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Biochemical composition and energy value of *Crassostrea gigas* (Thunberg) cultured in the bay of Marennes-Oléron

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Abstract

In the bay of Marennes-Oléron the dry flesh of *Crassostrea gigas* ranged from 29 to 52% proteins, 10 to 23% ash, 6 to 20% lipids and 0 to 4% carbohydrates of which 48.3±21.6% were glycogen. The energy value ranged from 18.84 to 23.47 joule.mg^{-1} ash free dry weight (mean 20.27 J.mg^{-1}). Reproductive effort varied from 17.8 to 55.9% dry weight for males, and 43.1 to 61.9% for females during the first and third year of reproduction respectively. A high energy value for female gametes (23.47 to 26.24 J.mg^{-1} dry tissue) was mainly due to a higher level of lipids (17.3 to 23% of dry tissue) in female gametes as compared to that in male gametes (5.9 to 12.3% of dry tissue). During the period of mass-loss which began in October and finished in March, the poor trophic conditions of the environment resulted in the use of 74.6% of glycogen, 44% of lipids and 36% of proteins to meet more than 50% of the requirements for basal metabolism.

Keywords : Biochemical composition, energy value, reproductive effort, winter loss of flesh, *Crassostrea gigas.*

Composition biochimique et teneur énergétique de Crassostrea gigas (*Thunberg*) *cultivée dans le bassin de Marennes-Oléron.*

Résumé

Dans le bassin de Marennes-Oléron, les constituants de la chair sèche des huîtres *Crassostrea gigas* fluctuent saisonnièrement de 29 à 52 % pour les protéines, 10 à 23 % pour les cendres, 6 à 20 % pour les lipides et 0 à 4 % pour les glucides, dont 48,3±21,6 % sont formés de glycogène. La valeur énergétique est comprise entre 18,84 et 23,47 joule.mg^{-1} de chair sèche sans cendre (moyenne de 20,27 J.mg^{-1}). L'effort de reproduction varie de 17,8 % à 55,9 % du poids sec pour les mâles, et, de 43,1 % à 61,9 % pour les femelles pour respectivement leur première et troisième année de reproduction. La forte valeur énergétique des produits émis par les femelles (23,47 à 26,24 J.mg^{-1} de tissu sec) est induite par une plus forte teneur en lipides des gamètes femelles (17,3 à 25 % de tissu sec) que des gamètes mâles (5,9 à 12,3 % de tissu sec). Pendant la période d'amaigrissement qui débute au mois d'octobre et se termine au mois de mars, les mauvaises conditions trophiques nécessitent l'utilisation de 74,6 % du glycogène, 44 % des lipides et 36 % des protéines pour assurer plus de 50 % du métabolisme basal.

Mots-clés : Composition biochimique, valeur énergétique, effort de reproduction, amaigrissement hivernal, *Crassostrea gigas.*

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By the use of culture methods such as harvest of spats, the annual and seasonal variations of climatic factors do not show close correlations with the variations of the production and biomass of the cultivated population of oysters in the bay of Marennes-Oléron (Héral *et al.*, 1986) in opposition to the sensitivity of the natural molluscan populations towards these climatic factors (Dow, 1983).

If the growth of molluscs was mainly in relation with the water temperatures (Bodoy, 1982; Hamon, 1983; Bachelet, 1984; Rodhouse *et al.*, 1984), it was also under the control of the amount of cultivated stock in the bay (Héral *et al.*, 1986), probably in relation with the carrying capacity.

In the same way, seasonal variations in the flesh of *Crassostrea gigas* cultivated in the bay of Marennes-Oléron (Deslous-Paoli, 1982; Bodoy *et al.*, 1986) depended directly on available food (Héral *et al.*, 1984). Several authors have described the proximate biochemical composition of *Crassostrea gigas* and showed that seasonal variations depended both on parameters as temperature and available phytoplankton and parameters as reproductive cycle and turnover of stored energy (Gabbott, 1982; Hawkins, 1985).

In the bay of Marennes-Oléron, the stocks of *Crassostrea gigas* increasing from 30 000 t to approximately 80 000 t (Héral and Deslous-Paoli, 1985; Héral *et al.*, 1986), beyond the optimum trophic capacity of the bay, have induced a decline both in growth rate and in oysters' condition. As this pattern of poor growth and physiological state of oysters induced by a change in stock size has been followed before 1972 by a large epizootic for the cupped oyster *Crassostrea angulata* (Héral and Deslous-Paoli, 1985), it is now useful to determine the level and changes in proximate biochemical composition and energy value of *Crassostrea gigas* in relation to reproductive cycle and environmental factors and to compare the results obtained in this study for *Crassostrea gigas* cultivated in an overstocked bay with those obtained for *Crassostrea gigas* cultivated in oyster ponds in the same area, at low density (Deslous-Paoli *et al.*, 1981 *a*; Zanette and Deslous-Paoli, 1983).

MATERIALS AND METHODS

Crassostrea gigas were cultivated at a density of $360/m^2$ in plastic boxes of $0.5\ m^2$. These boxes were placed on metallic tables, 40 cm off the ground, in an intertidal oyster bed from 1.6 m depth to the zero of the marine map (tidal coefficient 81), in the centre of the bay (*fig.* 1). Two different year classes were used. Oysters of the first year class were naturally settled on slate collectors in 1978 and where grown from January 1979 for 3 years. These oysters were separated from collectors when 15 months old. Oysters of the second year class were naturally collected in 1977, and grown for 1 year.

A sample of ten oysters was collected twice a month for the first year and once a month thereafter. The flesh was weighed and dried at 60°C for 72 hours. It was then pulverized in a mortar and analysed for its proximate biochemical components and energy value.

Proteins were determined using the Lowry *et al.* (1951) method after extraction with normal sodium hydroxyde. Total lipids were extracted with a mixture of chloroform and methanol (Bligh and Dyer, 1959) and analysed using the Marsh and Weinstein (1966) method; carbohydrates and glycogen, precipitated with 99% ethanol, were determined by the folin phenol method described by Dubois *et al.* (1956). Ash content was determined by igniting a subsample of dry tissue in a muffle furnace at 450°C for 24 hours. The energy content was determined using the method described by Héral and Deslous-Paoli (1983) with a Phillipson (1964) microcalorimeter. To understand the physiological state of *Crassostrea gigas* independently of growth and energy storage, the results will be expressed first as a percentage. Secondly, the absolute values will be used to define the seasonal storage and use of components and energy, and the reproductive effort. Because *Crassostrea gigas* spawn all their gametes at the same time, the reproductive effort could be calculated from the quantity of components or energy lost during the gamete emission.

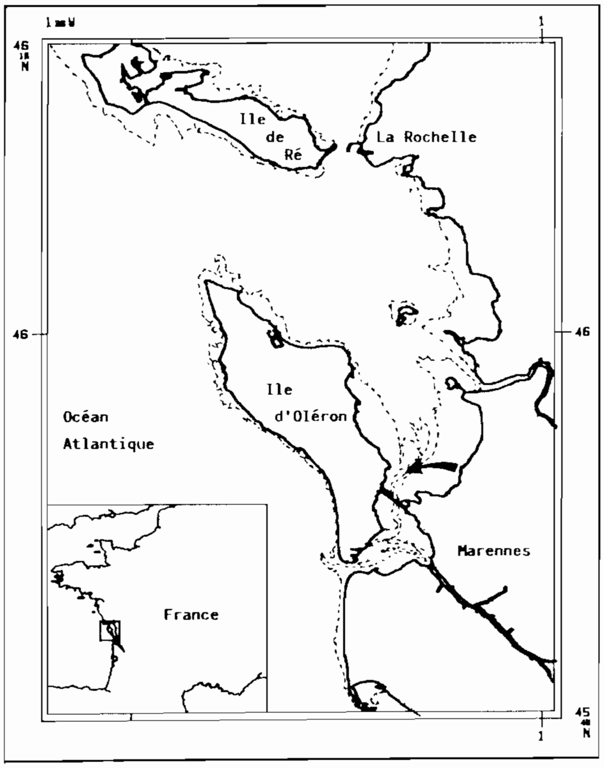

Figure 1. — Map of Marennes-Oléron bay and sample localities.

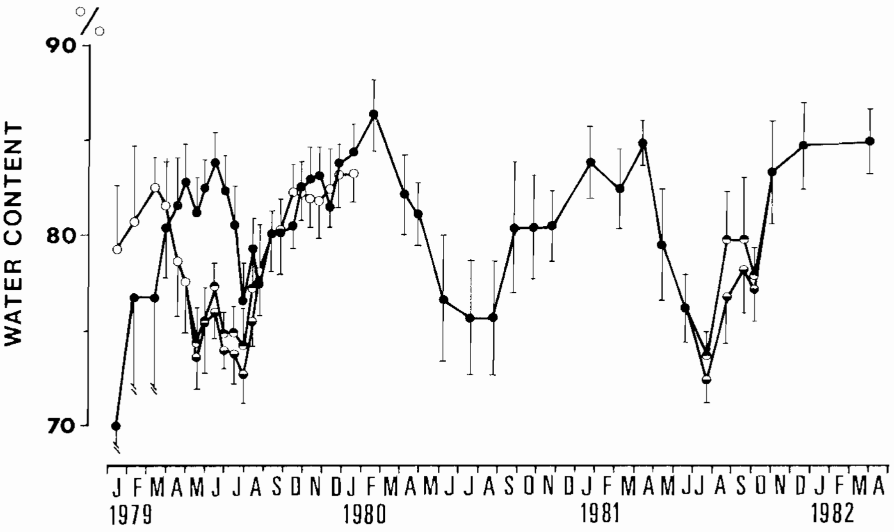

Figure 2. – Water content of the flesh of *Crassostrea gigas*: (●) oysters collected in 1978; (○) oysters collected in 1977; (◓) males; (◒) females.

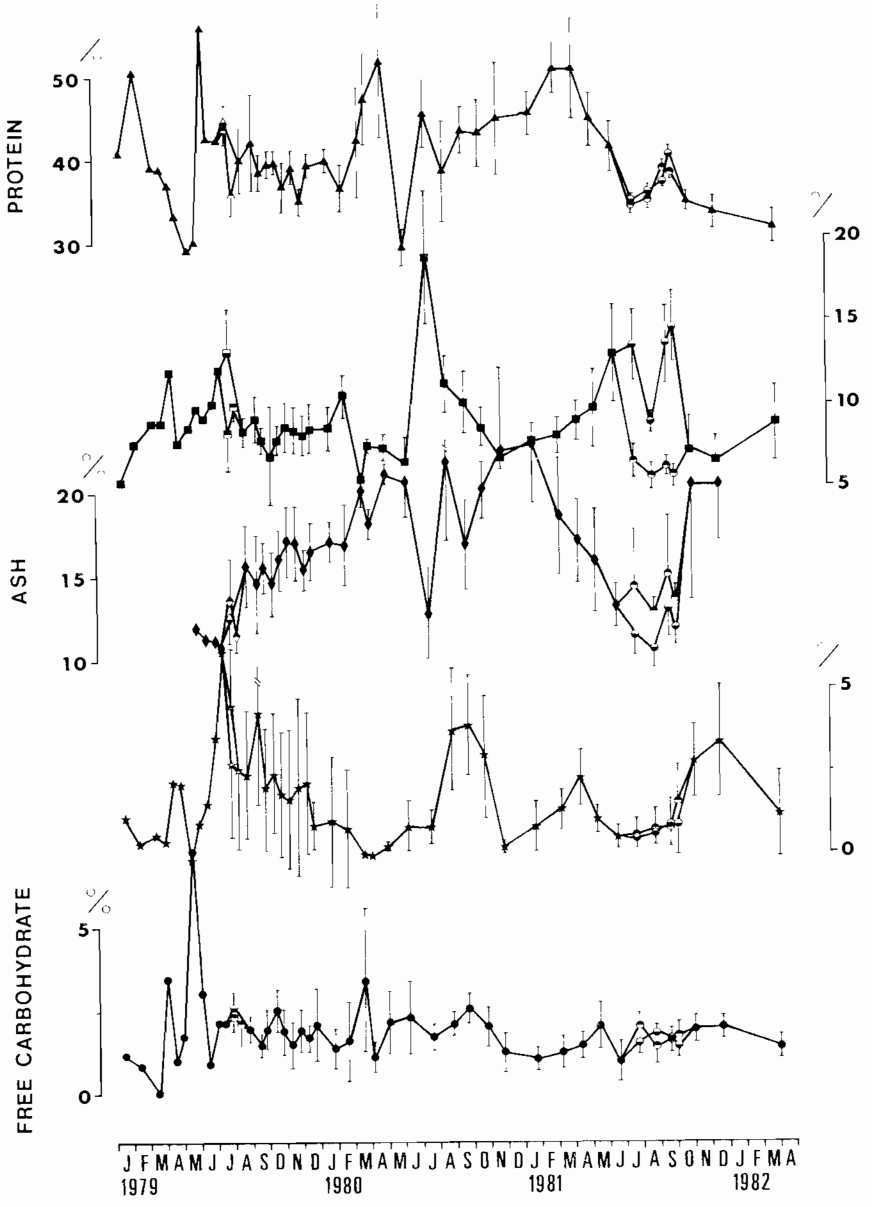

Figure 3. – Seasonal variation of the proximate composition of the dry flesh of *Crassostrea gigas* recruited in 1978. (▲) proteins; (■) lipids; (♦) ash; (★) glycogen; (●) free carbohydrates; (◒) females; (◓) males.

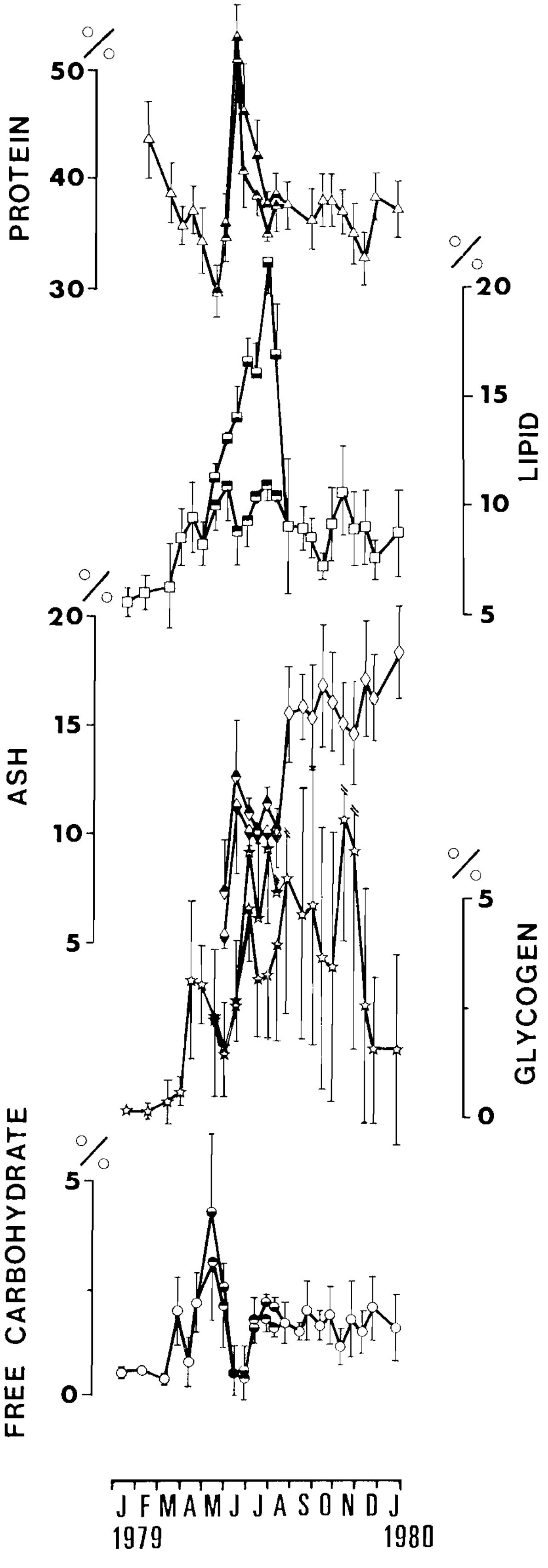

Figure 4. — Seasonal variation of the proximate composition of the dry flesh of *Crassostrea gigas* recruited in 1977. The open symbols are equivalent to the closed ones of the same shape in figure 3.

RESULTS

Changes in water content of the flesh followed a similar pattern every year, except for year 1 of growth (*fig.* 2). This pattern was characterized by a high water content of the tissues from the end of spawning to the end of winter. Thereafter, the water content decreased steadily to 75%, simultaneously with the buildup of gametes and the accumulation of biochemical reserves. During their first winter, oysters showed a low water content of 70%, which increased to 84% in the spring but declined again during the first short gametogenesis. After the spawning period, the water content of these young oysters was similar to that of older oysters.

Yearly differences in the proximate biochemical composition are shown in *figure* 3-4. In spring, the accumulation of energy reserves, which had been depleted in the winter months, along with flesh growth and gametogenesis, masked the clear scheme described for *Crassostrea gigas* grown in oyster ponds (Deslous-Paoli *et al.*, 1981 *a*). This pattern in which transformation of glycogen reserves into lipids intervened for the formation of gametes (Gabbott, 1975-1976; Lubet *et al.*, 1976), could be seen during the spring of 1981 (*fig.* 3) and of 1979 for the 2-year-old oysters (*fig.* 4). However a definite pattern was not observed in the other years studied, although a tendency may be seen. This might be explained by the monthly sampling, not accounting for the rapid spring variation of *Crassostrea gigas* energy reserves. Yet, these phenomena were quite obvious, when sampling was performed twice a month at the beginning of this study for the oysters in the bay of Marennes-Oléron as well as for oysters grown in ponds (Deslous-Paoli *et al.*, 1981 *a*).

For 1-year-old oysters, the increase of carbohydrate during March and May 1979 was followed by the accumulation of glycogen reserves. This increase was less in older animals; this was probably due to their increasing needs related to gametogenesis, causing an acceleration in the transformation of exogenous carbohydrate into glycogen during the depletion of glycogen reserves. The glycogen reserves were restored, after the spawning period, during the autumn or spring depending on the year; they were regularly depleted during the winter period in order to ensure the animal's survival when environmental conditions became unfavourable such as low temperatures and partial lack of food (Héral *et al.*, 1982).

In winter, the protein reserves were stable, increasing quickly during the spring as gametogenesis began, but decreasing all along the actual process of gamete production. Similarly, the ash content decreased regularly from the begining to the end of gametogenesis.

Table 1. – Quantities and percentage of the dry flesh (mg), the energy (kJ) and the proximate constitution of the flesh lost by males (♂) and females (♀) during the emission of gametes. ND : sex non determined.

	Oysters collected during 1978										Oysters collected during 1977			
Year	1979				1980		1981				1979			
Sex	♂		♀		ND		♂		♀		♂		♀	
	Q	(%)	Q	(%)	Q	(%)	Q	(%)	Q	(%)	Q	(%)	Q	(%)
Dry weight (mg)	128.2	17.8	447.4	43.1	810	42.9	1 510	55.9	1 930	61.9	850	45.2	1 030	50.0
Energy (kJ)	–	–	–	–	19.48	52.7	30.98	61.1	45.3	69.6	23.2	60.8	27.03	64.4
Proteins	86.7	27.7	236.3	51.1	435.7	51.0	502.6	55.2	663.7	61.9	330.8	46.7	415.1	52.3
Lipids	11.6	18.7	88.6	63.1	257.0	67.3	89.5	49.1	334.2	78.3	104.3	52.8	257.1	73.4
Free carbohydrates	5.7	33.7	16.6	59.8	9.46	30.1	30.0	57.9	22.9	51.2	14.7	48.2	27.0	63.1
Glycogen	14.3	44.3	11.5	39.0	–	–	–	–	–	–	48.6	50.6	33.0	41.0
Ash	4.1	4.4	42.6	32.3	66.1	27.7	151.8	40.5	125.5	36.0	29.1	15.2	41.2	20.2
	calculated from 24/7/79 to 21/8/79				calculated from 15/7/80 to 25/8/80		calculated from 20/7/81 to 28/10/81				calculated from 7/8/79 to 11/9/79			

The ash content increased and the lipid content decreased during the emission of genital products, showing the energy richness of the gametes (*table* 1 and 2). The energy value of the ash free dry weight (AFDW) of flesh fluctuated slightly during the year and was approximately 20.27 $J.mg^{-1}$ AFDW ($n=33$; $s=3.47$) (*fig.* 5). However, it appeared to be slightly higher at the end of gametogenesis (July and August). This results confirmed the values measured by Héral and Deslous-Paoli (1983).

Component levels in the wet tissue were similar to those of the dry flesh throughout the analysis except for glycogen, which made up $48.3 \pm 21.6\%$ of the carbohydrate (*fig.* 6). The sum of these components was about $68.3 \pm 7.7\%$ of the dry flesh. The variation in the carbohydrate-protein ratio pointed out two time periods where accumulation of carbohydrate reserves occurred (*fig.* 7); the first one being the spring at the begining of gametogenesis, and the second one in autum and the begining of winter. This ratio was, in any case, rather low approximately 0.097 ± 0.049. The lipid-protein ratio (*fig.* 7) showed the relationship between the accumulation of lipids and the reproductive period for 2 and 3 year old individuals. There was a significant relationship between the energy value of the flesh and the lipid-protein ratio ($n=24$, $r=0.628$).

The quantities and the percentages of dry flesh – *i. e.* the energy value and proximate biochemical components – used during gamete emission (*table* 1) clearly showed a sexual dimorphism, especially for oysters reproducing for the first year, as well as an increase in the average reproductive effort with age. This effort increased from 128.2 mg (17.8% dry weight) to 1 510 mg gamete weight (55.9% dry weight) between the first year and the third year of reproduction for males, and from 447.4 mg (43.1% dry weight) to 1 930 (61.9% dry weight) for females. The total waste of energy, due to loss of both proteins and lipids, followed the same pattern, and showed a high energy value in female gametes (23.47 $J.mg^{-1}$ of dry flesh in 1981 for the 3-year old oysters, and 26.24 $J.mg^{-1}$ of dry flesh in 1979 for the 2-year old oysters). This energy value was due to a higher quantity of lipids in female gametes with a value of 17.3 to 25.0% of dry tissue compared to that of 5.9 to 12.3% of dry tissue for male gametes (*table* 2). Meanwhile carbohydrate reserves remained rather low.

Table 2. – Composition of the products lost during the emission of gametes for males (♂) females (♀) and sex non determined (ND) of *Crassostrea gigas*.

	Oysters collected during 1978					Oysters collected during 1977	
Year	1979		1980	1981		1979	
Sex	♂	♀	ND	♂	♀	♂	♀
% proteins	67.7	52.8	53.8	33.3	34.4	38.9	40.3
% lipids	9.04	19.8	31.7	5.93	17.3	12.3	25.0
% free carbohydrates	4.4	3.7	1.2	1.99	1.19	1.7	2.6
% glycogen	11.2	2.6	–	–	–	5.7	3.2
% ash	3.2	9.5	8.16	10.1	6.5	3.4	4.0

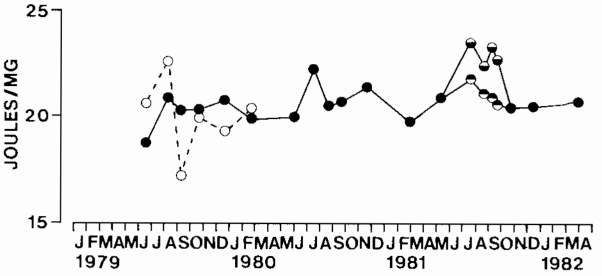

Figure 5. – Seasonal variation of the energy content of the flesh of *Crassostrea gigas* (joule . mg^{-1}).

Without taking into account the energy used in reproduction, the somatic variations alone showed flesh growth, the accumulation of reserves unused for reproduction between April and September as well as the use of these reserves during the rest of the year (*table* 3). The annual budget of the composition and use of the reserves was positive for 1 and 2-year old oysters, and negative for 3-year old individuals.

DISCUSSION

The average percentages of the proximate biochemical composition of *Crassostrea gigas* cultivated in the bay of Marennes-Oléron, are quite similar to those described in the literature (*table* 4), except for glycogen values. Despite its variations from one year to another due to environmental conditions (Deslous-Paoli *et al.*, 1981 *b*), the glycogen level remained lower than the one analysed in oysters grown in other countries and than the one found in oysters cultured in low density ponds (Gras and Gras, 1976; Deslous-Paoli *et al.*, 1981 *a*). On the other hand glycogen accounted for approximately 48.3 ± 21.6% of the total carbohydrate, being in accordance with the value of 55.8 + 28.8% total CHO obtained by Lee *et al.* (1975). However Deslous-Paoli *et al.* (1981 *a*) showed values ranging between 80.3 and 97.3% for oysters cultured in oyster ponds, Whyte and Englar (1982) recorded a value of 79.5% and Maurer and Borel (1986) analysed similar levels ranging from 65 to 100%. In the same way, this poor condition of the energy reserves as indicated by the carbohydrate protein ratio, may be due to an overstocking with respect to the carrying capacity of the bay of Marennes-Oléron (Héral and Deslous-Paoli, 1985; Héral *et al.*, 1986). After the introduction of *Crassostrea gigas* in the bay of Marennes-Oléron in 1970, oyster stocks reached 78 600 t as early as 1974 (Héral *et al.*, 1986), equivalent to the present level. At the same time a decline in both growth and the quality was recorded by Gras and Gras (1975). Although glycogen level was lower, its variation was similar to the cycle described by Jeng *et al.* (1979), Deslous-Paoli *et al.* (1981 *a*), Maurer and Borel (1986). The seasonal cycle for storage and use of glycogen, which is the main energy reserves for molluscs, reflected the complex interactions between food supply, both in quality (organic and mineral composition) and quantity (*fig.* 8) (Deslous-Paoli *et al.*, 1982), and growth and annual reproductive cycle. Contrary to the disconnected reproductive and energy storage cycle for *Mytilus edulis* (Widdows and Bayne, 1971; De Zwaan and Zandee, 1972; Emmett *et al.*, 1987), glycogen stored by *Crassostrea gigas* during the phytoplanktonic bloom in spring (*fig.* 8) was simultaneously used for both growth and lipid accumulation for the ovocytes build up during gametogenesis cycle (Lubet, 1959; Gabbott, 1976, 1982).

As has been shown by many authors in mussels (Griffith, 1981; Chaparro and Winter, 1983; Rodhouse *et al.*, 1984; Thomson, 1984), *Crassostrea virginica* (Dame, 1976), and *Ostrea edulis* (Rodhouse, 1978), for *Crassostrea gigas*, the reproductive effort increased with age or size, as well as with successive breeding period (Brown and Russel-Hunter, 1978) despite slower growth. This reproductive effort could reach 80 to 90% of the flesh weight for old bivalves (Griffith and King, 1979; Griffith, 1981; Thompson, 1984). This very high effort value was mainly due to the mode of reproduction in water, and to the length of the larval life, as seen in nudibranchs (Todd and Havenhand, 1983) and hatching bivalves (Rodhouse, 1978; Deslous-Paoli *et al.*, 1983). Moreover, the reproductive effort was increased by the high energy value of gametes, mainly in females, due to a high proportion of lipids and a low proportion of glycogen (Hatanaka, 1940; Krishnamoorthy *et al.*, 1979; Kim, 1980; Gabbott, 1983).

During the sexual resting period, the accumulation of energy reserves taking place from April to October, and their utilisation, from October to March, were closely related to the environmental conditions, and particularly with the availability of high quality food (Deslous-Paoli *et al.*, 1982; Whyte and Englar, 1982; Héral *et al.*, 1984) (*fig.* 8).

Table 3. – Build up (from March to October) and use (from October to March) of the reserves of *Crassostrea gigas* (△), the fraction corresponding to the gametes having been removed.

Period	13/3/79 ↗ 8/10/79		8/10/79 ↘ 17/3/80		17/3/80 ↗ 22/9/80		22/9/80 ↘ 9/4/81		9/4/81 ↗ 28/10/81		28/10/81 ↘ 30/3/82	
	△A	△%	△U	△%	△A	△%	△U	△%	△A	△%	△U	△%
Dry weight (mg)	783	11 186	−340	−43.0	610	135.6	−340	−32.1	470	65.3	−500	−42.0
Energy (kJ)	13.58	9 700	− 6.38	−46.5	11.08	151.0	− 6.24	−33.9	7.58	62.2	− 8.21	−41.5
Proteins (mg)	304.7	11 120	−114.9	−37.4	269.9	104.2	−102.3	−22.1	47.8	13.3	−197.4	−48.4
Lipids (mg)	63.1	9 420	− 38.4	−60.2	82.6	325.2	− 43.0	−39.8	27.9	42.9	− 29.6	−31.9
Free carbohydrates (mg)	19.9	33 167	− 2.1	−10.5	8.3	46.7	− 16.5	−63.2	12.2	127.0	− 13.6	−62.2
Glycogen (mg)	22.0	36 667	− 21.5	−97.4	39.6	6 947.4	− 22.6	−56.2	19.8	112.6	− 26.2	−70.2
Ash (mg)	–	–	− 24.8	−22.0	84.55	95.9	− 53.4	−30.9	103.8	87.0	− 91.3	−40.9

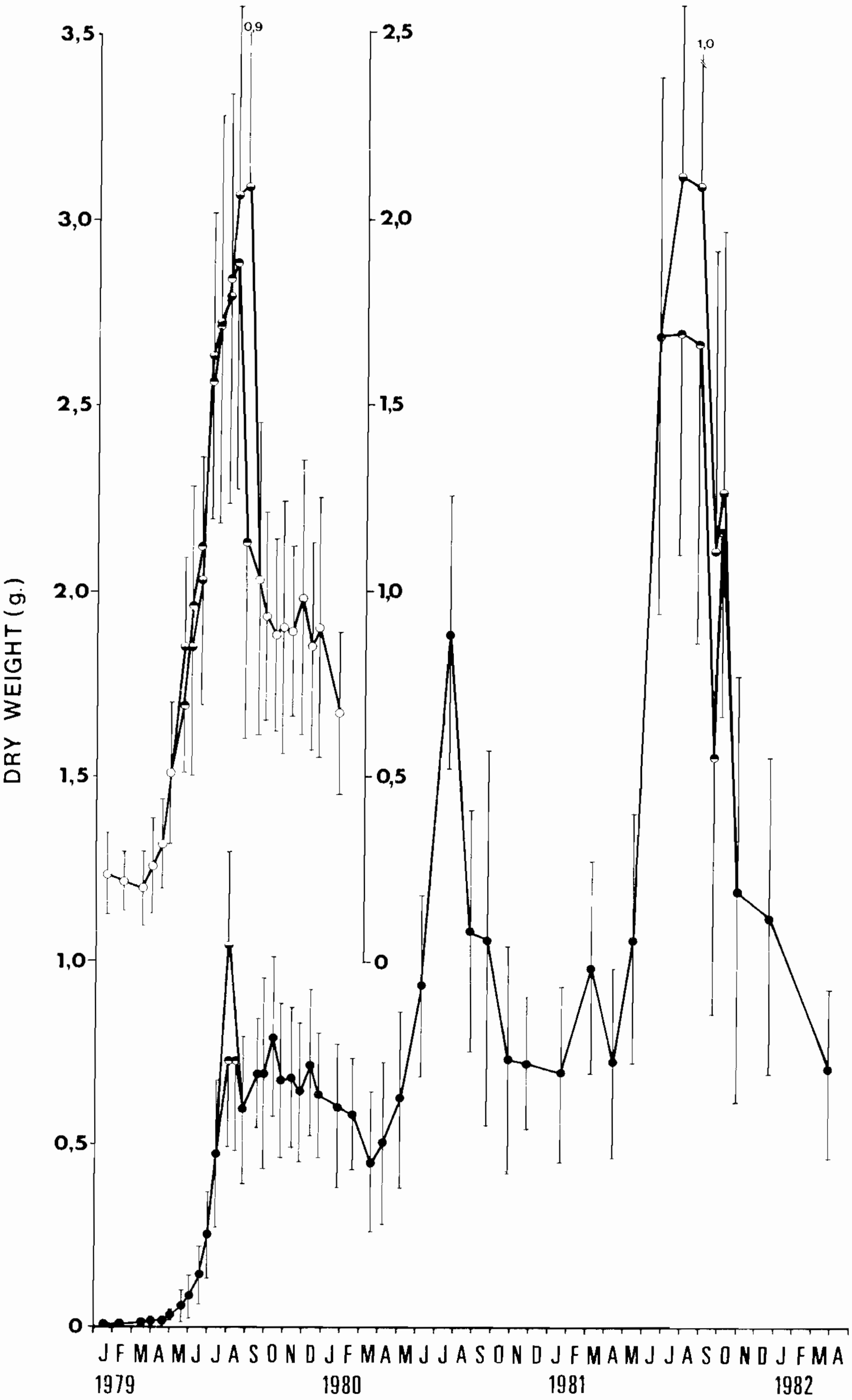

Figure 6. – Growth and seasonal change of the dry flesh weight of *Crassostrea gigas* recruited in 1978 (close circles) and in 1977 (open circles). (◒) females; (◓) males.

The use of the various energy reserves, *i. e.* 74.6 ± 20.9% of glycogen, 44 ± 14.6% of lipids, 36 ± 13.2% of proteins, analysed during the five and a half months of poor trophic conditions were similar to those obtained by Riley (1976) after 175 days of starvation, being 78% of carbohydrates, 63% of lipids, 55% of proteins. It may thus be hypothesized that it is a deficiency in the diet level that may cause a negative effect on growth (Héral *et al.*, 1983; Deslous-Paoli and Héral, 1984). The mean daily metabolic needs of oysters calculated from Riley's data (1976) during strict starvation of 125 and 175 days, was

Table 4. – Data from the literature on the proximate composition (% of dry tissue) and water content (% of fresh tissue) of *Crassostrea gigas*. (¹) measures of glycogen.

Authors	Countries	Proteins (%)	Lipids (%)	Carbohydrates (%)	Ash (%)	Water (%)
Sekine *et al.*, 1929	Japan	23 at 52	–	3 at 26 (¹)	–	–
Masumoto *et al.*, 1934	Japan	–	9 at 14	0.5 at 20 (¹)	5 at 10	80 at 90
Tully, 1936	British Columbia	46 at 55	12 at 16	12 at 25 (¹)	6 at 9	78 at 84
Hatanaka, 1940	Japan	46 at 58	–	–	–	–
Lin, 1969	U.S.A.	38 at 64	–	12 at 30 (¹)	–	–
Lee *et al.*, 1975	Korea	50 at 67	9 at 13	9 at 20	8 at 15	75 at 83
Gras and Gras, 1975	France	29 at 76	0.2 at 6	0.2 at 8	–	–
Walne and Mann, 1975	North Wales	55±3.3	–	11.6±2.2	20.9±1.7	–
Riley, 1976	U.S.A.	34 at 44	16 at 17	17 at 27	–	82 at 90
Gras and Gras, 1976	France (pond)	35 at 63	4 at 26	3 at 8 (¹)	–	–
Jeng *et al.*, 1979	Taiwan	48 at 68	6 at 18	0.2 at 14 (¹)	8 at 23	77 at 92
Kim, 1980	Korea	39 at 66	15 at 21	0.4 at 33	7 at 16	–
Deslous-Paoli *et al.*, 1981 *a*	France (pond)	35 at 56	8 at 23	0.5 at 10 (¹)	7 at 22	74 at 82
Whyte and Englar, 1982	British Columbia	30 at 62	4 at 14	22 at 30 (¹)	8 at 16	–
Seaman, 1985	Germany	33 at 54	8 at 15	9 at 30	8 at 16	–
Maurer and Borel, 1986	France	–	6 at 22	1 at 23	–	–
Present study	France	29 at 52	6 at 20	0 at 4	10 at 23	70 at 86

of approximately 67.6 J.day^{-1} (*table* 5). Therefore, oysters must have used their own reserves to meet 59% of their basal metabolic requirements during the winter of 1979-80, 46.4% in that of 1980-81 and 79.4% in that of 1981-1982. The differences seen in the use of endogenous reserves from one year to another resulted from a deficiency of food and temperature in the natural environment during 1981 (Héral *et al.*, 1984) (*fig.* 8) disturbing the oysters physiology, particularly for the processes of gametogenesis and spawning (Deslous-Paoli *et al.*, 1981 *b*). This disturbance, causing an important delay in spawning, must certainly have weakened the oysters at the beginning

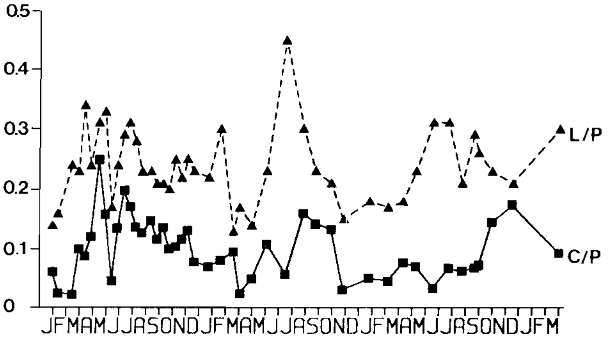

Figure 7. — Seasonal variation of the carbohydrate-protein ratio (■) and the lipid-protein ration (▲) for *Crassostrea gigas* recruited in 1978.

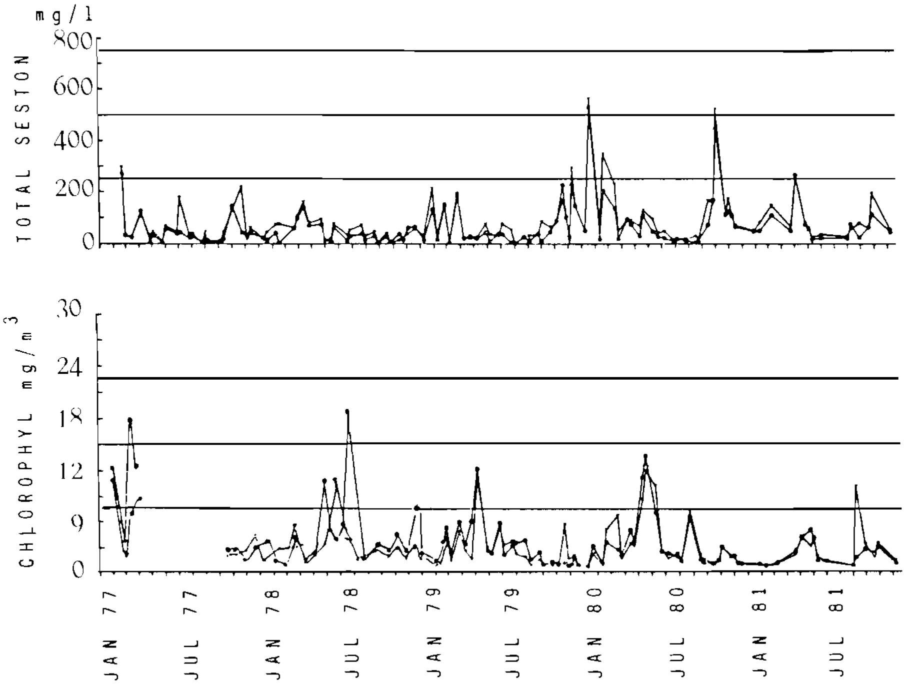

Figure 8. — Seasonal change in total seston and chlorophyll-*a* in surface and deep sea water in the bay of Marennes-Oléron (from Héral *et al.*, 1984.

Table 5. — Daily loss of reserves by *Crassostrea gigas* under starvation (data calculated from Riley, 1976) and during the winter in the bay of Marennes-Oléron.

Years	Number of days	Initial dry flesh weight (g)	Total loss of energy (kJ)	Dayly loss of energy (J)
1979-1980	160	0.79	6.38	39.88
1980-1981	199	1.06	6.24	31.36
1981-1982	153	1.19	8.32	53.66
Riley	175	1.0	12.02	68.71
(1976)*	125	1.0	8.32	66.54

* calculated from the energy coefficient of Brody (1945).

of the winter 1982; this consequently induced an increase in mortality at the end of the winter (Berthomé *et al.*, 1982).

Thus, the storage energy of mainly as glycogen, is linked with the quality of food available during phytoplanktonic blooms in spring and autumn. The energy use is in relation with endogenous parameters as growth and reproductive cycle during spring and summer, or exogenous parameters as temperature which acts on metabolic level, and as food quality, and high mineral charges, which are not able to satisfy the energy requirements during winter.

In an overstocked bay like Marennes-Oléron, the relationships between cultivated biomass, growth and physiological states do not allow a high energy storage (glycogen $<5\%$ dry flesh weight) contrary to what happened in oyster ponds with low density of oysters (glycogen $>10\%$ of dry flesh weight) (Deslous-Paoli *et al.*, 1981 *a*; and unpublished data); some climatic variations either during autumnal energy storage or during winter energy use, could induce an increase of oyster mortalities in early spring. In the same way, spring disturbances, directly acting upon the reproductive cycle and the delay of spawning, could induce the failure of spat settlement.

The setting of a regulation of the amount of cultivated biomass, with a best availability of food for each individuals could be advantageous all along the oyster culture cycle and for the quality of harvested oysters in December, for decreasing the mortalities at the end of winter and for the success of recruitment.

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