



# Shell morphology, growth and longevity of *Unio tumidus* (Bivalvia: Unionidae) from an archaeological site and contemporary population inhabiting the Oder estuary

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**Abstract** Mussel shells are often found in archaeological excavations and can provide information useful for ecological reconstruction and assessment of anthropogenic impact on waters. In this study, two sample groups of swollen river mussel (*Unio tumidus*) which occurred during the Early Middle Ages (EMS) and currently (MS) in the Oder river estuary (Baltic basin) were compared. Allometric shell growth, morphological characteristics of the shell (length, width, height and thickness), age structure and growth of mussels were analysed using the von Bertalanffy equation. All three types of allometric growth (isometry and both positive and negative allometry) were observed in the studied mussels. In both groups, typical values of shell length, width, height and thickness were recorded. However, higher values of

these morphological characteristics were recorded in the EMS group. Moreover, the EMS group, compared with the MS group of *U. tumidus*, was characterised by a higher longevity (12 and 10 years, respectively) and asymmetric length ( $L_{\infty}$ ) (93.09 and 83.23 mm, respectively). Both groups of mussels had a similar growth rate ( $k$ ). Larger shell sizes in the EMS group were probably caused by differential preservation and/or differential archaeological recovery, and resulted from differences in the age structure, especially higher mortality rate amongst individuals older than 6 years in the MS group.

**Keywords** Structure · Molluscs · Increase · Age · FSA

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## Introduction

Freshwater mussels are widely distributed throughout the world and are present in all continents except Antarctica (Graf & Cummings, 2006), but they are also severely endangered worldwide (Lopes-Lima et al., 2017; Böhm et al., 2020; Graf & Cummings, 2021). Their oldest representatives existed as early as during the Triassic period (Watters, 2001). Due to their filtration capacity, they play a significant role in the functioning of aquatic ecosystems, affecting the physical and chemical conditions, as well as the

structure and habitats of other organisms (Ziertitz et al., 2019). For example, Aldridge et al. (2007) observed a positive correlation between high densities of freshwater mussels and the diversity of other invertebrate taxa. On the other hand, a study by Vaughn & Hakenkamp (2001) showed that at high densities, mussels are able to significantly reduce phytoplankton biomass and reduce phosphorus content, leading to a better water transparency. Mussels as animals with a high ecological specialisation are good environmental bioindicators (Grabarkiewicz & Davis, 2008; Ganzei et al., 2020). Amongst the most remarkable freshwater bivalves are species belonging to the order of Unionida, which represents about 72% freshwater mussels (Lopes-Lima et al., 2018). The most numerous family of this order is Unionidae, which comprises 753 species in 153 genera (Graf & Cummings, 2021). In archaeological studies, they are a group of marker organisms used in “applied zooarchaeology” (Peacock et al., 2016) for the reconstruction of past climatic conditions, as well as the palaeoenvironment and its changes, including those of anthropogenic origin (Mitchell & Peacock, 2014; Mitchell, 2017; Peacock et al., 2017). Moreover, they widen our knowledge of the population composition and natural distribution (biogeography), biodiversity in various water types before changes related to human activity (Mitchell et al., 2016). The results of those studies also give some insight into the rate and direction of changes in the mussel population, allowing protection of the endangered species (Peacock et al., 2017). For the majority of known species we are currently aware of the environmental requirements; therefore, if we admit that both now and in the past the species have similar environmental requirements (Lyman, 2017), the presence or absence of a taxon in the environment is a proof of habitat modifications. Moreover, learning about biological diversity from distant past with the use of currently available novel laboratory techniques enables accurate and thorough identification of species translocation mechanisms (DiNapoli et al., 2021).

Unionids produce hard parts, which are found, despite taphonomic and diagenetic processes in sedimentary deposits and as such can be used in the reconstruction of ancient populations and species. These processes cause mechanical and chemical degradation of the shell by dissolution and recrystallization, resulting in their fragmentation, although the

shells are characterised by high resistance to crushing thanks to their structure (Barthelat et al., 2009), loss of colour, chemical dissolution and precipitation of calcite (Peacock et al., 2020). According to Wolverson et al. (2010) the factors influencing these processes include the discard process (e.g., height from which shells are dropped by people), orientation of deposition, disparity in burning amongst shellfish remains of different species, rate of disarticulation of valves, exposure to trampling, chemical weathering in acidic soils, soil formation processes, rates of deposition, sedimentation and erosion, archaeological recovery methods, modification of shells by predators, and shell shape and microstructure.

In Poland, remains of molluscs are found at archaeological sites much less frequently than those of vertebrates (Zabilska, 2012). In the case of molluscs, the most common remains found at archaeological sites in Poland are shells of mussels (Unionidae), in particular *Unio tumidus* Philipsson, 1788 (Dzięczkowski, 1998), which were used as food by the ancient residents (Kurzawska, 2015). The number of unionid shells found in the various archaeological layers indicates that they were also present in the waters surrounding the medieval Wolin, located in the Oder estuary, and used as additional food for the inhabitants (personal information from Prof. W. Filipowiak). Currently, a representative of the Unionidae family, *U. tumidus*, is an abundant species in the region (Wolnomiejski & Witek, 2013).

The aim of this study was (i) to compare the population structures (length and age), and (ii) to compare the longitudinal growth and shape of the shells of *U. tumidus*, between a shell midden excavated in Wolin town (Oder estuary) and shells from a contemporary population inhabiting the Oder estuary, with the two groups separated by approximately 1000 years.

## Material and methods

### Study site

The study material were shells of the mussel *Unio tumidus* originating from an archeological excavation (78 shells, called the Early Middle Ages group—EMS) and those harvested during fishing with a bottom dredge (88 shells, group harvested in the

twenty-first century—MS) in the northern part of the Szczecin Lagoon (Oder estuary). Material for the first group was collected from an archaeological excavation situated on the island of Wolin in the area of the old town of Wolin, approx. 60 m from the west bank of the Dziwna river (Oder estuary) (Fig. 1).

The excavation covered an area of 5 m × 20 m and reached a face located at a depth of 7 m. The studied shells were collected from layers corresponding to the following periods: tenth century, 1st half of the eleventh century, 2nd half of the eleventh century (Chełkowski et al., 2001). Shells for the second group were collected from the 2nd to 16th of October 2019 during fishing for macrozoobenthos using a bottom dredge at sites located in the Dziwna river and in the northern part of the Szczecin Lagoon (Oder estuary) within 1000 m of the excavation site.

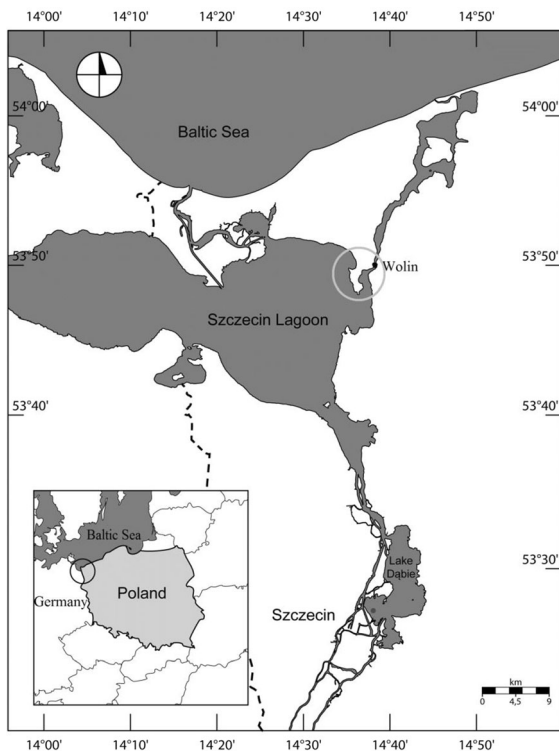
### Morphology and species identification

Shell morphology (including length, width, height and thickness) is one of the important qualities for biologists, allowing for species identification of the

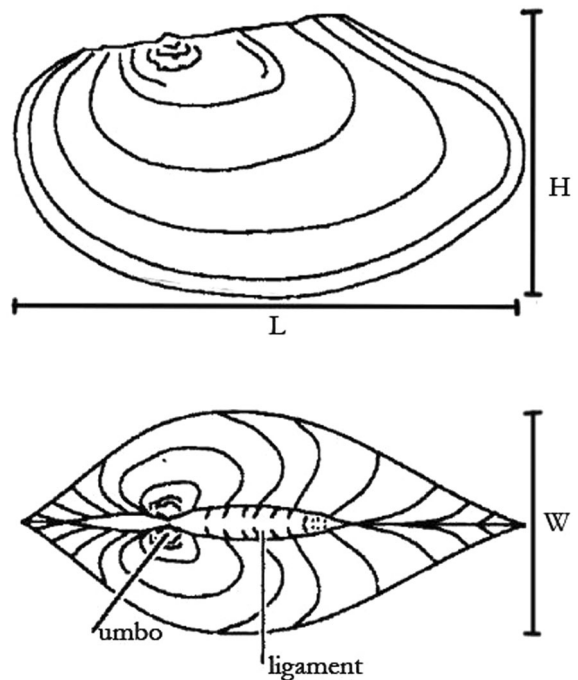
mussel (Aldridge, 1999; Rizhinashvili, 2008; Bogan & Roe, 2008). Of special importance are proportions between particular morphological features, which reflect the shape of the shell (Wolverton et al., 2010).

The collected shells were measured with an electronic calliper (0.01 mm measurement accuracy) to record the following parameters: maximum height ( $H$ ), maximum width ( $W$ ), maximum length ( $L$ ) (Fig. 2) (Aldridge, 1999; Wolverton et al., 2010) and the thickness of the valves ( $T$ ) (Ożgo et al., 2012). The thickness of the valves was measured at the centre of gravity of each valve. Centre of gravity is the point of contact of the valve with the surface on which it is placed concave side up. Of the harvested shells, only whole ones (non-fractured, retaining their umbo) and only those belonging to *Unio tumidus* were studied, whilst other ones were rejected.

After a logarithmic transformation ( $\log_{10}$ ) of the morphological measurements, a linear regression analysis was conducted ( $W-L$ ,  $H-L$ ,  $T-L$ ,  $W-H$ ,  $T-H$ ) using standard major axis regression (SMA) (Warton et al., 2012). The slope of the regression (allometric coefficient) was used as an indicator of the



**Fig. 1** Sampling site location



**Fig. 2** Standard measurements of the shell.  $H$ —maximum height,  $W$ —maximum width,  $L$ —maximum length (Aldridge, 1999, as modified)

type of differential growth, considering the 95% confidence intervals, calculated for each coefficient.

### Age and growth

Age was determined by counting the annual rings on the surface of mussel shells (Rizhinashvili, 2008; Johnsson et al., 2013), by 2 independent researchers. In order to confirm the compatibility of age and location of each annulus for 36 selected shells, a procedure described by Haag & Comments-Carson was used (2008). The shells were cut with the use of the Buehler Isomet low speed saw (Buehler Ltd., Evans-ton, IL, U.S.A.), with a diamond blade. Vernier callipers (0.01 mm measurement accuracy) were used to measure the length of individuals at each annulus. The growth of shells was described using the von Bertalanffy equation (Haag & Rypel, 2011):

$$L_t = L_{\text{inf}}(1 - e^{-K(t-t_0)})$$

where  $L_t$  is length (mm) at time  $t$  (age in years),  $L_{\text{inf}}$  is length (mm) at time infinity (the predicted mean maximum length for the population),  $K$  is a growth constant which describes the rate at which  $L_{\text{inf}}$  is attained (mm, year<sup>-1</sup>),  $t$  is age (years) and  $t_0$  is the time at which length = 0. The parameters of the above equation were calculated in the R programming environment with FSA packages, nlstools, magrittr, dplyr, nnet (Ogle, 2016).

The obtained data were used to calculate the maximum age that *Unio tumidus* reached in the early Middle Ages and currently, using the equation (Ziuganov et al., 1994):

$$t_m = -1/K \ln[1 - (L_m/L_\infty)]$$

where  $t_m$  is the maximum age and  $L_m$  is the maximum length.

### Statistical analysis

The data were tested for normality and homogeneity of variances by the Kolmogorov–Smirnov test and Levene’s test, respectively. If necessary, data were log-transformed to meet these assumptions. The significance level for all analyses was set at 0.05. The Wilcoxon test (Cohen & Cohen, 2008) was used to compare the values of the measured parameters, whilst Student’s  $t$ -test (Shahbaba, 2012) was used to

compare slope in the analysis of growth allometricity and isometry of the parameters measured. Stepwise discriminant analysis was used to identify the combination of variables that best separated the two groups (Bocard et al., 2018). Unless otherwise stated, statistical analyses were conducted with Statistica 13.0 (Statsoft Inc.), the R programming environment (R Core Team, 2013) and the R package nlme (Pinheiro et al., 2020).

## Results

### Shell morphology

The shells of *Unio tumidus* from the Early Middle Ages (EMS group) were characterised by a significantly greater length ( $L$ ), width ( $W$ ), height ( $H$ ) and thickness ( $T$ ) compared with the contemporary individuals (MS group) (Table 1). Moreover, the distribution of these parameters showed clear differences in shell size between the two groups (Fig. 3). The discriminant analysis (Table 2) indicated that the thickness, maximum length and height of shells are statistically significant variables which allow discriminating between the two studied groups of mussels. Cross-validation with the split-sample method indicated a 95.88% overall success rate (98.75% of the EMS group and 93.33% of the MS group were correctly assigned).

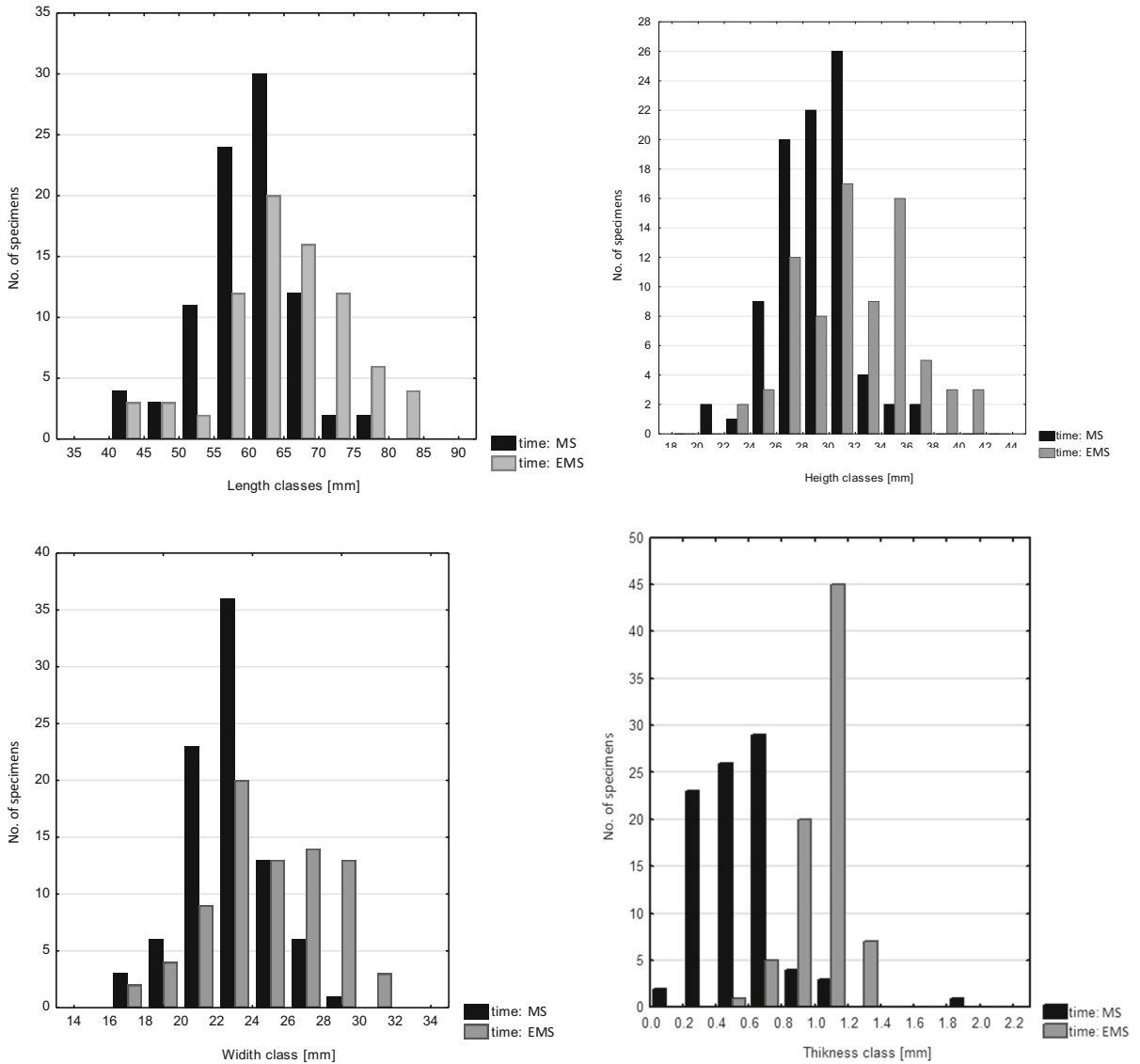
Regression equations for the shell morphology of the *U. tumidus* EMS and MS subgroups are given in Table 3. The equations demonstrate that all models were statistically significant (at  $P < 0.05$ ). Growth could mostly be considered as allometric (positive and negative), except  $T-L$ ,  $W-H$ ,  $T-H$  for the MS group for which isometric growth was recorded. By comparing the slope parameters ( $b$ ) of each regression between the mussel groups (Table 4), it was shown that statistically significant differences were present only in those regressions in which thickness ( $T$ ) was the independent variable.

### Age structure and growth

The comparative analysis between the methods of age determination (by counts of external annuli and by thin section) for 36 randomly selected mussels showed age compatibility for both methods in 31 individuals. Only

**Table 1** Morphometric data (mean ± SD) and the Wilcoxon test on *Unio tumidus* shells

<i>U. tumidus</i> group	<i>L</i> (mm) ± SD	<i>W</i> (mm) ± SD	<i>H</i> (mm) ± SD	<i>T</i> (mm) ± SD
EMS group	64.77 ± 9.20	24.81 ± 3.23	31.81 ± 4.08	1.03 ± 0.15
MS group	59.47 ± 6.78	22.46 ± 2.30	28.90 ± 2.86	0.56 ± 0.25
W statistic	4720	4980	4874	6466
<i>P</i> -value	0.00003099	0.000005519	0.000003095	0.000000000



**Fig. 3** Distribution of length (*L*), height (*H*), width (*W*) and thickness (*T*) of *Unio tumidus* shells from the Early Middle Ages (EMS) and present day (MS)

in 5 shells of mussels aged above 8 years, the mussel age was underestimated by 1 year using the method of counts of external annuli. Moreover, false annuli were

occasionally recorded in the study shells. In the case of thin-sectioning, the method enabled identification of false annuli, since real annuli could be analysed from

**Table 2** Results of discriminant analysis of the morphological characteristics of mussel shells

Variable	Wilk’s Lambda	F—remove	P	Tolerance
<i>L</i>	<b>0.378208*</b>	<b>30.0227*</b>	<b>0.000000*</b>	<b>0.063715*</b>
<i>H</i>	<b>0.327703*</b>	<b>3.9800*</b>	<b>0.047690*</b>	<b>0.108032*</b>
<i>W</i>	0.323197	1.6564	0.199894	0.118409
<i>T</i>	<b>0.818024*</b>	<b>256.8134*</b>	<b>0.000000*</b>	<b>0.373711*</b>

\*Significant values are indicated in bold type

**Table 3** Values of regression equations for *Unio tumidus* shell morphology and *P*-values of slope tests

	Group	<i>n</i>	Slope ( <i>b</i> )	Intercept ( <i>a</i> )	<i>r</i>	<i>F</i>	<i>P</i> value	Growth type	<i>t</i> -value	<i>P</i> value
$\log W \sim \log L$	EMS	78	0.863	− 0.389	0.93	948	0.000	A	30.79	< 0.00001
$\log H \sim \log L$		78	0.811	0.079	0.88	545	0.000	A	23.35	< 0.00001
$\log T \sim \log L$		78	0.939	− 3.885	0.73	207	0.000	I	14.38	< 0.00001
$\log W \sim \log H$		78	0.989	− 3.39	0.61	118	0.000	I	10.85	< 0.00001
$\log T \sim \log H$		78	0.989	− 3.397	0.61	118	0.000	I	10.85	< 0.00001
$\log W \sim \log L$	MS	88	0.75	0.045	0.759	271.7	0.000	A	16.48	< 0.00001
$\log H \sim \log L$		88	0.764	0.241	0.836	439.8	0.000	A	20.97	< 0.00001
$\log T \sim \log L$		88	3.142	− 13.479	0.828	415.9	0.000	A	20.39	< 0.00001
$\log W \sim \log H$		88	0.846	0.256	0.678	181.1	0.000	A	13.46	< 0.00001
$\log T \sim \log H$		88	3.549	− 12.582	0.738	242.5	0.000	A	15.57	< 0.00001

A allometric growth, I isometric growth

**Table 4** Comparison of correlation factors and regression of slope between the groups of mussels from early Middle Ages and present day

	Slope ( <i>b</i> )			<i>r</i>		
	<i>t</i> -value	DF	<i>p</i> -value	<i>t</i> -value	DF	<i>p</i> -value
$\log W \sim \log L$	1.829	162	0.069	3.981	162	<b>0.000103*</b>
$\log H \sim \log L$	0.909	162	0.364	0.968	162	0.334
$\log T \sim \log L$	− 13.087	162	<b>&lt; 0.000001*</b>	− 1.620	162	0.106
$\log W \sim \log H$	1.352	162	0.178	2.650	162	<b>0.008839*</b>
$\log T \sim \log H$	2.556	162	<b>0.0115*</b>	− 1.5577	162	0.121

\*Significant differences are indicated in bold type

the umbo to the shell margin. False annuli were characterised by an incomplete growth line in thin sections.

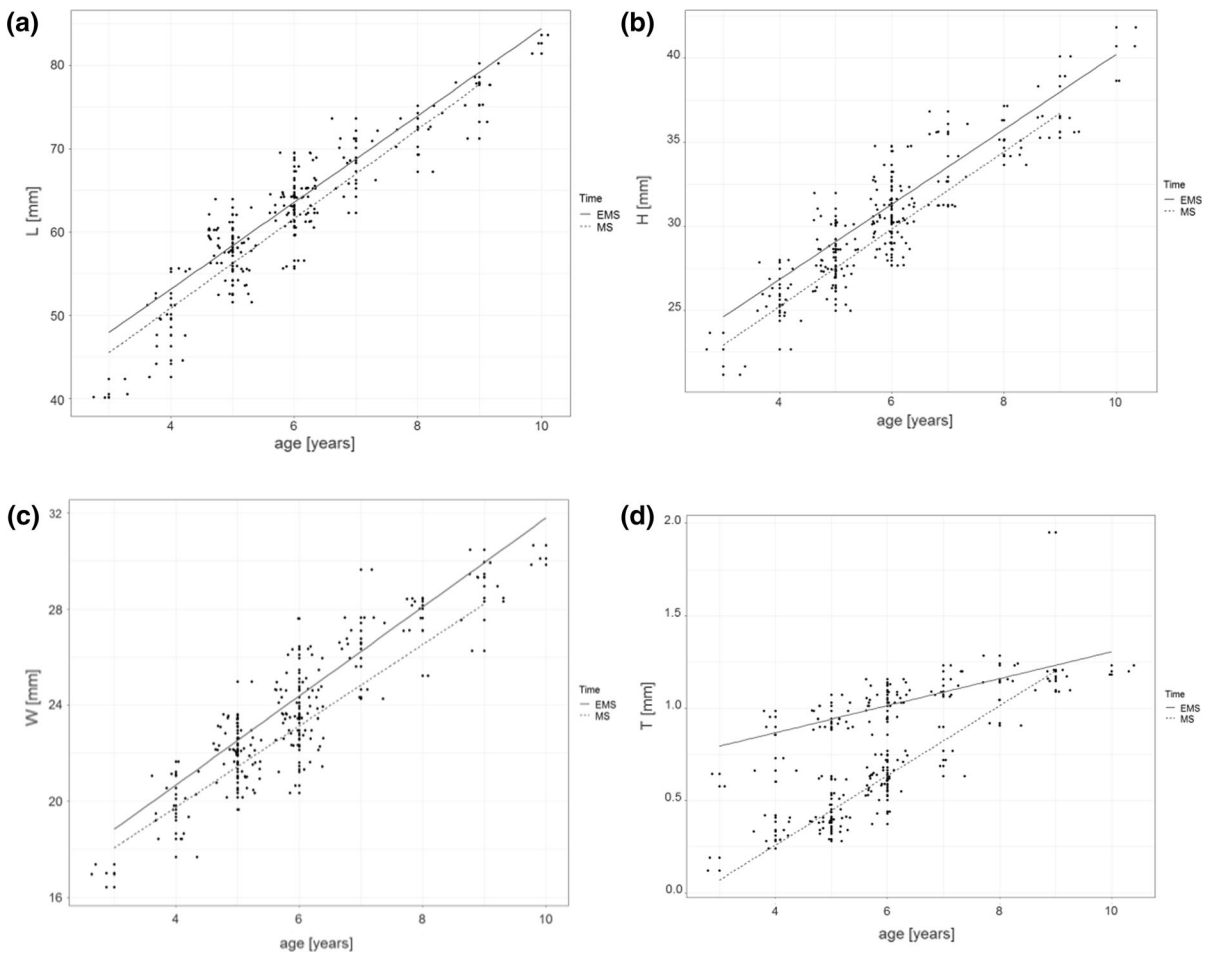
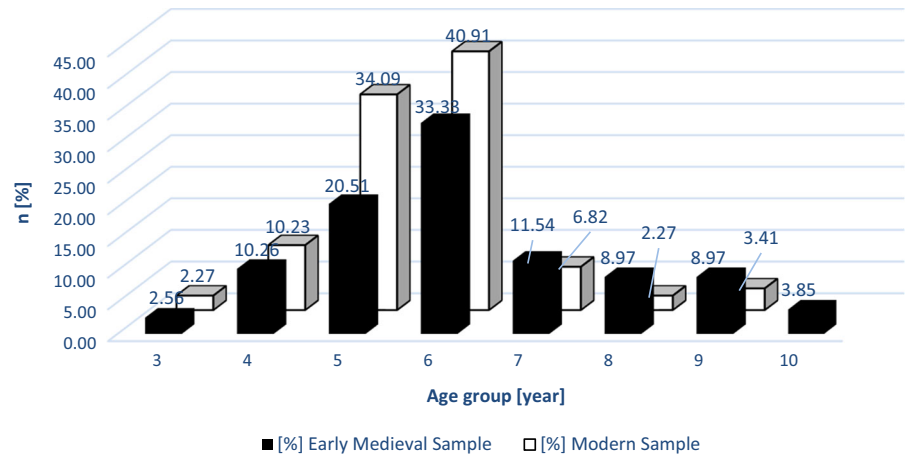
In the age structure of mussels, individuals aged 5 and 6 years prevailed in both groups (Fig. 4). Five-year-old individuals constituted 21.56%, and 6-year-old individuals constituted 33.33% of the EMS group. The corresponding values in the MS group were 34.09% and 40.91%, respectively. In the MS group, the proportion of older age groups (> 6 years) was only 12.50%, whilst in the EMS group, it was as high

as 33.33%, which means that mussel mortality rate in these age groups was higher in the contemporary individuals.

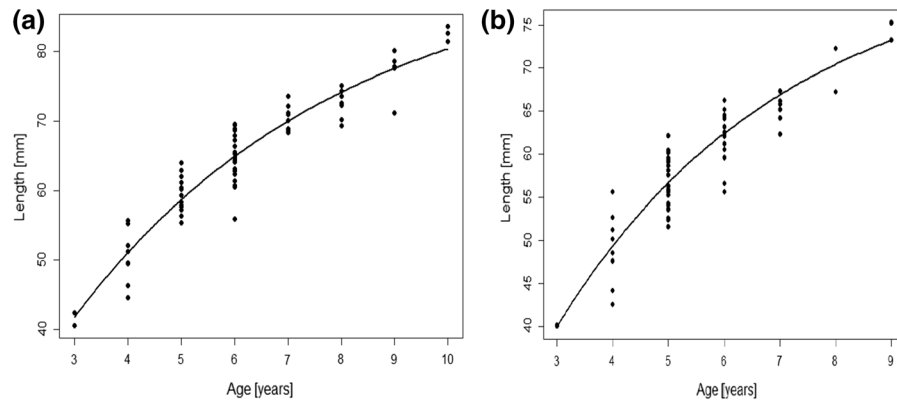
In individual age groups, the Early Middle Ages (EMS) mussels were characterized by greater length (*L*), width (*W*), height (*H*) and thickness (*T*) compared to modern mussels (MS) (Fig. 5a–d).

Figure 6 shows the growth of mussels from the EMS and MS groups based on the von Bertalanffy equation. The positions of growth curves and the equation parameters (Table 5) show that mussels in the

**Fig. 4** Age structure of mussels



**Fig. 5** Linear regression for *Unio tumidus* shell morphology. Regression between age [years] and length (a), height (b), width (c) and thickness (d) in time group



**Fig. 6** Comparison of the growth rates of mussels from the early Middle Ages (a) and present day (b)

**Table 5** Growth parameters for the investigated *Unio tumidus* populations from the Oder estuary

Group	Growth constant ( $k$ )	Asymptotic length ( $L_{\infty}$ ), mm	$t_0$	Maximum length ( $L_m$ ), mm	Maximum age (years)*
EMS	0.199	93.09	0.017	83.65	12
MS	0.243	83.23	0.309	75.32	10

\*Maximum age was calculated using the formula published by Ziuganov et al., (1994)

EMS group were characterized by higher longevity (maximum age for the EMS and MS groups was 12 and 10 years, respectively) and slightly higher asymptotic length ( $L_{\infty}$ ) ( $P = 0.0365$ ) compared with the currently occurring *U. tumidus*. Moreover, both groups showed similar growth rates, as indicated by parameter  $k$  ( $P = 0.0523$ ).

## Discussion

### Morphology

The unionid fauna of the Szczecin Lagoon includes all the species belonging to the genera *Unio* and *Anodonta* known to occur in Poland (Wolnomiejski & Witek, 2013). As in other waterbodies in this part of Europe, commonly observed species include *Unio pictorum* (Linnaeus, 1758), *Unio tumidus* and *Anodonta anatine* (Linnaeus, 1758), whilst those observed much less frequently include *Pseudanodonta complanata* (Rossmässler, 1835) and *Anodonta cygnea* (Linnaeus, 1758) (Masłowski, 1993). This is probably due to the habitat preferences of these species which is mainly found on the silt or sandy

bottom, rich in allochthonic organic matter (Abraszewska-Kowalczyk, 2002). The size of the *U. tumidus* shells from both the EMS and MS groups did not differ from the literature data. According to Piechocki & Wawrzyniak-Wydrowska (2016), the length of the *U. tumidus* shell in Poland ranges from 60 to 100 mm (max 130 mm), height 35–48 mm, width 25–37 mm. On the other hand, in the lake complex Crapina-Jijila in the Danube delta, bivalves were 48–68 mm long (Tudorancea, 1972). However, what is interesting is the statistically significant difference between the morphometric parameters of the mussel groups in our study. Individuals originating from the eleventh century had a greater shell length, width and height, and nearly twice the thickness. This may result from differential preservation, differential archaeological recovery, or both. For example, denser and thicker mussel shells preserve better than the thinner ones, because the latter are more susceptible to damage (Wolverton et al., 2010). Nevertheless, it seems that differential preservation affects mainly small and thin shells of young individuals. Aside to taphonomic changes, the mussel structure could have also been affected by “cultural filter” constituting selective human activity (human preferences or avoiding



certain species) (Mitchell, 2017). A decrease in the average shell length of this species, although over a relatively shorter period compared with our study (approx. 50 years), was also observed in the *U. tumidus* population in Lake Mikołajskie (Lewandowski & Kołodziejczyk, 2014). However, Peacock (2000) and Miller et al. (2014) reported usually larger dimensions in present-day mussels compared with the same species from Holocene archaeological excavations. These long-term disparities are likely to result from changes in the environmental conditions over many years due to progressive eutrophication, currently accelerated by human activity (Peacock & Mistak, 2008; Fritts et al., 2017) and temperature changes (Lundquist et al., 2019). As emphasised by numerous authors, climate changes over nearly 1000 years may also affect the age, growth and size of mussel shells (Holland et al., 2014; Lundquist et al., 2019). Especially because the first study group of mussels (EMS) probably lived in an optimal medieval climatic period, and the temperature differences between these periods were sufficiently high to have caused disproportions in their shell sizes (Schöne & Fiebig, 2009). This effect is more pronounced in freshwater, rather than marine species, since temperatures of fresh water are largely dependent on the air temperature, and habitats are often fragmentary, which limits the free movement of species with progressive environmental changes (Woodward et al., 2010). Moreover, it is common knowledge that freshwater mussels grow more slowly and reach more advanced age in the higher latitudes (Haag & Rypel 2011), where the air temperature is lower (Hu et al., 2018). Higher water temperature accelerates the photosynthesis of phytoplankton, one of the basic nutrient of mussels, which has a logarithmic effect on their growth rate. However, very large concentrations of food particles cause reduction in the filtration rates. Filtration rates of *Dreissena* mussel fed with *Nitzschia* diatoms were observed to increase up to 2 mg C/L with about 40% of assimilation performance. Plateau occurred above the level of 2 mg C/L (Wetzel, 2001). Mussel growth is affected not only by longevity, as claimed by Haag & Rypel (2011), or food amount (Wetzel, 2001), but also by the concentration of calcium and bicarbonates in water. Carey et al. (2013) indicate that a temperature increase causes an increase in the rate of growth of young *Epioblasma brevidens* (I. Lea, 1831) and *E. capsaeformis* (I. Lea, 1834), as

well as a decrease in the rate of growth. A different opinion was presented by Ganser et al. (2015) who showed that an increase in the temperature of water where Unionidae [*Amblema plicata* (Say, 1817), *Elliptio complanata* (Lightfoot, 1786), *Fusconaia flava* (Rafinesque, 1820) and *Lampsilis cardium* Rafinesque, 1820] mussels lived caused a change in the rate of metabolism, such that it might lead to a decrease in the energy necessary to survive, grow and reproduce.

#### Age and growth of mussels

In mussels, growth and longevity depend on species, sex and habitat conditions (Aldridge, 1999; Lundquist et al., 2019). Haag & Rypel (2011) observed that values of the growth constant  $K$  ranged from 0.05 [*Quadrula asperata* (I. Lea, 1861)] to 1.01 [*Toxolasma parvum* (Barnes, 1823)], whilst the same parameter in Unionini tribe was 0.323–0.412 (Ostrovsky et al., 1993). It should be noted that usually larger values are obtained for longevous mussel species (Hochwald, 2001). For example, Aldridge (1999) reported  $K = 0.075$  for a long-lived *U. tumidus* population in a Fenland waterway. In contrast,  $K$  value for the Oder estuary populations of this species in our study was 0.199 (EMS) and 0.243 (MS). These values fall within the range reported in the literature for *U. tumidus* populations in other European waters (Table 6).

Differences in the mussel growth in various waterbodies may result from the amount of nutrients and primary productivity (Strayer, 2014), which leads to higher amounts and availability of food for these mussels (Riccardi et al., 2016). Hinch et al. (1989) report that calcium and bicarbonate levels are important for the production of mussel shells, and their decline results in a decreased growth of the mussel size and thickness. These factors, as well as an increased water temperature (Lundquist et al., 2019) and other consequences of climate changes across the world may be the factors affecting the mussel growth in the long run. However,  $K$  values for the MS group compared with the EMS group did not reveal a significant difference. This indicates that the difference in the longitudinal growth rate of *U. tumidus* shells in the Szczecin Lagoon waters is very small (Fig. 6).

Haag & Rypel (2011), analysing data from 57 species and 146 populations of mussels, found a

**Table 6** Values of the von Bertalanffy equation parameters for the various *Unio tumidus* populations in European waters

Waterbody (country)	Growth constant	Asymptotic length ( $L_{\infty}$ ), [mm]	Maximum length ( $l_{max}$ ), [mm]	Maximum age (years)	Author	
Wicken Lode (England)	0.075	150.7	120	21	Aldrige (1999)	
Lake Lembolovskoe (Russia)	0.25	75.84	–	–	Rizhinashvili (2008)	
Lake Krasnoe (Russia)	0.09	100.30	–	–		
Gulf of Finland (Russia)	0.19	79.11	–	–		
Lake SestroretskRazliv (Russia)	0.08	124.30	–	–		
Oredezka river (Russia)	0.30	86.99	–	–		
Lake Loyanskoe (Russia)	0.38	76.14	–	–		
Lake Ladoga (Russia)	0.27	87.11	–	–		
Svir river (Russia)	0.31	71.59	–	–		
Kassel (Germany)	0.16	136.0	–	–	Nagel 1987	
Crapina-Jijila, Danube (Romania)	0.15	103.1	88.2	–	Tudorancea (1972)	
Thames river (England)	0.28	88.0	85.2	–	Negus (1966)	
Oder estuary	EMS	0.199	93.1	83.6	12	Own data
	MS	0.243	83.2	75.3	10	

significant positive correlation between the growth rate  $K$  and the longevity of the species. Amongst mussels, long-lived species mainly belong to the Margaritiferidae family (28–190 years), whilst short-lived species of a life span under 14 years belong to Anodontini (Haag & Rypel, 2011) and Unionini (Abraszewska-Kowalczyk, 2002). For example, Lewandowski & Kołodziejczyk (2014), whilst analysing the age structure of *U. tumidus* in the Pilica river (Poland), identified individuals aged 1–9 years, amongst which 2-year-old mussels prevailed in the Sulejowski reservoir, 4–5-year-old ones prevailed in the central Pilica river, whilst 1–4-year-old ones prevailed in the lower course of the Pilica. A much narrower age range (1–6 years) for the *U. tumidus* population of Lake Mikołajki was reported by Lewandowski & Kołodziejczyk (2014). Our study of mussels collected from archaeological excavations from the early Middle Ages and those currently inhabiting the Oder estuary demonstrated the presence of individuals aged 3–9 and 3–10 years, respectively, with a clear prevalence of individuals aged 5 and 6 in both groups. The maximum age, as defined using the formula by Ziuganov et al. (1994), which these groups of mussels could reach was 10 years with  $L_{\infty}$  of 83.2 mm for the MS group, and 12 years with  $L_{\infty}$  of 93.2 mm for the EMS group. These values are much lower than those reported by Aldrige (1999) for the

Fenland Waterway population (21 years), but large variations in the longevity of this species are known in the literature even between populations inhabiting waterbodies located at the same latitude. For example, Annie et al. (2013) in a population of this species from the Gullspång river recorded age groups of 4–20 years, with a clear prevalence of individuals aged 6 and 7 years. In turn, for Lake Kolungen these authors report an age range of 1–13 years, with the largest share of individuals aged 9–10 years. Differences in the age structure in various waterbodies result from mussel mortality rate at particular stages of development, which depends on the environmental conditions, predation and availability of natural habitats. As revealed in the studies of Strayer & Malcom (2012), high mussel mortality in the aqueous environment is caused by ammonia. Even at low concentrations, unionised ammonia is toxic for freshwater unionid mussels (Newton, 2003). Of importance are also changes in the natural flow of waters, which affect not only the habitats, but also the aquatic organisms (Randklev et al., 2015).

It should be noted that both groups in the Szczecin Lagoon were found to have an age distribution typical of stable populations of that species (Abraszewska-Kowalczyk, 2002; Lewandowski & Kołodziejczyk, 2014). The above may indicate that in both periods the population of the species was not threatened, despite

clear changes in the environmental conditions, also between the sampling periods (Borówka et al., 2002; Wolnomiejski & Witek, 2013). Currently, the Oder estuary together with the Szczecin Lagoon are a relatively strongly eutrophicated basin, with a high phosphorus and nitrogen content (Behrendt et al., 2008; Radziejewska & Schernewski, 2008; Friedland et al., 2019) and an oxygen content usually above  $8.0 \text{ mg dm}^{-3}$  (WIOŚ, 2018). Moreover, the basin has been undergoing dredging for more than 100 years (Wolnomiejski & Witek, 2013; Dąbkowski et al., 2017), which currently can lead to the destruction of many benthic species or elimination of their individual age groups (Weber, 2005). As a result of these activities, as well as the inflow of biogenic compounds from the Oder river catchment area, increased concentrations of nitrates, nitrites and phosphates can be observed alongside a periodic local decrease in the oxygen concentration in water (below  $6.2 \text{ mg O}_2 \text{ dm}^{-3}$ ) (WIOŚ, 2018), which according to Weber (2005) can reduce the period of *U. tumidus* active functioning to 83%. Nevertheless, it appears that these changes did not adversely affect the longitudinal growth of shells of *U. tumidus* population currently present in the Oder estuary. The above may be due to long-term changes in the environmental conditions and better adaptation of these organisms like mussels in river Ryck (Weber, 2005). Nevertheless, differences in longevity were observed between the EMS and MS groups in the examined waterbody. Shortening of the life span of *U. tumidus* in the contemporary individuals may be caused by factors associated with the trophy of the Szczecin Lagoon (Reis & Araujo, 2016).

Trophic changes in the Szczecin Lagoon waters observed in the recent decades (Wolnomiejski & Witek, 2013), caused by increased intensity of agricultural production and nutrient migration to surface waters (Burzyńska, 2019), may result in future elimination of numerous species sensitive to increased levels of nitrogen and phosphorus compounds. Such changes in the environmental conditions especially affect mussels (Cope et al., 2008), which are one of the most endangered groups of animals (Lopes-Lima et al., 2017; Böhm et al., 2020) How significant for the aqueous environment the freshwater mussels are is shown by the fact that they highly support water purification by filtering off bacteria from the water column (Othman et al., 2015). The most common

factors considered in the assessment of the mussel resources and planning of conservation works include the present state of the population or variability over short periods of time. This may lead to erroneous conclusions regarding the changes in the species abundance, distribution and composition of groupings, and may result in non-effective conservation works (Wolverton & Lyman, 2012; Dombrosky et al., 2016; Wolverton & Randklev, 2016). Therefore, zooarchaeological studies should be considered in ecological and conservation science, since understanding the causes of current state of resources requires long-term historical perspective.

## Conclusions

A comparative analysis of the contemporary (MS) and Early Middle Ages (EMS) shells of the *Unio tumidus* mussels revealed significant differences in the morphometric parameters. Regarding both the whole sample and particular age groups, a higher mean length ( $L$ ), width ( $W$ ), height ( $H$ ) and thickness ( $T$ ) of EMS vs MS mussels was observed, which considering a similar growth rate ( $K$ ) in both groups, may result from differential preservation and/or differential archaeological recovery. At the same time, EMS mussels, as compared with MS mussels, were characterised by a higher longevity (12 and 10 years, respectively), higher asymptotic length ( $L_{\infty}$ , 93.1 and 83.2 mm, respectively) and maximum length ( $L_{\text{max}}$ , 83.6 and 75.3 mm, respectively), which also resulted in higher morphometric parameters ( $L$ ,  $W$ ,  $H$ ,  $T$ ) of shells in this group of mussels.

The present studies have increased our knowledge of the *U. tumidus* and its distribution in the Oder estuary over long periods, but they also reveal the need of further exploratory analyses in the context of environmental and infrastructural changes of the analysed area affecting the distribution and biology of these environmentally valuable aquatic organisms. Moreover, these studies show the role of zooarchaeological studies in the assessment of the state and structure of the mussel (*U. tumidus*) population and their usefulness in a better understanding of changes taking place in the aqueous environment. However, the assessment of the length and age structure of mussels must also take account of taphonomic processes, because due to shell decomposition and

crystallization they make it difficult to draw correct conclusions regarding the changes taking place over the years.

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