



OPEN Millennial-scale changes in size and growth of *Unio pictorum* (L. 1758) and *U. tumidus* (Philipsson, 1788), in the Oder river

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Unio pictorum (L. 1758) and *Unio tumidus* (Philipsson, 1788) are common bivalve molluscs from the Unionidae family, with significant ecological importance in aquatic ecosystems. Their shells are essential for species identification and can also be used to assess changes in population structure, individual growth, and body form under varying environmental conditions. The aim of this study was to: (i) compare the individual size and shape of shells, (ii) assess length growth, and (iii) analyse population structures (based on length and age) of the bivalve molluscs *Unio pictorum* and *Unio tumidus* between specimens from the early medieval period (EMS) and those currently found (MS) in the Oder River near Szczecin, Poland. EMS shells were collected from archaeological excavations in cultural layers dated to the 10th and 11th centuries. They were located at three sites in Szczecin, approximately 500–700 m from the Oder River. MS specimens were collected using a bottom dredge between 12 and 21 May 2024 from sites within 1,000 m of the excavation area. For both groups, measurements included size, age, growth (using the von Bertalanffy model), and morphometric characteristics (length [L], height [H], width [W]), as well as the Elongation Index and Convexity Index. The shells of *Unio pictorum* and *U. tumidus* from the modern sample (MS) exhibited statistically significantly greater length, width, and height compared to those from the early medieval sample (EMS). At the same time, lower values of the Convexity Index and, in *U. pictorum*, the Elongation Index were recorded in the MS group. The length and age structure of both species in the MS group was dominated by larger and older individuals relative to the EMS group. The growth of contemporary *Unio pictorum* and *U. tumidus* can be considered moderate compared to other present-day populations, with maximum predicted ages of eight and nine years, respectively, and asymptotic lengths (L_{∞}) of 93.85 mm and 87.03 mm. In contrast, in the EMS group, the maximum predicted age and asymptotic length were 10 years and 70.12 mm for *U. pictorum*, and 6 years and 96.25 mm for *U. tumidus*, respectively. Higher values of the ϕ' and P growth indices in the MS group indicate that both species are currently growing at a faster rate than their early medieval counterparts (EMS). The observed differences in individual and population characteristics of *Unio pictorum* and *U. tumidus* between present-day specimens (MS) and those from the early Middle Ages (EMS) are attributed to long-term changes in temperature, nutrient availability, and water regime over the past 1,000 years.

Keywords Molluscs, *Unio pictorum*, *U. tumidus*, Age-length interactions

Fifty-five species of bivalve molluscs have been recorded in the inland waters of Europe¹ of which 16 belong to the Unionidae family². Unionidae represent a major group of freshwater bivalves, accounting for approximately two-thirds of all freshwater bivalve species³. Among their representatives are *Unio pictorum* (L., 1758) and *U. tumidus* (Philipsson, 1788), both commonly found in European waters⁴. *Unio pictorum* is distributed from western Europe (including Spain and Portugal) to the Urals and the Caucasus, with its southern range extending into Romania and Bulgaria⁴. In contrast, *U. tumidus* has a more limited range, occurring in European waters from France to Russia⁴. Both species are common in standing and flowing waters^{4,5} typically found near shores where they form large shoals alongside *Anodonta anatina*⁶. In such aggregations, the wet biomass of bivalves can

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exceed 11 kg per m², with densities reaching up to 80 individuals per m². These species prefer sandy or muddy substrates, avoiding gravel and soft silt, and are frequently found among macrophytes⁸.

Unio tumidus and *U. pictorum* are typically filter feeders⁹. This feeding strategy contributes to water purification by removing suspended solids from the water column and reducing the abundance of microorganisms¹⁰ which is crucial for the functioning of aquatic ecosystems¹¹. According to 6, the filtration rate of *Unio pictorum* ranges from 3.2 to 4.6 L·h⁻¹ per individual, while for *U. tumidus* it ranges from 2.1 to 2.4 L·h⁻¹. Furthermore, 12 note that selective filtration of planktonic organisms by bivalves can lead to restructuring of planktonic communities. In ecosystems, bivalves also serve as hosts for parasites^{13,14}. Conversely, their larval stage (glochidia) is parasitic on various fish species¹⁵. Additionally, these bivalves are used by ostracophilic fish, such as *Rhodeus sericeus roseus*, as sites for egg deposition⁴. According to⁴ *U. tumidus* is highly resistant to water pollution, including heavy metals, and can even survive in the vicinity of sewage discharge sites.

Shells serve as a protective element for the bivalve body¹⁶ and play a significant habitat-forming role in aquatic environments^{16–18}. They also provide attachment surfaces for numerous epizootic organisms¹⁹. Shells are a key feature in the identification of individual bivalve species. For instance, *Unio tumidus* is distinguished by its broadly rounded anterior and tapering posterior shell, while *U. pictorum* displays a much more elongated shell shape⁴. Additionally, *Unio tumidus* typically has a greater shell height at the same length compared to *U. pictorum*²⁰. However, shell morphology in bivalves may be influenced by various factors, including habitat conditions, sex, parasitic infections, and genetic variation^{20,21}.

Bivalves are estimated to have first appeared during the Cambrian period, approximately 541 million years ago²² with historical records of their presence dating back to antiquity¹⁷. For over 6,000 years, these organisms have served as a source of food and material for ornamental objects among communities living near water bodies¹⁷. Their shells have been found in refuse pits of early medieval settlements situated near water, where inhabitants discarded food waste^{23,24}. However, their remains were never predominant at these sites, as fish consistently formed the core of the human diet^{17,25}. Despite their limited dietary role, bivalve shells from archaeological contexts provide valuable material for study, offering insights into species biology and local environmental conditions²⁶. These remains allow for the analysis of long-term changes in bivalve morphology^{23,27} as well as more abrupt changes over shorter time spans^{28,29}. Numerous archaeological sites across Europe have yielded such findings, particularly in Central Europe^{23,30}. Among the best-known sites are excavations in Wolin on the Szczecin Lagoon²³ as well as those in Szczecin, where remains of aquatic animals fished from the Oder River during the early medieval period have also been uncovered³¹. Compared to the Szczecin Lagoon, the Oder River has a higher water flow rate (approximately 570–580 m³·s⁻¹)^{32,33} and contains elevated levels of nutrients and biogens that support high mussel density and influence population structure^{32,33}.

The bivalves *Unio pictorum* and *U. tumidus* recovered from early medieval excavations along the Oder River have not previously been the subject of zoological research. Their discovery enabled an analysis of changes in selected biological and population traits over the past millennium. The aim was to: (i) compare individual size and shell shape, (ii) assess length growth, and (iii) examine population structures (in terms of length and age) of *Unio pictorum* and *U. tumidus* between specimens from the early medieval period (EMS) and those found today (MS) in the Oder River near Szczecin.

Results

Shell morphology

Table 1 presents the main characteristics describing the linear dimensions and weight of both bivalve species from each period (EMS and MS groups). In both *Unio pictorum* and *U. tumidus*, modern individuals were characterized by statistically significantly greater shell length, width, and height, as well as higher individual shell weight (Mann–Whitney U test, $p < 0.0001$).

The Elongation Index and Convexity Index values for both bivalve species are presented in Table 2. The results indicate that, for both species, individuals from the EMS group had more convex shells, as reflected by higher Convexity Index values. Additionally, in *U. pictorum*, a higher Elongation Index was recorded for individuals from the early medieval period, suggesting that their shells were more elongated compared to those from the MS group.

Group	L (mm) ± SD	H (mm) ± SD	W (mm) ± SD	Shell weight (g)
<i>U. pictorum</i>				
EMS group	41.69 ± 5.25	19.00 ± 2.38	14.44 ± 1.63	3.60 ± 0.96
MS group	59.19 ± 4.16	27.9 ± 1.35	19.32 ± 0.84	7.06 ± 1.18
In Statistic	123	14	109	205.5
p-value	<0.0001	<0.0001	<0.0001	<0.0001
<i>U. tumidus</i>				
EMS group	40.45 ± 8.81	20.72 ± 4.20	15.53 ± 3.21	4.36 ± 2.47
MS group	58.16 ± 8.46	29.26 ± 4.06	20.54 ± 2.54	9.36 ± 3.89
In Statistic	2286	2358.5	3570.5	4198
p-value	<0.0001	<0.0001	<0.0001	<0.0001

Table 1. Linear dimensions (L, H, W) and shell weight of *Unio pictorum* and *U. tumidus* from EMS and MS groups.

U. pictorum			U. tumidus	
Group	Elongation Index	Convexity Index	Elongation Index	Convexity Index
EMS group	219.40 ± 4.10	76.14 ± 1.73	194.93 ± 5.14	74.991 ± 1.97
MS group	211.88 ± 5.64	69.23 ± 1.13	198.6 ± 3.15	70.40 ± 1.67
In Statistic	23,055	24,460	23,731	25,594
p-value	<0.0001	<0.0001	<0.0001	<0.0001

Table 2. Comparison of elongation index and convexity index values between EMS and MS clam groups (U-Mann-Whitney-Wilcoxon test) for both species studied.

Regression	Group	n	SMA Model	Linear model					Growth type	Isometric test of Statistic*	
			Slope (b)	Intercept (a)	x	r ₁	F	p-value		p-value	r ₂
<i>U. pictorum</i>											
W ~ L	EMS	153	0.875	1.655	0.307	0.975	5852	<0.0001	A	<0.0001	-0.987
H ~ L		153	0.987	0.243	0.450	0.986	1039	<0.0001	A	<0.0001	-0.808
W ~ H		153	0.886	1.530	0.680	0.983	8919	<0.0001	A	<0.0001	-0.995
W ~ L	MS	162	0.581	8.071	0.190	0.877	1144	<0.0001	A	<0.0001	-0.992
H ~ L		162	0.671	9.182	0.316	0.941	2586	<0.0001	A	<0.0001	-0.992
W ~ H		162	0.867	2.880	0.590	0.895	1379	<0.0001	A	<0.0001	-0.917
<i>U. tumidus</i>											
W ~ L	EMS	181	0.959	0.578	0.370	0.965	5042	<0.0001	A	<0.0001	-0.859
H ~ L		181	0.953	0.919	0.489	0.987	14,180	<0.0001	A	<0.0001	-0.931
W ~ H		181	1.007	0.069	0.746	0.955	3803	<0.0001	A	<0.0001	0.291
W ~ L	MS	174	0.813	3.820	0.287	0.985	11,350	<0.0001	A	<0.0001	-0.988
H ~ L		174	0.948	1.490	0.477	0.992	22,550	<0.0001	A	<0.0001	-0.956
W ~ H		174	1.010	2.933	0.602	0.991	19,580	<0.0001	A	<0.0001	-0.985

Table 3. Values of regression equations for *Unio pictorum* and *U. tumidus* shell morphology and p-values of slope. r₍₁₎– value of r calculated in linear model, r₍₂₎– value of r calculated by SMATR, * H0-slope not different from 1, from SMATR-R package, A - allometric growth, I isometric growth.

The regression equations for the linear parameters of *Unio pictorum* and *U. tumidus* shells in the EMS and MS subgroups are presented in Table 3. The high regression coefficient values (r₁), ranging from 0.877 to 0.992, along with p-values < 0.00001, indicate that all models were statistically significant. The shell growth of both *Unio pictorum* and *U. tumidus* from both periods can be classified as allometric.

Length structure of the mussel population

Among *U. pictorum* from the EMS group consisting of 153 specimens, the 40.0–50.0 mm length class was the most common, representing 58.5% of individuals. In contrast, in the MS group containing 162 specimens, the 50.0–60.0 mm and 60.0–70.0 mm classes dominated, together accounting for 97.5% of the specimens. For *U. tumidus*, the EMS group of 182 specimens was primarily composed of individuals in the 30.0–40.0 mm and 40.0–50.0 mm length classes, which together made up 76.0% of the sample. In the MS group comprising 175 specimens, individuals in the 50.0–60.0 mm and 60.0–70.0 mm classes predominated, comprising 73.8% of the total (Fig. 1). Overall, larger specimens of both *Unio pictorum* and *U. tumidus* were recorded in the modern populations compared to those from the early medieval period.

Age and growth rate

In terms of the age structure of *U. pictorum*, the highest abundance of mussels in the EMS group was found at age 5+, which accounted for 49.0%, while in the MS group they were at age 6+ (53.7%). For *U. tumidus*, the EMS group was dominated by individuals aged 3+ (55.5%), while the MS group was dominated by individuals aged 4+ (36.0%) (Fig. 2).

The growth of bivalve molluscs from the EMS and MS groups for *Unio pictorum* (A) and *U. tumidus* (B), based on the von Bertalanffy equation, is illustrated in Fig. 3, with the equation parameters provided in Table 4. The positioning of the growth curves indicates that individuals from the MS group of both species reached greater lengths at corresponding ages compared to those from the EMS group. Additionally, the higher values of the ϕ' and P indices in the MS group, as shown in Table 5, suggest that the modern populations (MS) of both species exhibit faster growth rates than their early medieval counterparts (EMS).

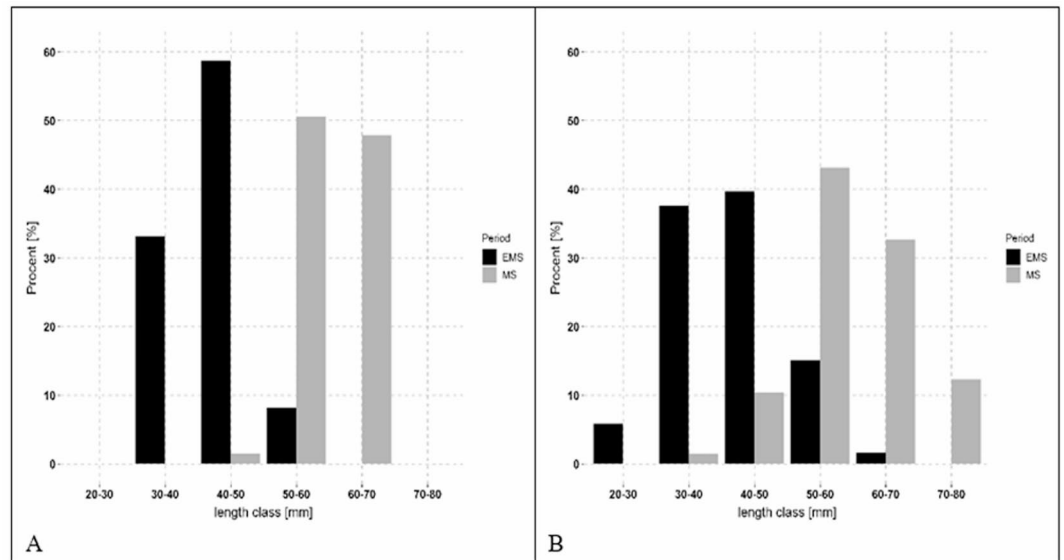


Fig. 1. Distribution of length (L) of *Unio pictorum* (A) and *U. tumidus* (B) shells from the Early Middle Ages (EMS) and present day (MS).

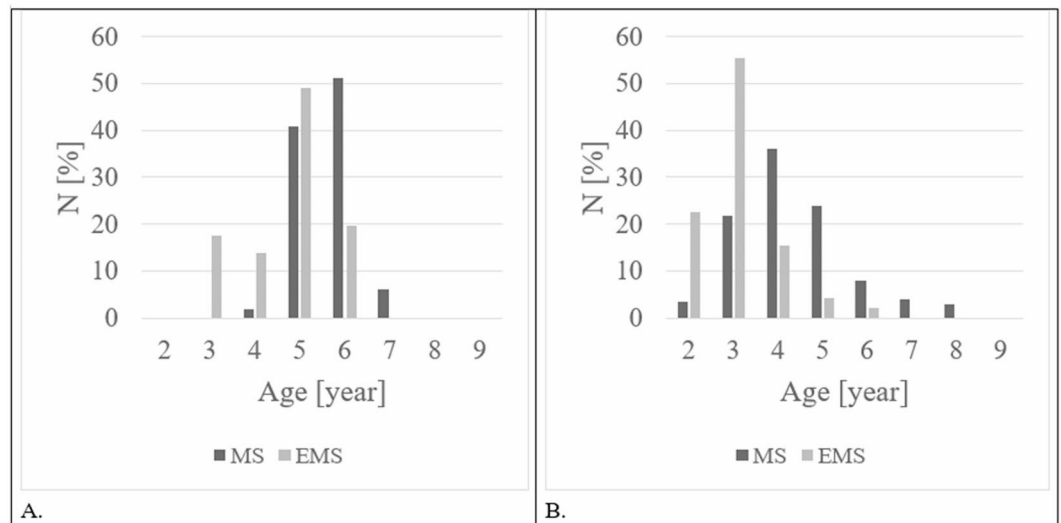


Fig. 2. Distribution of age of *Unio pictorum* (A) and *U. tumidus* (B) shells from the Early Middle Ages (EMS) and present day (MS).

Discussion

Unio pictorum and *U. tumidus*, found in European waters, are characterized by a maximum shell length of up to 140 mm for both species¹. In Polish waters, the shell length of *Unio tumidus* typically ranges from 60 to 100 mm (with a maximum of 130 mm), while for *U. pictorum* it ranges from 70 to 100 mm (with a maximum of 138 mm)⁴. The measurements obtained for the populations of these species in the Oder River fall within these reported ranges. However, in early medieval specimens, both the mean shell dimensions (length, width, and height) and their ranges were smaller compared to modern individuals. Our findings, showing that contemporary specimens are larger than those from the past, are consistent with the results of²⁴ who compared modern bivalves with specimens dated to around 850 BC. The authors suggest that archaeological samples containing many small shells indicate successful recruitment, whereas no evidence of recruitment was found among the large individuals in modern samples³⁵. In the case of the EMS and MS specimens analysed in this study, reproduction and recruitment of *Unio pictorum* and *U. tumidus* currently inhabiting the Oder River appear to be sufficient, as indicated by the high densities of these bivalves⁵.

Miller et al.³⁶ and Peacock³⁷ also reported larger sizes in modern bivalves compared to the same species found in Holocene archaeological sites. These differences are likely the result of long-term environmental changes,

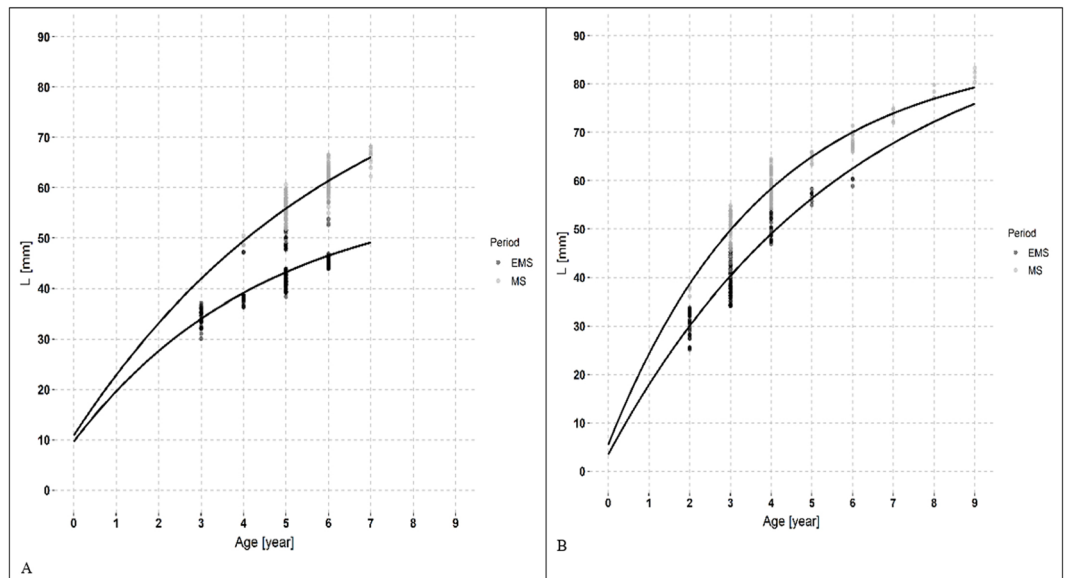


Fig. 3. Comparison of growth rates of the bivalves *Unio pictorum* (a) and *U. tumidus* (b) from the early Middle Ages (EMS) and present day (MS).

Group	Growth constant (k)	Asymptotic length (L_{∞}), mm	t_0	Maximum length (L_m), mm	Maximum age (years)*
<i>U. pictorum</i>					
EMS	0.170	70.12	-0.250	57.2	10
MS	0.156	93.85	-0.787	68.2	8
<i>U. tumidus</i>					
EMS	0.168	96.25	-0.217	63.0	6
MS	0.261	87.03	-0.246	79.4	9

Table 4. Parameters of the von Bertalanffy equation for *Unio pictorum* and *U. tumidus* from medieval (EMS) and modern (MS populations). * Maximum age was calculated using the formula published by Ziuganov et al.³⁴.

Group	<i>U. pictorum</i>		<i>U. tumidus</i>	
	φ'	P	φ'	P
EMS	2.922	4.768	3.192	5.176
MS	3.139	5.111	3.296	5.236

Table 5. Value of φ' and P coefficients for *U. pictorum* and *U. tumidus*.

including increasing eutrophication—now accelerated by human activities^{35,38}—as well as temperature fluctuations³⁹. Currently, elevated water temperatures and high levels of nutrients and food availability in the Oder River⁴⁰ may be contributing to the faster growth (see Fig. 3) and larger body sizes (Table 1; Fig. 1) observed in present-day bivalves. Conversely, the smaller sizes of *Unio pictorum* and *U. tumidus* from the early medieval period may be influenced by differential preservation, differential archaeological recovery methods, or both⁴¹. Generally, smaller, denser, and thicker mussel shells tend to preserve better than thinner ones, which are more prone to damage⁴². Furthermore, since modern shells were collected by hand rather than by sieving sediments, larger specimens may have been more easily detected and collected⁴³.

The bivalves shell morphology is an important taxonomic feature. In the nineteenth century, approximately 4,000 species were described based on shell morphology alone⁴⁴ though in recent years the number of recognized species has been revised⁴⁵. However, the high morphological plasticity of shells remains a significant challenge, as it often leads to taxonomic misidentification^{46,47}. Numerous studies have highlighted the influence of long-term climate change on bivalve shell size and form^{39,48}. According to⁴⁹ water temperature and productivity are the most important environmental factors shaping shell morphology. In addition⁵⁰, emphasize the role of river discharge, turbulence, and water depth, as also noted by⁵¹ and⁵². It is likely that changes in environmental conditions in the Oder River over the past millennium⁵³ have influenced the shell morphology of *Unio pictorum*

and *U. tumidus*. This is particularly plausible given that, as⁵⁴ observed, shell morphology is phenotypically plastic and primarily shaped by environmental conditions. Consequently, individuals from modern populations in the Oder River—where trophic and food resources are currently abundant⁴⁰—had longer, wider, and higher shells than those from the early medieval period. They also exhibited lower Convexity Index values, and, in the case of *U. pictorum*, a higher Elongation Index compared to early medieval specimens, which likely inhabited less fertile environments⁵³. Nonetheless, it should be acknowledged that phenotypic plasticity in response to environmental variation also has a genetic component⁵⁵ and should not be viewed merely as environmental noise obscuring the relationship between heritability and phenotype⁵⁶.

It is generally accepted that individual bivalve growth follows the von Bertalanffy growth curve^{23,57,58}. Bivalves continue to grow throughout their lives, and in temperate climates, a period of winter growth arrest—when water temperatures fall below approximately 12 °C⁵⁹—leads to the formation of an annual growth ring, visible as a dark band on the shell. However, as noted by⁶⁰, ring formation may also be triggered by environmental disturbances. Despite this, bivalve growth patterns offer valuable insights into their living conditions and historical population dynamics⁶¹. The lengths achieved by individuals in different age groups reflect environmental factors such as water quality and food availability^{62,63}, which explains the considerable variation in growth observed for *Unio pictorum* and *U. tumidus* (Table 6).

The lengths attained in individual years of life by *Unio pictorum* and *U. tumidus* from the Oder River are consistent with data reported for other populations of these species (Table 6), and the von Bertalanffy growth parameters calculated in this study align with those from other research sites (Table 7). Generally, both species exhibit their highest growth rates in the first year of life, ranging from 15 to 23 mm for *Unio pictorum* and from 13 to 22 mm for *U. tumidus*. In the subsequent two years, growth rates average around 10 mm for both species and gradually decline thereafter. Based on annual growth rates, individuals of both species currently inhabiting the Oder River can be classified as moderate-growing bivalves, similar to populations in Wicken Lode, England⁶⁵ and the Szczecin Lagoon²³. The calculated growth coefficients for *Unio pictorum* ($K=0.156$ – 0.170) and *U. tumidus* ($K=0.129$ – 0.172) are also within the average range for these species and fall within the broader ranges reported for European populations: $K=0.121$ – 0.245 for *Unio pictorum* and $K=0.075$ – 0.286 for *U. tumidus*^{28,65}.

However, clear differences in shell length growth were observed between the early medieval (EMS) and modern (MS) specimens of bivalves from the Oder River, particularly in *U. pictorum*. This is supported by the higher values of the growth indices ϕ' and P in the MS group (Table 5). These differences are likely attributable to changes in environmental conditions in the river, especially water temperature and fertility, both of which significantly influence bivalve growth⁶². According to⁶⁷ the period between 950 and 1250 AD, known as the Medieval Climate Anomaly (MCI), was characterized by relatively warm conditions in Europe. Nevertheless, water temperatures in the Oder River during that time were likely slightly lower than present-day levels⁴⁰. Additionally, a study by⁵³ indicates that water fertility (i.e., productivity) in the Oder River was considerably lower in the early medieval period. These conditions likely contributed to the differences in growth observed between the two time periods. As noted by⁶² freshwater mussels generally grow more slowly and live longer at higher latitudes, where lower air temperatures prevail. Reduced water temperatures limit bivalve feeding rates⁶⁸; in winter, although filtration continues, food particles are often rejected as inedible seston⁶⁹. This can lead not only to growth stagnation but also to increased mortality during colder periods⁷⁰. In contrast, higher water temperatures promote phytoplankton development—a primary food source for bivalves—thus enhancing their growth rates^{71–73}.

Location (author)	Age (year)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>U. pictorum</i>															
Lake Sapanca, Turke ⁶⁴	17	32	43	52	58	65	70	74	78	81	84	87	90		
Thames River, England -data from 2022 ²⁸	15	24	32	38	42	48	51	53	55	55					
Thames River, England - data from 1964 ²⁸	18	30	40	48	53	58	60	62	64	68	70	72			
Wicken Lode, England ⁶⁵	17	30	40	48	58	63	68	76	78	83	84	90	87	90	98
Oder River, Poland - Medieval data (Own data)	20	28	34	39	43	47	49	51	53	54	55	56			
Oder River, Poland - Modern data (Own data)	23	33	42	49	56	61	66	70	74	77	79	81	83		
<i>U. tumidus</i>															
Oder River, Poland - Medieval data (Own data)	17	30	40	49	57	63	69	73	77	80	83	85			
Oder River, Poland - Modern data (Own data)	20	31	40	49	56	63	69	74	78	82	86	89			
Thames River, England -data from 2022 ²⁸	15	23	30	38	41	45	48	50	51	53					
Thames River, England - data from 1964 ²⁸	22	39	51	60	68	71	76	79	81	83	85				
Lake Viinjärvi, Finland ⁶⁶	15	28	41	52	58	63	71	80	82						
Wicken Lode, England ⁶⁵	19	30	40	48	53	60	65	73	77	83	87	92	95	103	105
Szczecin Lagoon - Medieval data ²³	17	30	42	51	59	65	70	74	78	80					
Szczecin Lagoon - Modern data ²³	13	28	40	49	57	62	67	70	73	75					

Table 6. Comparison of length (mm) at age for *Unio pictorum* and *U. tumidus*.

Waterbody (Country)	K - growth constant	Asymptotic length (L_{∞}), [mm].	t_0	Maximum length (L_{∞}), [mm].	Maximum age [years]	Author
<i>U. pictorum</i>						
Thames River (England) – 1964	0.245	74.3	– 0.112	–	–	28
Thames River (England) – 2020	0.187	67.6	– 0.324	–	–	28
Lake Sapanca (Turkey)	0.190	96.2	–	90	–	64
Wicken Lode (England)	0.121	115.3	–	108	22	65
King's Dyke (England) - Modern data	0.214 ± 0.047	79.0 ± 8.1	– 0.146 ± 0.17	–	–	24
River Nene (England) - Modern data	0.243 ± 0.034	91.8 ± 5.4	– 0.090 ± 0.129	–	–	
Must Farm1 (England) - Ancient data	0.158 ± 0.063	71.5 ± 16.9	– 0.426 ± 0.241	–	–	24
Must Farm2 (England) - Ancient data	0.184 ± 0.031	76.8 ± 6.2	– 0.149 ± 0.144	–	–	
Odra River (Poland)	0.156	93.85	– 0.787	68.2	8	Own data - modern probe
Odra River (Poland)	0.170	70.125	– 0.25	57.2	10	Own data - medieval probe
<i>U. tumidus</i>						
Wicken Lode (England)	0.075	150.7	–	120	21	65
Gulf of Finland (Russia)	0.190	79.11	–	–	–	91
Lake Ladoga (Russia)	0.270	87.11	–	–	–	
Oder Estuary, Medieval data (Poland)	0.199	93.1	0.017	83.6 5	12	23
Oder Estuary, Modern data (Poland)	0.243	83.2	0.309	75.32	10	
Lake Viinijärvi (Finland)	0.150	114	–	98.4	13	65
Thames River (England) – 1964	0.286	87.8	– 0.037	–	–	28
Thames River (England) – 2020	0.239	58.9	– 0.205	–	–	28
Oder River (Poland)	0.129	111.04	– 0.504	79.4	10	Own data - modern probe
Oder River (Poland)	0.172	97.08	– 0.105	63	6	Own data - medieval probe

Table 7. Comparison of the parameters of the von Bertalanffy equation for different populations of *Unio pictorum* and *U. tumidus*.

An important factor influencing the growth of filter-feeding organisms, in addition to food availability, is the nutrient content of the water⁶³. According to data presented by⁵³ the process of eutrophication in the Oder River began in the 8th century AD, coinciding with the destruction of oak and beech forests in the area of present-day Szczecin. Initially slow, eutrophication accelerated significantly during the post-industrial era, and today the Oder is considered a highly eutrophicated river with elevated nutrient levels⁴⁰. This increase in nutrient content may enhance food availability for filter-feeding bivalves, enabling them to attain larger body sizes⁶⁰.

In addition, differences in bivalve growth may also result from long-term changes in the hydrological regime²⁴. According to⁷⁴ the period during which the EMS mussel groups originated was marked by frequent floods and river surges in Poland, leading to increased water flow. Haag and Rypel⁶² suggest that such increases in flow may be negatively correlated with mussel growth. In contrast, under present-day conditions of reduced flow and lower water levels, a positive correlation between flow and growth has been observed, as slower currents can enhance food availability for filter feeders^{63,68}. However, higher energy demands for survival under high-flow conditions may counteract growth⁷⁵. Additionally, the instability of flow regimes during the large floods of the early medieval period^{74,76} may have further limited bivalve growth compared to the more stable, low-flow conditions of the 21st century⁷⁷. A positive relationship between bivalve growth and flow stability was also demonstrated by⁷⁸ who found that greater stability in water flow was associated with increased bivalve size.

The production of these mussels is affected by various factors, including water pollution, habitat degradation, a decline in the number of host fish and the presence of invasive species^{79,80}. Water pollution significantly reduces the production of filter-feeding mussels and limits their presence⁸¹. Unfortunately, the section of the Oder River under study is located in a heavily industrialised area (cities of Szczecin and Police). Industrial activity significantly impacts water quality, causing major increases in pollution and periodic decreases in oxygen content⁴⁰. Decreases in oxygen content⁸² and increases in pollution⁸³ lead to reduced mussel production and high mortality rates, particularly among juveniles. The regulatory changes made to the river since the 19th century, including the concrete reinforcement of riverbanks, the removal of aquatic vegetation, and dredging, are important factors limiting the production of these organisms in the Oder River and leading to the degradation of their habitats⁸⁴. These works have been most intensive in the past 50 years, resulting in a decrease in macrozoobenthos species diversity, as well as changes to the resources and structure of ichthyofauna^{85,86}. Ichthyofauna, especially benthic species such as bream, roach and tench, can reduce mussel production by feeding on them⁸⁷. However, fish

also promote the movement of mussel larvae (in the glochidium stage) by carrying them, thus facilitating the colonisation of new water bodies⁸⁸.

Competition with other bivalves, particularly species capable of colonising a variety of underwater structures – such as the zebra mussel *Dreissena polymorpha* – plays a significant role in shaping Unionidae biomass⁸⁹. Large concentrations of this invasive species are currently present in the lower Oder River, including the Szczecin Lagoon. Despite the pollution of the Oder by a chemical plant in the town of Police, *D. polymorpha* populations have been recorded at levels reaching approximately 91,000 tonnes⁹⁰.

Thus, increased temperatures, higher water fertility, and other consequences of climate change – including declining water levels and reduced flow – may be key factors influencing bivalve growth over the long term^{39,48}. These factors also appear to have played a major role in shaping the evolution of individual size, shell morphology, growth patterns, and population structure of *Unio pictorum* and *U. tumidus* in the Oder River over the past millennium.

Methods

The study material consisted of shells of the bivalves *Unio pictorum* and *U. tumidus*, obtained from archaeological excavations (early medieval EMS group) and modern specimens harvested during fishing with a bottom dredge in the Oder River in 2024 (MS group). A total of 315 specimens of *Unio pictorum* (153 medieval and 162 modern) and 355 specimens of *U. tumidus* (181 medieval and 174 modern) were analysed. The EMS group comprised shells recovered from archaeological excavations at three sites: (1) Szczecin Mścięcino (located at an unspecified distance from the Oder River), (2) Szczecin Rynek Warzywny, and (3) Szczecin Zamek Książąt Pomorskich (both situated approximately 500 m from the Oder River) (Fig. 4). The shells were obtained from cultural layers dated to the 10th and 11th centuries³¹. Shells from the MS group were collected from bivalves caught between 12 and 21 May 2024 using a bottom dredge at sites in the Oder River within 1,000 m of the archaeological site.

Methods

The collected bivalves were identified to species level based on the criteria provided by⁴. Morphometric measurements were taken following the scheme proposed by⁶⁵ as modified by²³ using a NOWA 2000 (China) electronic calliper (± 0.01 mm) connected to a computer. The measurements included maximum shell length (L), maximum shell height (H), and maximum shell width (W) (Fig. 5;²³).

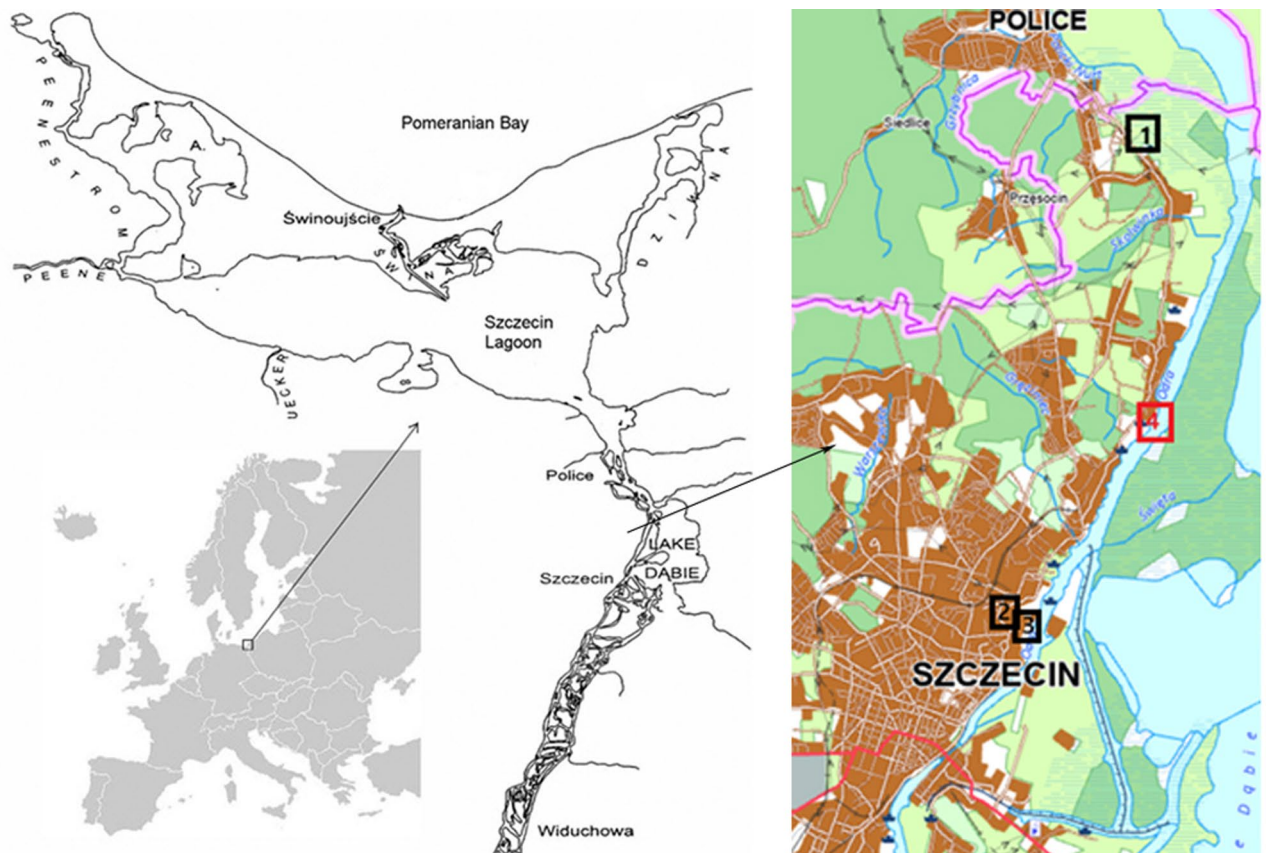


Fig. 4. Location of early medieval excavation sites (1 - Szczecin Mścięcino, 2 - Szczecin Zamek, 3 - Szczecin Rynek Warzywny) and 4 - fishing sites of the currently occurring mussels *Unio pictorum* and *U. tumidus* (Szczecin River Odra).

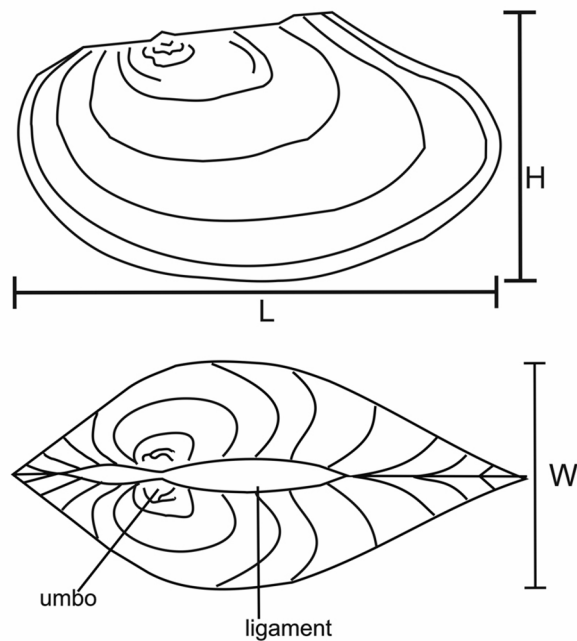


Fig. 5. Standard measurements of the shell. H-maximum height, W-maximum width, L-maximum length^{23,65}.

An analysis of the relationships $H \sim L$, $W \sim L$ and $W \sim H$ was conducted following⁶⁵ and the type of growth for H and W was assessed²³. Based on Shingleton (2010), the relationship is called isometric when $b = 1$, positively allometric when $b > 1$, and negatively allometric when $b < 1$.

Shells were weighed using an Axis electronic scale (Radwag, Poland) with a precision of 0.01 g. The age of the bivalves was estimated by counting the growth rings visible on the shell surface after cutting the shells into thin sections.⁹³ Growth rates were determined using the von Bertalanffy growth function^{57,58} as shown in Eq. (1):

$$L_t = L_\infty \times (1 - e^{-K(t-t_0)}) \quad (1)$$

where L_t is length (mm) at time t (age in years), L_∞ 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_∞ is attained (mm, year⁻¹) t is age (years) and t_0 is the time at which length = 0.

The parameters of the von Bertalanffy equation were calculated in the R programming environment in the FSA, nlstools, magrittr, dplyr packages⁹⁴.

Following³⁴ the maximum age that the studied bivalve species can reach in this water body was calculated according to Eq. (2):

$$A_{max} = -1/K \times \ln[1 - (L_m/L_\infty)] \quad (2)$$

where A_{max} is the maximum age and L_m is the maximum length.

The phi-prime index (ϕ' - Eq. (3)) and overall growth performance (index P - Eq. (4)) were also calculated⁹⁵:

$$\phi' = \log_{10} K + 2 \times \log_{10} L_\infty \quad (3)$$

$$P = \log_{10} (K \times L_\infty^3) \quad (4)$$

These indices are now widely used to assess the health of bivalves^{96,97}.

In addition, Elongation index (Eq. (5)) and Convexity index (Eq. (6)) were calculated according to^{98,99}:

$$Elongation\ index = (L/H) \times 100 \quad (5)$$

where: L - individual shell length, H - individual shell height.

$$\text{Convexity index} = (W/H) \times 100 \quad (6)$$

where: W - individual shell width, H - individual shell height.

Statistical analyses

The Shapiro–Wilk and Levene tests were used to assess the normality of distribution and homogeneity of variance, respectively, while the Breusch–Pagan test was applied to check for heteroscedasticity¹⁰⁰. Comparisons between clams from the early medieval (EMS) and modern (MS) samples were conducted using the Mann–Whitney U test (also known as the Wilcoxon rank-sum test)¹⁰⁰. A p-value ≤ 0.05 was considered statistically significant. If this threshold was met, the null hypothesis of no differences between EMS and MS samples was rejected in favour of the alternative hypothesis indicating statistically significant differences.

In addition, following the methodology of¹⁰¹ regression analysis of the linear parameters was conducted using the SMATR package in the R programming language. This package was also used to determine the type of growth by comparing the calculated *b* value to the reference value of 1, as proposed by⁹². A p-value < 0.05 was considered statistically significant, allowing the rejection of the null hypothesis that there was no difference between the calculated *b* value and 1. All statistical analyses were performed using R software (version 4.4.1,¹⁰²) along with the required packages.

Data availability

Dataset available upon request from corresponding author.

Received: 21 May 2025; Accepted: 13 August 2025

Published online: 20 August 2025

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Acknowledgements

The authors are thankful to Derek H. Oogle for his help in the interpretation of growth rate assessment using the von Bertalanffy method.

Author contributions

P.C. conducted fieldwork; J.D., P.C., A.B. conceptualized the research; J.D. formal data analysis; J.D., P.C., A.B. prepared draft manuscript; A.B. and P.C. reviewed and commented on the manuscript; A.B. and P.C. edited throughout. All authors reviewed the manuscript.

Funding

This research received no external funding.

Declarations

Competing interests

The authors declare no competing interests.

Statement confirming

The reporting in the manuscript follows the recommendations in the ARRIVE guidelines.

Additional information

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