Seasonal changes in the Mya arenaria (L.) population from Inner Puck Bay

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> > **KEYWORDS**

Mya arenaria Population dynamics Biochemical composition Inner Puck Bay

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Abstract

Morphometric relationships, the growth rate, sex distribution and annual fluctuation in dry flesh weight, biochemical composition and energy value of the sublittoral bivalve Mya arenaria (L.) from Inner Puck Bay were studied from May 1994 to April 1995.

M. arenaria grows rapidly during the first year of its life, after which the growth rate decreases. The oldest individual was 5 years old and 53 mm long. Judging from the sex distribution and analysis of biochemical composition, the soft-shell clam breeds in June–July. Analysis of the growth rate and the age distribution confirms the theories that specimens of M. arenaria found in low latitudes reach a smaller maximum size and grow more slowly than those living in higher latitudes.

The biochemical composition was determined in the 20–30 mm length class. The mean percentages of the main components of dry flesh were: proteins 47.54 ± 6.0 (male), 51.28 ± 7.7 (female); carbohydrates 9.28 ± 3.7 (male), 10.40 ± 4.0 (female); glycogen 5.74 ± 2.8 (male), 6.72 ± 3.5 (female); lipids 8.67 ± 1.8 (male), 8.79 ± 1.3 (female).

Analysis of lipid and carbohydrate (glycogen) content in tissues of the soft-shell clam yielded the highest values in the residue (gonads and hepatopancreas). The lipid level is much higher in early spring, before spawning, than in autumn, when gonad development begins.

The highest energy values are reported for August (20.82 J mg⁻¹ in both sexes), the lowest for October (14.38 J mg⁻¹ in males and 14.98 J mg⁻¹ in females).

Seasonal changes in energy values are mainly connected with the availability of food and reproduction cycle.

1. Introduction

Even though the soft-shell clam, Mya arenaria, is a very common species in Inner Puck Bay, its growth and population dynamics have only been occasionally investigated. Information about this species can be found in Mulicki (1957), Żmudziński (1967), Wenne and Wiktor (1982) and Żmudziński (1990). It must be pointed out that none of these investigations concentrated on M. arenaria; their purpose was to provide a brief, general characterisation of the bay's ecosystem. There is no data on the biochemical composition of this species.

The purpose of the present investigation is to examine in detail the growth rate, sex distribution, biochemical composition and energy values of the soft-shell clam population in Inner Puck Bay.

2. Material and methods

All the samples were taken at Rzucewo every month from May 1994 till April 1995 (except the winter months) (see Figs. 1 and 2, Tab. 1) from an area of 1 m^2 .

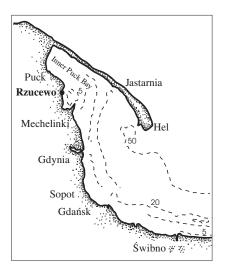


Fig. 1. The sampling site

Individual specimens of M. arenaria were divided into 10 mm length classes; length, height and width were measured with vernier callipers.

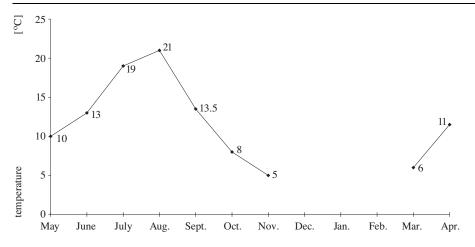


Fig. 2. Seasonal changes in seawater temperature

Table 1. Type of sediment, salinity and depth at the sampling site

Sediment type	Organic matter	Salinity	Depth
gravel and sand	< 1%	av. $7.5~\mathrm{PSU}$	$\sim 1 \text{ m}$

Wet weight was recorded for the whole organism (both shell and body) and separately for the shell and for the body. The flesh was dried at 60°C for 48 h to constant dry weight (d.w.). D.w. was determined both in the whole body and in the separate tissues – siphon, muscles, mantle, gills and residue.

The biomass of the samples in each month was calculated according to the equation: biomass = mass of sample (g) / area (m²). In our case the area was equal to 1 m^2 .

Microscopic examination of gonadal tissues enabled each individual to be assigned to one of three categories: male, female or immature (Brousseau, 1987).

Age classes were determined by counting annuli (Newcombe, 1936).

Morphometric relationships were estimated using the following equations:

$$S = aL + b, (1)$$

$$W = aL^b, (2)$$

where

S – height or weight,

L – length,

a, b – parameters of the equation.

The parameters a and b were estimated.

The relationship between age and shell length was estimated using the von Bertalanffy equation (Brousseau and Baglivo, 1987).

The 20–30 mm length group was used in the determination of the biochemical composition of whole organisms in each month. Moreover, in October 1994 and March 1995 the lipid, carbohydrate and glycogen contents were determined in soft tissues, *i.e.* siphon, muscles, mantle, gills and the residue (containing gonads and hepatopancreas).

Protein content was determined according to Lowry's method (Lowry *et al.*, 1951). Lipids were extracted from the bivalve bodies with 2:1 chloroform-methanol (Blight and Dyer, 1959) and then determined by the Marsh and Weinstein method (1966). The quantities of carbohydrates and glycogen were determined as described by Dubois *et al.* (1956).

The energy values were calculated on the basis of the biochemical composition using standard conversion factors: 39.57 J mg^{-1} for lipids, 23.65 J mg^{-1} for proteins and 17.16 J mg^{-1} for carbohydrates (Brody, 1945).

3. Results and discussion

3.1. An investigation of the population

Fig. 3 shows the number of individuals per m^2 and the biomass fluctuations in Inner Puck Bay soft-shell clam population in each month. The average density of *M. arenaria* there was 129 indiv. m^{-2} , which is higher than the results obtained by Munch-Petersen (1973) – av. 96 or

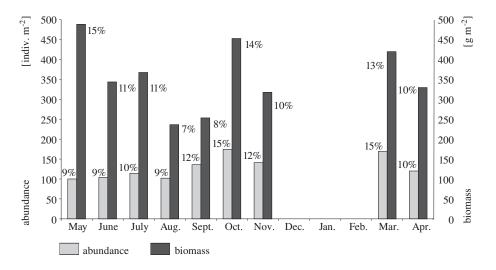


Fig. 3. The number of indiv. m^{-2} and the biomass of *M. arenaria* samples in each month

Pfitzenmeyer (1972) – av. 100. Further, the biomasses obtained are much higher than those published by Wenne and Wiktor (1982), who found the biomass of M. arenaria in Inner Puck Bay to be 84 g m⁻².

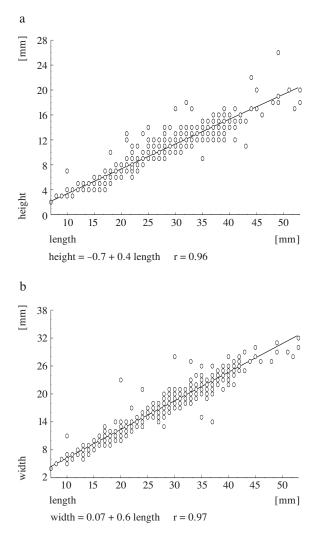
M. arenaria is a bioecious pelecypod, the sexes of which are distinguishable only after examination of the gonads. Of 978 individuals examined, 358 were male and 300 female (Tab. 2). It is therefore reasonable to assume equal numbers of the sexes in the population, which is in good agreement with the results obtained by Pfitzenmeyer (1972), Munch-Petersen (1973) and Brousseau (1987). No evidence of hermaphroditism or protandry was forthcoming, which suggests that these are rather rare phenomena in *M. arenaria*. Coe and Turner (1938) found only 3 hermaphrodites in more than 1000 individuals, Munch-Petersen (1973) found only 1 in 110 individuals examined, and Brousseau (1987) none at all.

Month			Sez	2			Tota	ıl
	mal	е	fema	le	immat	ure		
	[indiv.]	[%]	[indiv.]	[%]	[indiv.]	[%]	[indiv.]	[%]
May	41	41	54	54	5	5	100	100
June	51	49	39	37.5	14	13.5	104	100
July	52	45.5	37	32.5	25	22	114	100
September	52	43.5	38	32	29	24.5	119	100
October	33	30	35	31	44	39	112	100
November	44	31.5	22	15.5	75	53	141	100
March	44	26	47	28	78	46	169	100
April	41	34	28	23	51	43	120	100
Total	358	36	300	31	321	33	979	100

Table 2. Numbers and percentages of the different sexes of M. arenaria in Inner Puck Bay in each month

Fig. 4 shows the allometric relationship of M. arenaria in the bay. The estimated parameters of the equation linking length and width, length and height, length and total wet weight, length and body wet weight, and length and body dry weight for each month are shown in Tab. 3. It must be pointed out that the result obtained for the Inner Puck Bay population of M. arenaria differs from the data obtained by other investigators (see Tab. 4). The differences between these parameters are attributable to the effects of substrate, temperature, salinity *etc.* found at all these sites. Analysis of parameter a in the length-weight relationship suggests that M. arenaria spawns during June–July, which is in good agreement with the analysis of biochemical composition.

The age-shell length relationship is shown in Fig. 5. Clearly, *M. arenaria* from Inner Puck Bay grows rapidly during the first years of life, after which the growth rate decreases. This agrees well with the results obtained by others (Munch-Petersen, 1973; Feder and Paul, 1974; Brousseau, 1979; Brousseau and Baglivo, 1987). An inverse relationship exists between growth rate and age, a feature common to a number of bivalves. Growth rates within a species are commonly found to increase with rising temperature. Accordingly, bivalves occurring in lower latitudes attain a smaller maximum length than those living in higher latitudes. These differences are attributed to metabolic compensation and an extended growing season (Brousseau, 1979).



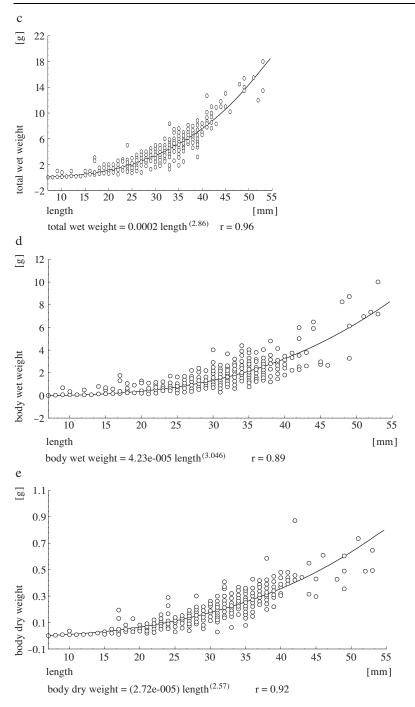


Fig. 4. Morphometric relationships of M. arenaria between: length and height (a), length and width (b), length and total w.w. (c), length and body w.w. (d), and length and body d.w. (e)

Month		Para	ameters					
	a	b	r	n				
	The relation	The relationship between length and width						
May	0.759	0.59	0.97	100				
June	-0.0066	0.62	0.96	104				
July	0.0527	0.62	0.98	114				
August	-0.24	0.61	0.98	102				
September	0.04	0.61	0.96	119				
October	0.159	0.61	0.95	112				
November	0.12	0.61	0.98	141				
March	0.17	0.61	0.98	169				
April	-0.075	0.63	0.98	120				
Average	0.07	0.61	0.97	1081				
	The relation	nship betwee	n length and he	eight				
May	-0.26	0.39	0.93	100				
June	-0.20 -0.38	0.39	0.93 0.97	100				
July	-0.58	0.39 0.42	0.97	104				
August	-0.33 -0.74	0.42 0.40	0.95	114				
September	-0.74 -0.85	$0.40 \\ 0.41$	0.93	102				
October	-0.54	0.41 0.39	0.93	113				
November	-0.54	0.39	0.98	112				
March	-0.72	0.39	0.98	141				
April	-0.93	0.39	0.98	120				
Average	-0.69	0.4	0.96	1081				
	The relation	nship betwee	n length and to	otal w.w.				
May	0.017	2.3	0.97	100				
June	0.0017	2.25	0.95	104				
July	0.0004	2.69	0.98	114				
August	0.0002	2.84	0.97	102				
September	0.0013	2.22	0.83	119				
October	0.0007	2.48	0.94	112				
November	0.0006	2.51	0.96	141				
March	0.0003	2.76	0.99	169				
April	0.0006	2.52	0.96	120				
Average	0.0002	2.51	0.96	1081				
	The relation	nship betwee	n length and be	odv w.w.				
May	0.0012	2.22	0.95	100				
June	0.0012 0.0012	2.22 2.05	$0.93 \\ 0.92$	100				
June	0.0012	2.00	0.32	104				

Table 3. The estimated parameters of equations 1 and 2 for each month

Month		Parame	ters	
	a	b	r	n
	The relations.	hip between le	ength and bod	y w.w.
July	0.0006	2.89	0.93	114
August	0.0001	2.72	0.95	102
September	0.001	2.07	0.78	119
October	0.001	2.12	0.93	112
November	0.0005	2.31	0.94	141
March	0.0004	2.24	0.94	169
April	0.0005	2.23	0.94	120
Average	0.000043	3.046	0.89	1081
	The relations	hip between le	ength and bod	y d.w.
May	0.0001	2.19	0.88	100
June	0.00036	1.86	0.9	104
July	0.00035	1.82	0.89	114
August	0.0003	1.86	0.89	102
September	0.0005	1.68	0.76	119
October	0.0004	1.76	0.86	112
November	0.00001	2.75	0.95	141
March	0.0003	1.87	0.89	169
April	0.0004	1.78	0.89	120
Average	0.000027	2.57	0.92	1081

Table 3. (continued)

a, b – estimated parameters of eqs. (1) and (2);

r – correlation coefficient;

n – number of individuals.

Table 4. Comparison of morphometric relationships obtained by other au	thors
and those characteristic of M . arenaria from Inner Puck Bay	

Relationship	Param	eters	Site	References
	a	b		
height = a + b length	0.077	1.63	Wadden Sea	Zwarts (1991)
	0.3	0.53	Danish estuary	Munch-Petersen (1973)
	0.7	0.4	Inner Puck Bay	this paper

Relationship	Paramet	ers	Site	References
	a	b		
width $= a + b$ length	$0.93 \\ 0.46 \\ 3.03$	$1.66 \\ 1.41 \\ 1.57$	Long Island Sound	Brousseau and Baglivo (1987)
	0.07	0.6	Inner Puck Bay	this paper
total w.w. = $a \text{ length}^b$	23.4	3.02	Alaska	Feder and Paul (1974)
	0.0002	2.86	Inner Puck Bay	this paper
body w.w. $= a \text{ length}^b$	27.75	3.037	Alaska	Feder and Paul (1974)
	4.23e-0.05	3.046	Inner Puck Bay	this paper
body d.w. = $a \text{ length}^b$	48.51	3.25	Alaska	Feder and Paul (1974)
	2.72e-0.05	2.57	Inner Puck Bay	this paper

Table 4. (continued)

a, b – estimated parameters of eqs. (1) and (2).

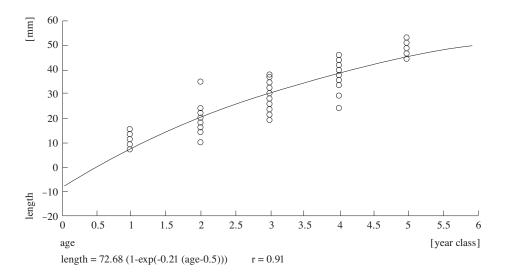


Fig. 5. Calculated von Bertalanffy growth-rate curve (length vs. age)

The available data (Tab. 5) confirm these patterns in M. arenaria. The growth rate was not determined separately for males and females, because most studies assume that there is no sexual dimorphism in the growth patterns, a fact confirmed by Brousseau (1979).

Site	Р	'aramete:	\mathbf{rs}
	L_{∞}	k	t_0
Long Island Sound (Brousseau and Baglivo, 1987)	81.12 60.89 72.56	$0.05 \\ 0.05 \\ 0.06$	$\begin{array}{c} 0.5 \\ 0.5 \\ 0.5 \end{array}$
Danish estuary (Munch-Petersen, 1973)	60.10	0.3	-0.11
this paper	72.68	0.21	0.5

Table 5. The relationship between age and shell lengthfor M. arenaria from different sites

k – growth rate;

 L_{∞} – asymptotic length.

k and L_{∞} – these two parameters are population-dependent and were estimated.

References		А	.ge [year	·s]	
	1	2	3	4	5
this paper	12.55	19.26	30.23	37.44	49.89
Newcombe (1936)	4.4	19.6	31.3	41.7	49.8
Munch-Petersen (1973)	15.82	27.16	34.79	37.47	47
Feder and Paul (1974)	13.41	17.73	26.04	30.87	39.01

 Table 6. Mean lengths in each age class

As a group, bivalves are relatively long-lived. For instance, *M. arenaria* has lived up to 17 years in the Bay of Fundy, and 10–12 years in the waters off Massachusetts (Brousseau, 1979). Shells reach a length of 70 mm in the Baltic Sea (Żmudziński, 1990) and 120 mm in oceanic waters (Tardent, 1993). In the present study the oldest individual was 5 years old and 53 mm long. This could be due to the uniqueness of Inner Puck Bay and its geographical location. The results shown in Tab. 6 confirm these conclusions.

 t_0 – this parameter represents the age 0. In the present study t_0 was fixed at 0.5, the end of the valiger or free-swimming stage, a period of about 14 days prior to settlement;

3.2. Biochemical composition

The percentage contents of proteins, lipids, carbohydrates, glycogen and energy in the body of M. arenaria are summarised in Tab. 7.

The protein content (Fig. 6a) was the highest in comparison with other biochemical compounds. Their average percentage calculated on the basis of all months was 45.13% d.w. in males and 49.3% d.w. in females. Seasonal changes were less evident than in the case of other compounds. The protein content in *M. arenaria* was higher than in *Cardium glaucum* from the same area, which varied between 30.82% and 37% d.w. (Wołowicz, 1991). The seasonal changes in protein content in other molluscs tended to differ from those found in *M. arenaria*. Unfortunately, there is at present too little evidence to explain this.

The average percentage lipid content (Fig. 6b) calculated on the basis of all months was 8.67% d.w. in males and 8.78% d.w. in females. The highest values in other molluscs from this region were found in Mytilus edulis – 16.15% in females, 16.28% in males (Brudkowska and Szaniawska, 1988), in C. glaucum - 9.77% in females, 10.82% in males, and in Macoma balthica from Inner Puck Bay – 11.7% (Wenne and Styczyńska-Jurewicz, 1985). The seasonal changes in lipid levels are similar to those found by other investigators: Pazikowska and Szaniawska (1988) reported maximum levels in March–April, as did Wołowicz (1991) in May. In all cases post-spawning minima were recorded. The lipid level probably falls more rapidly in July–August (because of spawning) than in the middle of summer (during the non-reproductive period), when this level remains low. In autumn, when gametogenesis starts, it again increases owing to the build-up of lipid reserves in the developing eggs. The second increase in lipid content (after November), though not as great as in the previous spring, could be related to pre-winter phytoplankton blooms and storage energy (Wenne and Styczyńska-Jurewicz, 1985).

The carbohydrate (glycogen) content (Fig. 6c) varied between 15.65% (13.20%) and 5.57% (2.88%) d.w. in females. In males it varied between 12.77% (8.31%) and 4.07% (2.06%) d.w. The seasonal trends in carbohydrate and glycogen contents in M. arenaria are similar when compared with results obtained for the M. balthica population in Inner Puck Bay (Wenne and Styczyńska-Jurewicz, 1985). The carbohydrate content in M. arenaria is high in comparison with that in other molluscs from this area. Lower carbohydrate levels were found in M. edulis – 4.83% d.w. in females and 4.39% d.w. in males (Wołowicz, 1991), and in C. glaucum – 6.4% d.w. in females, 6.34% d.w. in males (the respective glycogen contents: 2.65 and 2,62%) (Wołowicz, 1991). The seasonal variations in glycogen content.

Month				% of dry weight	weight				Energy value	· value
I	pro	proteins	lipids	ds	carboh	carbohydrates	glycogen	ogen	$[J mg^{-1} d.w.]$	¹ d.w.]
I	male	female	male	female	male	female	male	female	male	female
May	44.80	47.18	10.52	10.13	11.61	13.72	6.71	8.31	18.33	19.49
June	54.97	50.67	10.80	10.32	11.82	12.87	8.31	5.77	20.91	20.09
July	52.10	48.80	11.28	10.89	12.77	15.65	7.00	13.20	20.73	20.82
August	53.19	53.19	8.23	8.23	15.36	15.36	11.00	11.00	20.82	20.82
September	38.49	45.70	7.46	8.36	8.30	7.87	5.09	4.70	14.61	16.48
October	41.36	40.82	6.35	7.05	6.81	8.19	4.45	5.39	14.38	14.98
November	50.62	65.28	7.51	8.59	6.00	5.77	3.45	3.29	16.69	20.46
March	44.82	58.58	7.25	7.88	4.07	5.57	2.06	2.88	16.56	18.55
April	I	I	8.62	7.64	6.82	8.63	3.61	5.93	I	I

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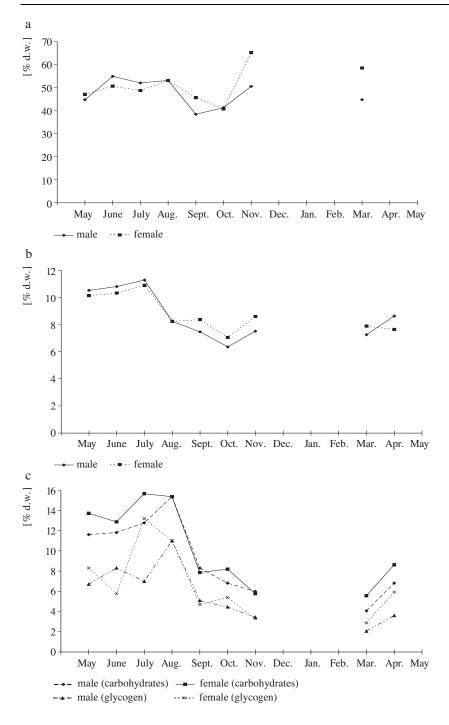


Fig. 6. Seasonal variations in biochemical composition: proteins (a), lipids (b), carbohydrates and glycogen (c)

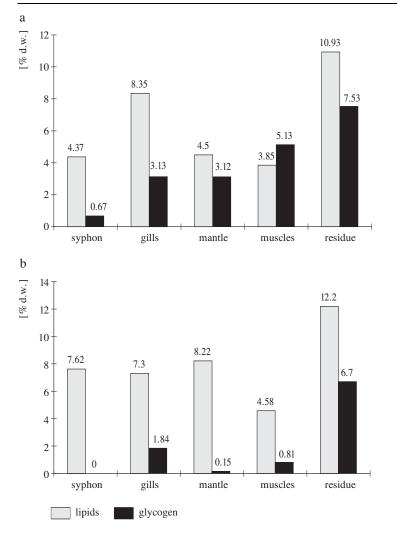


Fig. 7. Comparison of lipid and glycogen contents in separate tissues of *M. arenaria* in October (a) and March (b)

Glycogen reserves built up in the summer decrease rapidly in autumn, with minima being reached the following spring, when the lipid content is high. These seasonal changes are related to the annual reproductive cycle. Glycogen reserves accumulated in summer are converted during gametogenesis into lipids stored in the maturing eggs and subsequently utilised by the larvae as an energy store during the first stages of life (Gabbott, 1976). This is in good agreement with the results obtained from tissue analysis. Comparison of the lipid and glycogen contents in the separate organs, especially the siphon, mantle and muscle, indicates that in early spring (March), before spawning, the lipid level is much higher than in autumn, when gonadal development begins. In October the differences between the glycogen and lipid levels are not so distinct (Fig. 7).

In the tissues analysed, the highest total lipid concentration was found in the residue (containing hepatopancreas and gonads). The lipid levels recorded there are higher than those found in whole organisms, which suggests that lipids accumulate in these organs (Tab. 8).

Type of		% of dry weight	
tissue	lipids	carbohydrates	glycogen
October 1994			
syphon	4.37	1.80	0.67
gills	8.35	9.59	3.13
mantle	4.50	5.39	3.12
muscles	3.85	7.76	5.13
residue	10.93	11.08	7.53
Average	6.40 ± 3.1	7.12 ± 3.7	3.92 ± 2.6
March 1995			
syphon	7.62	0.66	0
gills	7.30	3.27	1.84
mantle	8.22	0.23	0.15
muscles	4.58	2.25	0.81
residue	12.20	9.25	6.70
Average	7.98 ± 2.7	3.13 ± 3.6	1.90 ± 2.8

Table 8. Comparison of lipid, carbohydrate and glycogen contentin each tissue of M. arenaria in October and March

The highest carbohydrate and glycogen levels were found in the residue; there too they were higher than those recorded for whole organisms. A high glycogen content was found in muscles in October (Tab. 8). The highest lipid content in the hepatopancreas (Jarzębski *et al.*, 1986), hepatopancreas and gonads was also found in *M. balthica* (Wenne and Polak, 1989).

The fact that during gametogenesis the lipid content increases to a maximum before spawning and drops to a minimum thereafter is typical for those species in which lipids are stored mainly in the gonads, *e.g. M. edulis* (Drzycimski, 1961; Williams, 1969).

The lowest lipid content in the major tissues of *M. arenaria* was found in the muscles, a level similar to that in *Macoma balthica* (Wenne and Polak, 1989). It has been reported that molluscan muscles store glycogen rather

than lipids as a major energy source and can utilise glycogen for rapid contractions. The results noted in October agree with this observation. The March glycogen level in all tissues (even in muscles) was lower than the lipid level. The high lipid content could be related not only to the reproductive cycle but also to phytoplankton blooms as it was found to be high in all the organs, not just in the gonads. The accumulation of lipids as storage material in clams living at low temperatures, like the species living in the Baltic Sea, has already been noted (Wenne and Styczyńska-Jurewicz, 1985).

The mean energy value of M. arenaria from Inner Puck Bay is 17.88 J mg⁻¹ d.w. in males and 18.96 J mg⁻¹ d.w. in females (Tab. 7). The highest values were recorded in summer, the lowest in early autumn. The energy values recorded by other investigators were higher than in M. arenaria: M. balthica 20.23–25.38 J mg⁻¹ (Szaniawska et al., 1986), M. edulis 19.16–22.12 (Pazikowska and Szaniawska, 1988). Food availability and the reproductive cycle are the main reasons for the seasonal variability in the energy value. The high energy level noted in May–August is correlated with high levels of lipid (before spawning) and carbohydrates (due to phytoplankton blooms). The decrease in the energy value after September is explained by a fall in the carbohydrate content, whereas the increase in the energy values in autumn is associated with lipid accumulation.

4. Conclusions

- High correlation coefficients of the morphometric relationships (Fig. 4) confirm the hypothesis that M. arenaria grows according to the equations: S = aL + b and $W = aL^b$. Parameter b in equation $W = aL^b$ is close to 3, and is indicative of isometric growth of the Inner Puck Bay population of M. arenaria.
- In Inner Puck Bay, *M. arenaria* grows rapidly during the first year of its life, after which the growth rate decreases (Fig. 5). An inverse relationship exists between growth rate and age, a common feature in a number of bivalves.
- A decrease in lipid content in July indicates that *M. arenaria* probably spawns in June–July, a fact confirmed by the impossibility of sexing the animals in August.
- The results of biochemical analysis suggest that lipids and carbohydrates are stored in *M. arenaria*.

- A high lipid level, probably due to spawning, and confirmed by high lipid concentrations in the gonads (see Fig. 7) was noted in spring. This could also be related to the spring phytoplankton bloom, a fact confirmed by the high concentration of lipids in all tissues (see Fig. 7).
- In summer, carbohydrates are built up as energy sources and are then probably converted into lipids during gametogenesis. The high lipid level in autumn may also be related to the second, autumn phytoplankton bloom and the build-up of energy to be used in the subsequent winter.

References

- Blight E. G., Dyer W. F., 1959, A rapid method of total lipid extraction and purification, Can. J. Biochem. Physiol., 37, 911–917.
- Brody S., 1945, Bioenergetics and growth, Reinhold, New York, 30 pp.
- Brousseau D. J., 1979, Analysis of growth rate in M. arenaria using the von Bertalanffy equation, Mar. Biol., 51, 221–227.
- Brousseau D. J., 1987, A comparative study of the reproduction cycle of the soft-shell clam, M. arenaria in Long Island Sound, J. Shellfish Res., 6, 7–15.
- Brousseau D. J., Baglivo J. A., 1987, A comparative study of age and growth in M. arenaria (soft-shell clam) from three populations in Long Island Sound, J. Shellfish Res., 6, 17–24.
- Brudkowska J., Szaniawska A., 1988, Seasonal changes of energetic value and lipids content in female and male of Mytilus edulis (L.) from Gulf of Gdańsk, Stud. i Mater. Oceanol., 54, 165–177, (in Polish).
- Coe W. R., Turner H. J., 1938, Development of the gonads and gametes in the soft shell clam (Mya arenaria), J. Morphol., 62, 91–111.
- Dubois M., Gilles K. A., Hamilton J. K., Reberts P. A., Smith F., 1956, Calorimetric methods for determination of sugars and related substances, Analyt. Chem., 28, 350–356.
- Drzycimski I., 1961, Nutrition, chemical composition and possibilities for utilization of the sea mussel, Mytilus edulis (L.), from the Southern Baltic, Ann. Biol., 18, 209–210.
- Feder H. M., Paul A. J., 1974, Age, growth and size-weight relationships of the soft-shell clam, M.arenaria, in Prince William Sound, Alaska, Proc. Natn. Shellfish Ass., 64, 45–52.
- Gabbott P. A., 1976, Energy metabolism, [in:] Marine mussels: their ecology and physiology, B. Bayne (ed.), Cambridge Univ. Press, Cambridge, 293–300.
- Jarzębski A., Wenne R., Habermehl G., 1986, Anatomical distribution of lipids and sterols in Macoma balthica (L.), Comp. Biochem. Physiol., 85 (B), 135–137.
- Lowry O. H., Rosebrough N. J., Farr A. L., Randall R. J., 1951, Protein measurement with the folin phenol reagent, J. Biol. Chem. 193, 193, 263–275.

- Marsh J. B., Weinsten D. B., 1966, Simple charring method for determination of lipids, J. Lipid Res., 7, 574–576.
- Mulicki Z., 1957, Ecology of the more important Baltic invertebrates, Pr. Mor. Inst. Ryb., Gdynia, 9 (A), 313–377, (in Polish).
- Munch-Petersen S., 1973, An investigation of a population of the soft clam (M. arenaria L.) in a Danish estuary, Medd. Danm. Fisk.-og Havunders., 7, 47–73.
- Newcombe C. L., 1936, Validity of concentric rings of M. arenaria (L.) for determining age, Nature, 137, 191–192.
- Pazikowska G., Szaniawska A., 1988, Variations in energy and lipid content from the Gulf of Gdańsk, Oceanologia, 25, 99–107.
- Pfitzenmeyer H. T., 1972, Tentative outline for inventory of molluscs: M. arenaria (soft- shelled clam), Chesapeake Sci. Suppl., 13, 182–184.
- Szaniawska A., Wołowicz M., Wenne R., 1986, Energetic value of the body of Macoma balthica (L.) from the Gulf of Gdańsk, Oceanologia, 24, 55–62.
- Tardent P., 1993, *Meeresbiologie*, Thieme Verlag, Stuttgart, 192 pp.
- Wenne R., Wiktor K., 1982, Benthic fauna of the inshore waters of Gdańsk Bay, Stud. i Mater. Oceanol., 39, 138–169, (in Polish).
- Wenne R., Styczyńska-Jurewicz E., 1985, Microgeographic differentiation in condition and biochemical composition of Macoma balthica (L.) from the Gdańsk Bay (South Baltic), Pol. Arch. Hydrobiol., 32, 175–194.
- Wenne R. Polak L., 1989, Lipid composition and storage in tissues of the bivalve Macoma balthica, Biochem. Syst. Ecol., 17, 583–587.
- Williams C. S., 1969, The effects of Myticola interstinalis on biochemical composition of mussels, J. Mar. Biol. Ass. U. K., 46, 161–173.
- Wołowicz M., 1991, Geographical differentiation of population of Cardium glaucum (Bivalvia). Hypothesis relative to origin of species and migration ways, Gdańsk Univ. Press, Gdańsk, 88–110, (in Polish).
- Zwarts L., 1991, Seasonal variation in body weight of the bivalves Macoma balthica, Scrobicularia plana, M. arenaria and Cerastoderma edule in the Dutch Wadden Sea, Neth. J. Sea Res., 28, 231–245.
- Zmudziński L., 1967, Zoobenthos of Gdańsk Bay, Pr. Mor. Inst. Ryb., Gdynia, 14 (A), 47–80, (in Polish).
- Żmudziński L., 1990, *The Baltic animal world*, Wyd. Szk. i Pedag., Warszawa, 132, (in Polish).