H., Kluytmans J.H., Zandee D.I., Cadée G.C., 1980, *Tissue composition and reproduction of *Mytilus edulis* in relation to food availability*, Neth. J. Sea Res., 14 (3–4), 349–361.
- Pieters H., Kluytmans J.H., Zurburg W., Zandee D.I., 1979, *The influence of seasonal changes on energy metabolism in *Mytilus edulis* (L.). 1. Growth rate and biochemical composition in relation to environmental parameters and spawning*, [in:] *Cyclic phenomena in marine plants and animals*, E. Naylor & R. G. Hartnoll (eds.), Pergamon Press, New York, 285–293.
- Pliński M., 1995, *Phytoplankton of the Gulf of Gdańsk in 1992 and 1993*, Oceanologia, 37 (1), 123–135.
- Porter J., Dyrzynda P., Ryland J., Carvalho G., 2001, *Morphological and genetic adaptation to a lagoon environment: a case study in the bryozoan genus *Alcyonidium**, Mar. Biol., 139 (3), 575–585.
- Riisgård H. U., Kittner C., Seerup D. F., 2003, *Regulation of opening state and filtration rate in filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, *Mya arenaria*) in response to low algal concentration*, J. Exp. Mar. Biol. Ecol., 284 (1–2), 105–127.
- RIKZ, RIZA, 2009, Waterbase, National Institute for Coastal and Marine Management, Institute for Inland Water Management and Waste Water Treatment, The Netherlands, (available at <http://www.waterbase.nl/index.cfm?taal=en>).
- Ruiz C., Martinez D., Mosquera G., Abad M., Sánchez J.L., 1992, *Seasonal variations in condition, reproductive activity and biochemical composition of the flat oyster, *Ostrea edulis*, from San Cibrao (Galicia, Spain)*, Mar. Biol., 112 (1), 67–74.
- Russell P. J. C., 1972, *Biological studies on *Cardium glaucum*, based on some Baltic and Mediterranean populations*, Mar. Biol., 16 (4), 290–296.
- Rygg B., 1970, *Studies on *Cerastoderma edule* (L.) and *Cerastoderma glaucum* (Poiret)*, Sarsia, 43, 65–80.
- Sarà G., 2007, *Sedimentary and particulate organic matter: mixed sources for cockle *Cerastoderma glaucum* in a shallow pond, Western Mediterranean*, Aquat. Living Resour., 20 (3), 271–277.
- Sastry A. N., 1979, *Pelecypoda (excluding Ostreidae)*, [in:] *Reproduction of marine invertebrates. Vol. V. Molluscs: pelecypods and lesser classes*, A. C. Giese & J. S. Pearse (eds.), Acad. Press, New York, 113–292.
- Schmidt-Nielsen K., 1990, *Animal physiology. Adaptation and environment*, Cambridge Univ. Press, Cambridge, 601 pp.
- Smaal A. C., Stralen M. R., 1990, *Average annual growth and condition of mussel as a function of food source*, Hydrobiologia, 195 (1), 179–188.
- Stora G., Arnoux A., Galas M., 1995, *Time and spatial dynamics of Mediterranean lagoon macrobenthos during an exceptionally prolonged interruption of freshwater inputs*, Hydrobiologia, 300–301 (1), 123–132.

- Stora G., Gilbert F., Dupont E., Ré C., Picon P., 2004, *The dynamics of macrobenthic populations in the central and coastal parts of the Berre Lagoon*, Report, GIPREB, COM, Univ. Méditerranée, France, 19 pp., (in French).
- Sukhotin A. A., Lajus D. L., Lesin P. A., 2003, *Influence of age and size on pumping activity and stress resistance in the marine bivalve *Mytilus edulis* L.*, J. Exp. Mar. Biol. Ecol., 284 (1–2), 129–144.
- Tarnowska K., Chenuil A., Nikula R., Féral J.-P., Wołowicz M., 2009, *Complex genetic population structure of bivalve (*Cerastoderma glaucum*) living in highly fragmented lagoon habitat*, Mar. Ecol.-Prog. Ser., (in revision).
- Taylor A. C., Venn T. J., 1979, *Seasonal variations in weight and biochemical composition of the tissues of the queen scallop, *Chlamys opercularis* from the Clyde Sea area*, J. Mar. Biol. Assoc. U.K., 59 (3), 605–621.
- Wasmund N., Nausch G., Matthäus W., 1998, *Phytoplankton spring blooms in the southern Baltic Sea – spatio-temporal development and long-term trends*, J. Plankton Res., 20 (6), 1099–1117.
- Wenne R., Klusek Z., 1985, *Longevity, growth and parasites of *Macoma balthica* L. in the Gdańsk Bay (South Baltic)*, Pol. Arch. Hydrobiol., 32 (1), 31–45.
- Wenne R., Styczyńska-Jurewicz E., 1985, *Age-dependence of condition and lipid and carbohydrate contents in *Macoma balthica* (L.) from the Gdańsk Bay (South Baltic)*, Pol. Arch. Hydrobiol., 32, 65–70.
- Wenne R., Styczyńska-Jurewicz E., 1987, *Gross biochemical composition of the bivalve *Macoma balthica* from the Gulf of Gdańsk (Southern Baltic)*, Mar. Biol., 96 (1), 73–78.
- Wilson J. G., 1990, *Effects of temperature changes on infaunal circalittoral bivalves, particularly *T. tenuis* and *T. fibula**, [in:] *Expected effects of climatic changes on marine coastal ecosystems*, J. J. Beukema (ed.), Kluwer Acad., Amsterdam, 93–97.
- Wilson J. G., Davis J. P., 1984, *The effect of environmental variables on the oxygen consumption of the protobranch bivalve *Nucula turgida* (Leckenby & Marshall)*, J. Mollus. Stud., 50 (2), 73–77.
- Wilson J. G., Elkaim B., 1991, *Tolerances to high temperature of infaunal bivalves and the effect of geographical distribution, position on the shore and season*, J. Mar. Biol. Assoc. U.K., 71 (1), 169–177.
- Wilson J. G., Elkaim B., 1997, *Seasonal and geographical differences in oxygen consumption with temperature of *Cerastoderma glaucum* (Poiret) and a comparison with *C. edule* (L.)*, Estuar. Coast. Shelf Sci., 45 (5), 571–577.
- Wołowicz M., 1987, *A comparative study of the reproductive cycle of cockles *Cardium glaucum* (Poiret 1789) and *C. hauniense* (Petersen, Russell 1971) – (*Bivalvia*) from the Gdańsk Bay*, Pol. Arch. Hydrobiol., 34 (1), 91–105.
- Wołowicz M., 1991, *Geographical differentiation of *Cerastoderma glaucum* Bruguiere (*Bivalvia*) populations. Hypothesis concerning the origin and migration pathways*, Wyd. UG, Gdańsk, 151 pp., (in Polish).

- Wołowicz M., Sokołowski A., Bawazir A.S., Lasota R., 2006, *Effect of eutrophication on the distribution and ecophysiology of the mussel Mytilus trossulus (Bivalvia) in southern Baltic Sea (the Gulf of Gdańsk)*, *Limnol. Oceanogr.*, 51 (1, part 2), 580–590.
- Yukihira H., Klumpp D. W., Lucas J. S., 1998, *Effects of body size on suspension feeding and energy budgets of the pearl oysters Pinctada margaritifera and P. maxima*, *Mar. Ecol.-Prog. Ser.*, 170, 119–130.
- Zandee D. I., Kluytmans J. H., Zurburg W., Pieters H., 1980, *Seasonal variations in biochemical composition of Mytilus edulis with reference to energy metabolism and gametogenesis*, *Neth. J. Sea Res.*, 14 (1), 1–29.
- Zaouali J., 1974, *The malacological fauna of the Lake of Tunis (northern and southern parts) and its channels*, *Haliotis*, 4, 179–186, (in French).