

Assessment of energetic requirements of reared molluscs
and of their main competitors.

by

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INTRODUCTION :

In the context of aquaculture in open sea, the amount and quality of food is variable according to the season and the physical flux in the ecosystem (carrying capacity ecosystems). Thus, to predict the potential production of a cultivated ecosystem, it is mandatory to know the seasonal changes in organisms energy balance of cultivated organisms. These changes result from the environmental variability either in the temperature or, more significantly in the nutrients supply (Bayne and Newell, 1983).

The techniques of physiological energetics allow to understand the adaptations of the energy balance in bivalve molluscs and to calculate the complete energy budget all over the seasonal variations of the field. Such studies are few, they include research on individual organisms or on a whole population. These researchs have been done on *Scrobicularia plana* (Hughes, 1970), *Crassostrea gigas* (Bernard, 1974 ; Kim, 1980 ; Héral and al., 1983 ; Deslous-Paoli and Héral, 1984) *Mercenaria mercenaria* (Hibbert, 1977), *Mytilus edulis* (Bayne and Widdows, 1978 ; Widdows, 1978 ; Rosenberg and Loo, 1983 ; Thompson, 1984a ; Hawkins and al., 1985), *Mytilus chilensis* (Navarro and Winter, 1982), *Perna perna* (Berry and Schleyer, 1983) and a gastropod competitor *Crepidula fornicata* (Deslous-Paoli and al., 1985).

The synthesis on physiological energy has been done by Bayne and Newell (1983) on molluscs (bivalves and gastropods). Here we will try to make a complementary synthesis especially on oysters which are with mussels the main species of cultivated molluscs, with reference of one trophic competitor (*Crepidula fornicata*).

In this synthesis we only speak about particulate matter as food. The dissolved substances and their uses by suspension feeding bivalves are not discussed here because nobody takes it into account in the energy budget. Although the use of dissolved A.A. and carbohydrates have been proved on *Mytilus edulis* (Pequignat, 1973 ; Jorgensen, 1982, 1983 ; Wright, 1982) and on *Saccostrea commercialis* (Nell et al., 1983).

1. The components of the energy budget

The equation of energy budgets for marine benthic invertebrates was first discussed by Crisp (1971). This equation describes the net energy exchange in the individual organisms under steady state conditions :

$$C = P + R + F + U$$

$$\text{with } P = P_g + P_s + P_r + P_e \text{ (Lucas, 1982) and } F = F' + F''$$

where C (consumption) is the energy content of food consumed ; P (production) is the energy incorporated in P_g (growth of somatic flesh), P_s (secretory products such as organic parts of the shell, mucus, byssus), P_r (reproductive products) and P_e (eliminated products). R is the energy equivalent of metabolic heat losses, F is the energy content of the not ingested food and not absorbed one that is voided respectively as pseudofeces (F') and feces (F''), U is the energy of excretion products like urine.

In the diagram of figure 1, we show that in bivalvia the ingested energy (I) is the filtrated food (C) which passes through the mouth ($I = C - F'$). The efficiency with which the filtrate ration was ingested is the ingestion efficiency (I/C). The ingested ration is difficult to estimate in marine lamellibranchia, because of the difficulty to separate pseudofeces (F') and feces (F'') especially for species with siphons. Thus in the main study, especially for studies made on the field, the absorption efficiency (Ab/C) is calculated from the filtrated energy (C) (Widdows, 1978) and not from the ingested one (I) and the absorbed ration is $Ab = C - F = I - F''$. From the absorbed ration, Bayne and Newell (1983) define two main sources of loss which are the losses of products of protein metabolism (U) and those to the heat increment (R'). Unlike Bayne and Newell (1983) the mucus is not considered as an excretory product (U) but as secretory product like shell and/or byssus (P_s). R' (heat increment) and R'' (metabolic energy losses) are never separated and constitute the total metabolic loss ($R = R' + R''$) (Bayne and Newell, 1983) which is estimated by the oxygen consumption. The assimilated

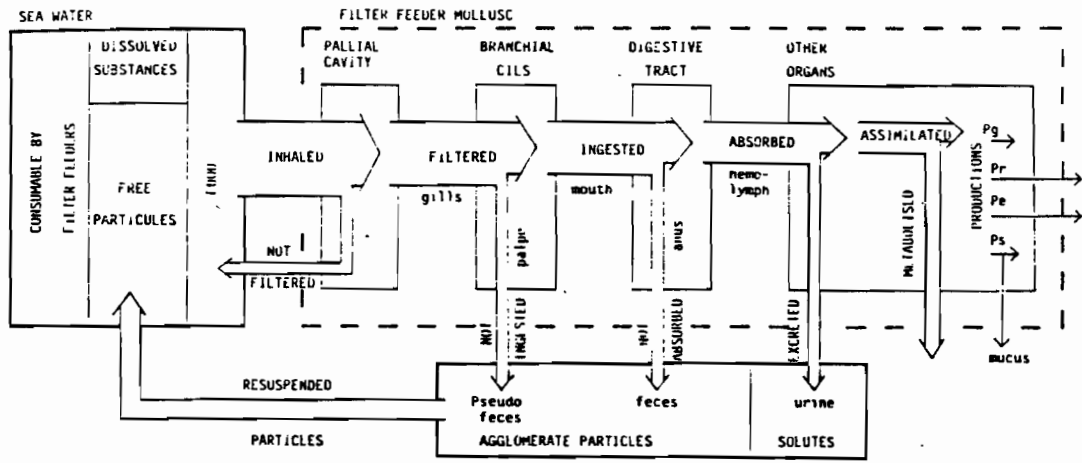


Figure 1 : Synthetic diagram of the energy flow between food and filter feeding molluscs (redraw from Lucas, 1982).

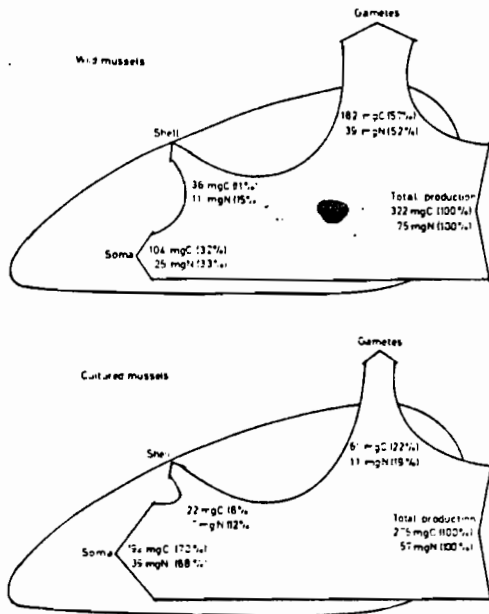


Figure 2 : *Mytilus edulis* : Allocation of carbon and nitrogen in wild and cultured mussels (from Rodhouse et al., 1984).

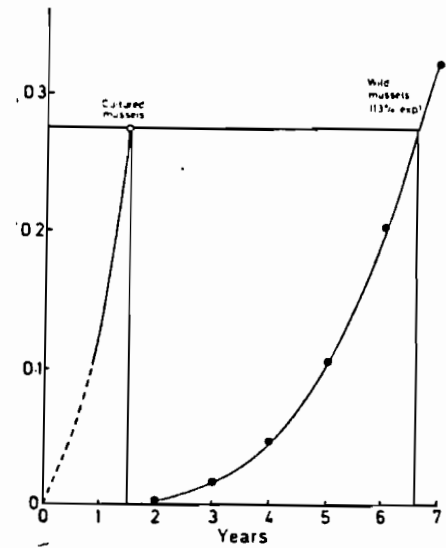


Figure 3 : *Mytilus edulis* : cumulative production of wild and cultured mussels (from Rodhouse et al., 1984).

ration (As) can be expressed as $As = R + P = C - F - U$, where the energy available for production (P) is partitioned between somatic growth (Pg), secretory products (Ps), production of gametes (Pr) and eliminated products (Pe) (Lucas, 1982). This last term (Pe) is not taken into account for individual energy balance, except when flat fish eat the siphon of *Scrobicularia plana* for exemple (Hodgson, 1982).

Some confusion arises between absorption and assimilation in a number of papers. This is due to the fact that the excretion product (U) was often neglected. The definition of efficiencies has been reviewed for its ecological interest (Lucas, 1982) and physiological interest (Lucas and Shafee, 1983).

$$\text{Assimilation efficiency} = \frac{As}{C} = \frac{P + R}{C} = \frac{C - F - U}{C} = \frac{P + R}{P + R + F + U}$$

$$\text{Gross production efficiency} = \frac{P}{C} = \frac{Pg + Pr + Ps + Pe}{C} = \frac{P}{P + R + F + U}$$

$$\text{Net production efficiency} = \frac{P}{As} = \frac{Pg + Pr + Ps + Pe}{As} = \frac{P}{P + R}$$

$$\text{Gross growth efficiency} = \frac{Pg}{C} = \frac{Pg}{P + R + F + U} = \frac{Pg}{Pg + Pr + Ps + Pe + R + F + U}$$

$$\text{Net flesh growth efficiency} = \frac{Pg}{As - Pg} = \frac{Pg}{Pr + Ps + Pe + R}$$

2. Populations energetics

A review of the population energy budget has been done by Bayne and Newell (1983) where all the components are expressed in percent of consumption (C) (table 1). We added some new results in the table 2 which exclusively concerns field studies.

In that case, the production ~~is~~^{em} not only influenced by growth of individuals but also by the immigration of new ones. Losses are due to mortality emigration and the reproductive effort of the whole population (Verhagen, 1982). The input of energy from immigration happened in Pg and Ps whereas the output of energy mortality and emigration act on Pe, and the reproductive effort on Pr.

Table 1 : Basis components of the population energy budgets of marine suspension and deposit feeders in percent of consumed energy. Mean values calculated ignoring the values for *Tellina tenuis* and taking values for only years 2 and 10 for *Patinopecten* and *Chlamys* respectively (from Bayne and Newell, 1983).

Organism	Feces (F)	Absorbed ration $A = (C - F)$	Gross production efficiency $P_R + P_r = P/C$			Respiration (R)	Net respiratory cost $(R/A) \times 100$	Urine (U)	Net production efficiency $(P_R + P_r)/A \times 100$	Reference
<i>Mercenaria mercenaria</i>	58.7	41.3	5.6	4.7	10.3	18.7	45.3	12.3	35.5	Hibbert (1977)
<i>Ostrea edulis</i>	30.7	69.3	6.4	5.5	11.9	29.0	28.4	—	17.2	Rodhouse (1979)
<i>Scrobicularia plana</i>	39.3	60.7	6.6	6.2	12.8	47.9	21.0	—	21.0	Hughes (1970)
<i>Macoma balthica</i>	40.0	60.0	—	—	18.0	42.0	70.0	—	30.0	Warwick et al. (1979)
<i>Patinopecten yessoensis</i> (yr 1)	21.1	79.9	39.7	1.6	41.3	39.2	49.1	—	24.9	Fuji and Hashizume (1974)
<i>P. yessoensis</i> (yr 2)	34.6	65.4	21.8	4.9	26.9	41.6	66.7	—	40.8	Fuji and Hashizume (1974)
<i>P. yessoensis</i> (yr 3)	32.5	67.5	19.6	8.2	27.8	47.9	70.9	—	41.2	Fuji and Hashizume (1974)
<i>Tellina tenuis</i>	90.0	10.0	1.0	0.8	1.8	6.7	67.0	—	18.0	Trevallion (1971)
<i>Aulacomya ater</i>	41.5	58.4	—	—	9.2	49.2	84.2	—	15.7	Griffiths and King (1979a, 1979b)
<i>Hydrobia ventrosa</i>	37.0	63.0	—	—	21.0	20.7	32.8	—	33.3	Koloed (1975b)
<i>Chlamys islandica</i> (yr 5)	66.6	33.4	11.0	1.7	12.7	20.7	62.0	—	37.9	Vahl (1981b)
<i>C. islandica</i> (yr 10)	74.2	25.8	2.6	2.7	5.4	20.4	79.2	—	20.8	Vahl (1981b)
<i>C. islandica</i> (yr 15)	74.8	25.2	1.4	3.3	4.8	20.4	80.9	—	4.8	Vahl (1981b)
<i>Mytilus edulis</i>	54.0	45.9	8.9	4.8	13.7	25.8	56.1	6.4	29.8	Bayne (unpublished)
Mean \pm SD	45.6 ± 14.0	54.4 ± 14.0	8.7 ± 6.8	4.8 ± 1.2	14.4 ± 6.6	33.0 ± 12.6	53.7 ± 23.0	—	27.1 ± 8.8	

Table 2 : Annual energy budget of filter feeders molluscs calculated for field population in percent of consumed energy.

Organism	Pe	Pg	Ps	Pr	R	F'	F''	U	As/C	P/As	Auteurs
<i>Mytilus edulis</i>	←33.4→			46.5	←20→		-	-	80	42	Rosenberg and Loo, 1983
<i>Perna perna</i>	←19.3→		3.4	19.1	←58→		-	-	42	55	Berry and Schleyer, 1983
<i>Crassostrea gigas</i>	←4.5→		18.2	18.2	←54.5→		4.5	-	41	56	Bernard, 1974
<i>Crassostrea gigas</i>	2.1	15.3	0.4	2.7	35	17.2	27.3	-	56	37	Kim, 1980
<i>Crassostrea gigas 1</i>	-	2.8	1.4	0.9	21.1	←73.8→		-	26	19	Deslous-Paoli and Héral, 1984
<i>Crassostrea gigas 2</i>	-	0.2	0.8	3.5	23	←72→		-	28	16	Héral et al., 1983
<i>Crepidula fornicata</i>	4.6	1.6	0.8	48	45		-	-	55	13	Deslous-Paoli et al., 1985

- 1 1 year old oysters
- 2 2 years old oysters

For example, Rodhouse et al. (1984) compared the resource allocation in two populations of *Mytilus edulis*. One is cultivated, the other is wild, when the total cumulative production is approximately equal. They define considerable differences in resource allocation (fig. 2) which are mainly due to the structure composition of the two populations (fig. 3). In the cultivated population, all the mussels are young (less than eighteen months old) with very low reproductive effort (P_r) and high somatic production (P_g). In the wild population the highest proportion of old mussels with very high reproductive effort (P_r) and low somatic growth (P_g) inverts the resource allocation in the production. Therefore the study of energy budget of a population must be done in the same time that structure and dynamic study of the population.

Steady state conditions are rarely encountered for populations because of the continuously increasing or decreasing of biomass depending on the season, it is preferable to calculate monthly energy budgets rather than annual ones (Lucas and Shafee, 1983). Nevertheless some of the components of the equation are difficult to determine on the field (C , U , R). They necessitate experimental determination. But the application of laboratory-based studies to the field situation presents many problems (Bayne and Newell, 1983). These problems are related in laboratory to consumption and absorption under different trophic levels and different trophic quality, to respiration and excretion with starved or not starved organisms and to the physiology of the organisms tested in laboratory.

3. Parameters acting on physiological energy

3.1. Field study

Some endogenous parameters act on the physiological energy, the age or the size class and the seasonal physiological state of an organism.

Rodhouse (1978) finds an age-dependent annual repartition of energy in *Ostrea edulis* (fig. 4) as, Vahl (1981) for *Chlamys islandica* and Deslous-Paoli et al. (1985) for *Crepidula fornicata* according to the position along the chain. As the individual ages, a greater proportion of P is due to the gametes production (Bayne and Newell, 1983) and the somatic tissues (P_g) and shell product (P_s) declines to zero when the animal has reached its maturity.

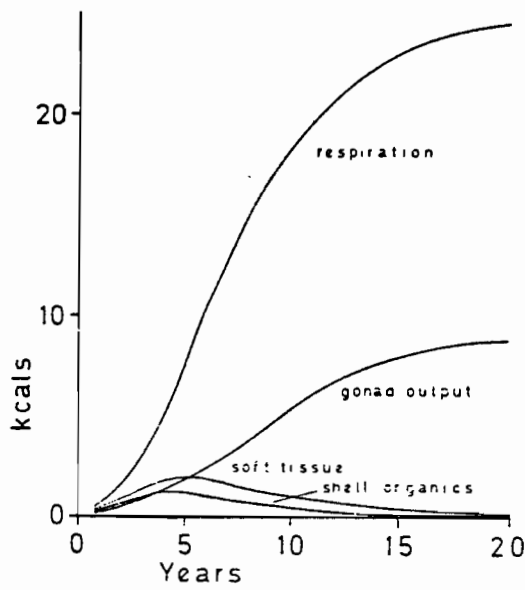


Figure 4 : Age-dependent annual production of soft tissue, shell organics, gonad output and respiration in an oyster *Ostrea edulis* (from Rodhouse, 1978).

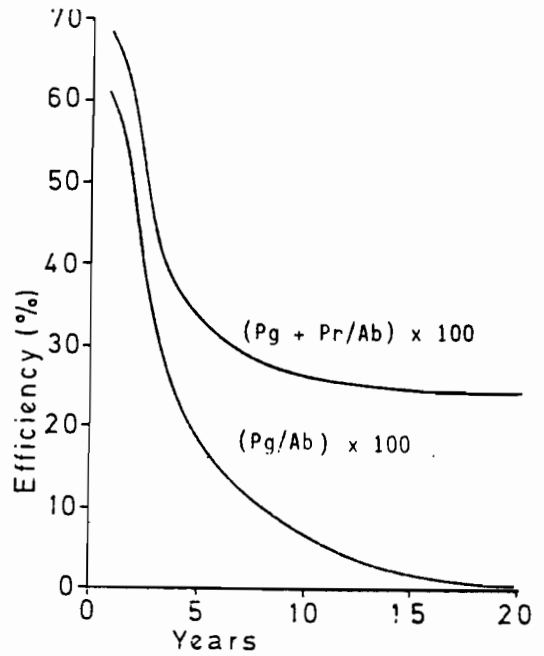


Figure 5 : Net growth efficiency $(P_g + P_r/Ab)$ and net growth efficiency of somatic tissue (P_g/Ab) in oysters *Ostrea edulis* (from Rodhouse, 1978).

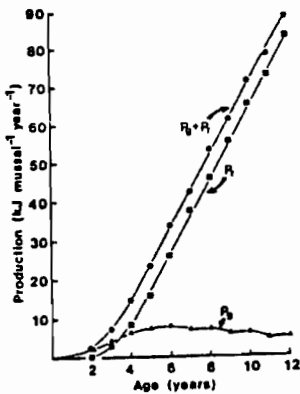


Figure 6 : *Mytilus edulis*. Somatic production (P_{gi} ▲), gamete production (P_{ri} ■) and total production ($P_g + P_{ri}$ ●) in individuals from Bellevue (from Thompson, 1984b).

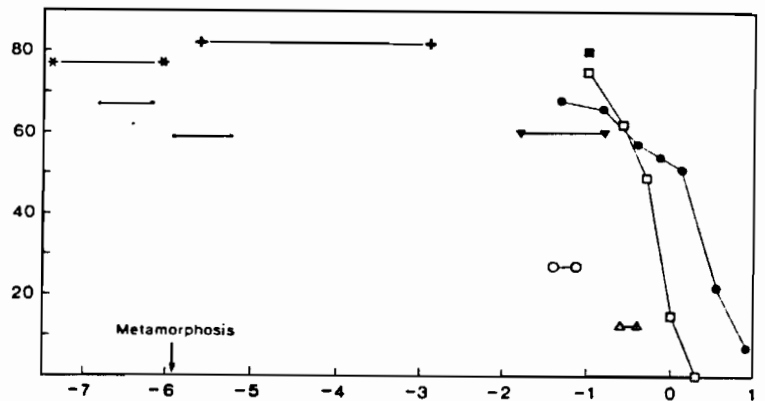


Figure 7 : From Jorgensen, 1976).

Relationship between body weight and net growth efficiency in *Mytilus edulis*.

- * Veligers, Isefjord, Denmark, June (Jorgensen, 1952).
- Veligers and young post-metamorphic stages, growth in the laboratory (Bayne, 1965). Oxygen consumption from Zeuthen (1947).
- + Øresund, Denmark, summer, recalculated from Thorson (1946, p. 460). Oxygen consumption from Zeuthen (1947).
- La Jolla, Calif., USA. August-November (Coe, 1945). Oxygen consumption from Thompson & Bayne (1974), highest level.
- ▼ Oslo fjord, Norway, August-September (Bohle, 1970). Oxygen consumption from Thompson & Bayne (1974), highest level.
- Norfolk, England. Maximum values obtained in laboratory (Thompson & Bayne, 1974).
- Mass., USA, feeding ^{14}C -labelled *Dunaliella tertiolecta* (Gilfillan, 1975).
- ▲ Mass., USA, aquaculture experiments (Tenore et al., 1973).
- Weser Estuary, FRG. maximum values in laboratory (Winter, 1974).

(Salzwedel, 1980), the net production efficiency may become relatively constant but the energy input in P_r increases (fig.5) and in the older organisms, the allocation of all available surplus energy to the production of gametes (fig.6) ultimately sets the limits on size (Bayne and Newell, 1983). The relationship between the net growth efficiency and size of organism (fig.7) is identical to the one concerning the age. When a population is studied, the population structure must be taken into account to allocate energy to P_g and P_r (fig. 8). It is mainly due to a different mortality rate between younger and older individuals and the middle ones.

The physiologically dependent partition of energy is mainly due to the period of gametogenesis (fig. 9). For some molluscs, such as *Mytilus edulis*, somatic and gonadal growth occurred at different times. This is not the case for *Crassostrea gigas* which must perform at the same time, in spring and summer somatic growth and gametogenesis (fig. 10-11) (Kim, 1980 ; Héral et al., 1983 ; Deslous-Paoli and Héral, 1984). Shafee and Lucas (1982) give a detailed analysis of the reproductive effort of *Chlamys varia* as well as Vahl (1981) for *Chlamys islandica*. Depending on the season, the energy used to produce gametes is taken either from endogenous food reserves (september) or from exogenous food (june) because at that time somatic and gonadal growth occurred together.

In each species the endogenous parameters (gametogenesis and growth) and the exogenous parameters (temperature, food) are closely related, set in seasonal context, and condition both the reproduction effort and the timing of reproductive events (Newell et al., 1982 ; Sastry, 1979). *Mytilus edulis* populations cultivated in different places, where the environmental stress are more or less reduced, have differently developed their reproductive efforts (fig. 12).

The impact of environmental changes (Zandee et al., 1980) depends on the age or size of individuals as Thompson (1984a) sees on *Mytilus edulis* (fig. 13) about scope for growth. The younger *Crassostrea gigas* does not exhibit a negative growth during winter (Deslous-Paoli and Héral, 1984) whereas the two years old *Crassostrea gigas* shows negative growth during the same season (Héral et al., 1983) (table 3). Smaller individuals were more able to compensate the metabolic energy losses, than the larger one. This is linked with

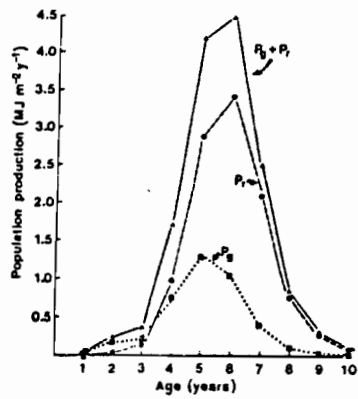


Figure 8 : *Mytilus edulis*. Production by the population at Bellevue. ■ somatic production $(P_g)_i$ ● gametes production $(P_r)_i$ ▲ total production $(P_g + P_r)$ (from Thompson, 1984b).

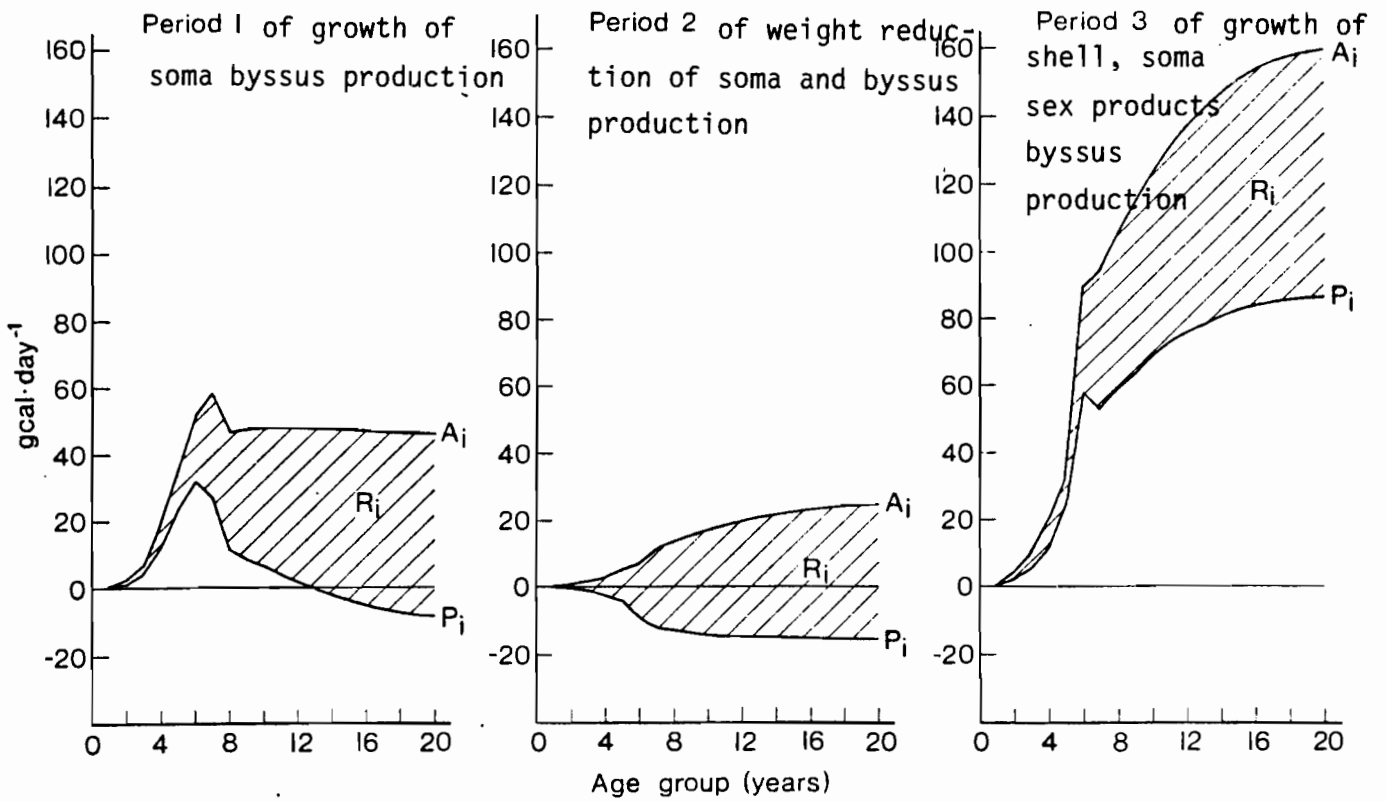


Figure 9 : Age-specific energy budget of *C. islandica* in summer, autumn and winter, and in spring (from Vahl, 1981).

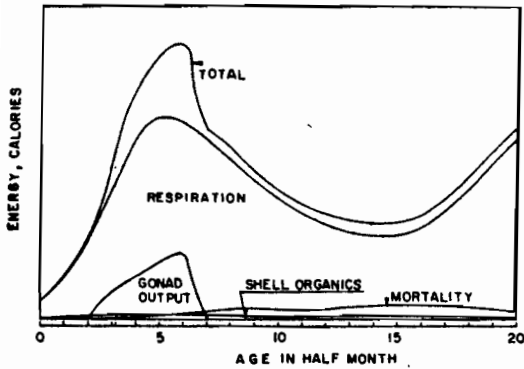


Figure 10 : Age specific distribution of energy loss by oysters population. (from Kim, 1980).

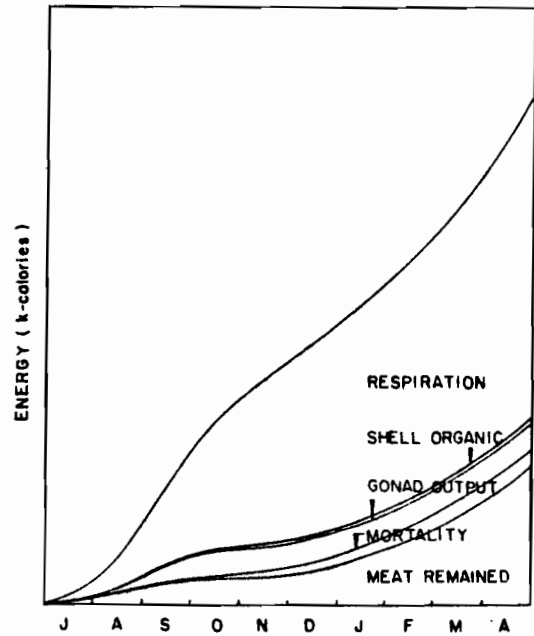


Figure 11 : Cumulative energy used by the population of the oyster *C. gigas* in the culture bed. (from Kim, 1980).

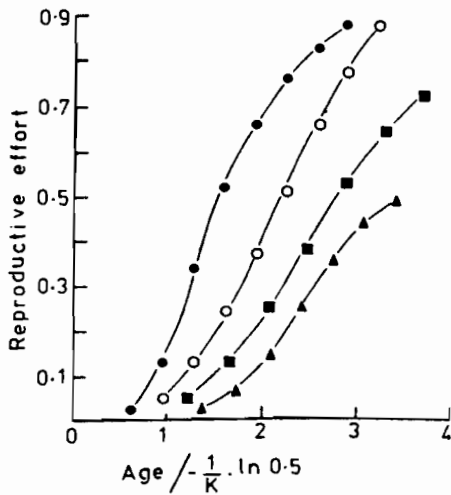


Figure 12 : Reproductive effort, calculated as P_r/P of *Mytilus edulis* from four populations, related to age standardized for growth rate

● Bellevue, Newfoundland. (From R.J. Thompson, unpublished date). ○ Lynher ;
 ■ Mothecombe ; ▲ Cattewater. (All southwestern England ; from Bayne and Widdows, 1978 and Bayne et al., 1983). (from Bayne and Newell, 1983).

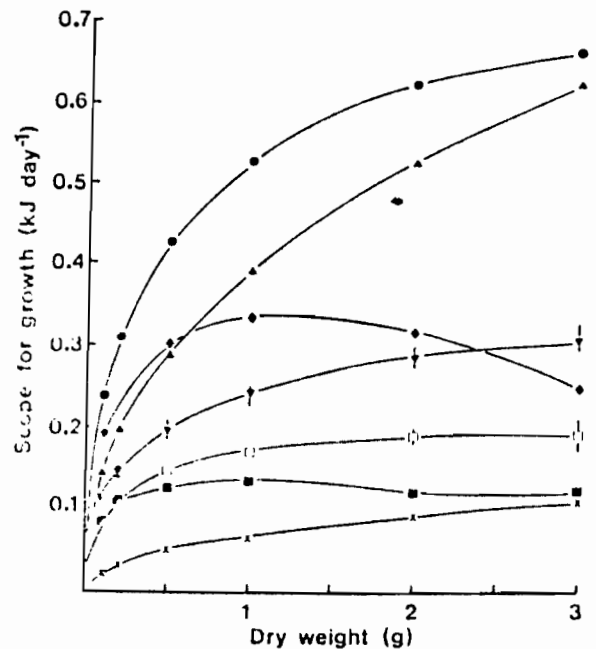


Figure 13 : From Thompson, 1984a.

Mytilus edulis. Scope for growth as a function of dry weight. (●) 16th October 1980, (▲) 24th June 1980, (◆) 28th July 1980, (▼) 19th December 1979, 12th March 1980, 10th September 1980 (mean + range), (□) 7th November 1979, 22nd January 1981 (mean + range), (■) 29th April 1980, (x) 11th December 1980

Date	Pg	Pr	Ps	R	F	P	A	C
12.02.79	0,07	-	0,04	0,572	0,10	0,11	0,68	0,78
28.03.79	0,13	-	0,03	0,742	1,10	0,16	0,90	2,00
25.04.79	0,52	-	0,09	2,845	1,69	0,61	3,46	5,15
28.05.79	1,51	-	0,31	7,065	1,18	1,82	8,89	10,07
26.06.79	5,53	-	0,99	15,108	2,09	6,52	21,63	23,72
24.07.79	8,97	-	2,96	25,106	34,79	11,93	37,04	71,83
21.08.79	2,73	6,49	0,72	17,441	116,07	9,94	27,39	143,46
24.09.79	2,81	-	0,98	18,521	93,54	3,79	22,31	115,85
22.10.79	-0,69	-	2,18	14,249	22,76	1,49	15,74	38,50
20.11.79	-0,99	-	-0,20	13,909	6,37	-1,19	12,72	19,09
18.12.79	-0,34	-	1,02	15,443	36,66	0,68	16,12	52,78
21.01.80	-0,79	-	0,02	11,40	108,9	-0,77	10,63	119,53
20.02.80	-0,43	-	0,02	10,26	15,5	-0,42	9,84	25,34
17.03.80	-4,50	-	0,70	13,09	450,9	-3,80	9,29	460,19
1.04.80	3,28	-	1,56	21,45	29,4	4,84	26,29	55,69
1.05.80	2,71	-	0,56	22,60	24,1	3,27	25,87	52,97
2.06.80	6,92	-	0,26	27,62	13,1	7,18	34,8	47,90
15.07.80	2,71	21,78	2,93	38,64	83,0	27,42	66,06	149,06
25.08.80	2,77	16,75	0,49	26,61	77,6	20,01	46,62	124,22
22.09.80	-1,86	-	1,02	24,82	64,7	-0,84	23,98	88,68
27.10.80	-12,08	-	-0,27	18,52	72,4	-12,35	6,17	78,57
24.11.80	-0,57	-	1,70	15,65	53,5	1,13	16,78	70,28
23.01.81	-0,73	-	-0,22	14,43	10,5	-0,95	13,85	24,35

Table 3 : Daily energy balance of oysters cultivated at density of 200 per square meter. Oysters settle in July 1978. (Redraw from Heral et al., 1983 ; Deslous-Paoli and Heral, 1984). Values in Kcal.

the energy expended for food intake by filtration (Bayne and Newell, 1983). The older mollusc can not obtain their maintenance ratio from natural food and must use their endogenous reserves.

Storage of carbohydrates, lipids and proteins usually occurs during spring when food is abundant, and for some species, such carbohydrates reserves are immediately used for gametogenesis (Gabbot, 1976). For others species, these reserves will be used in winter to fulfil the metabolic requirements when the food scarce. As suggested by Sundet and Vahl (1981) for *Chlamys islandica*, the younger individuals of *Crassostrea gigas* invest in rapid growth, during a more longer period than older one, with the risk to not possess large reserves for winter food shortage. In contrast, mature *Crassostrea gigas* stop their growth one month before spawning (August), first because all the available energy production is utilized for gametogenesis as Barber and Blake (1981) said for *Argopecten irradians*, and secondly to store reserves after spawning to winter.

The use of available food on the field seems to be related with the quantity and the quality of the particulate food, Widdows and al. (1979a) give a schematic diagram summarising the effect of particle concentration on feeding and digestive system (fig. 14). The pseudofeces production occurs when a threshold concentration of seston is reached in water (Foster-Smith, 1975). In the field, it is difficult to separate pseudofeces production (F'') and feces production (F') and the two are usually considered together as biodeposition. Sornin et al. (1983) describe a relationship between seston concentration and the amount of biodeposition product by *Crassostrea gigas* (fig. 15). Up to 97 % by weight of processed material may be rejected from the mantle cavity (Hyllberg and Gallucci, 1975). An annual mean of 75 % of the energy filtered, as protein, lipid and carbohydrate, is rejected as biodeposition by *Crassostrea gigas* (Héral et al., 1983 ; Deslous-paoli and Héral, 1984) whereas only 45 % is rejected by *Crepidula fornicata* (Deslous-Paoli et al., 1985). For *Crepidula fornicata*, the seasonal biodeposition represent from 26 per cent of the filtered energy in June, to 68 % in December. For *Crassostrea gigas* in Marennes-Oleron the energy loss by feces

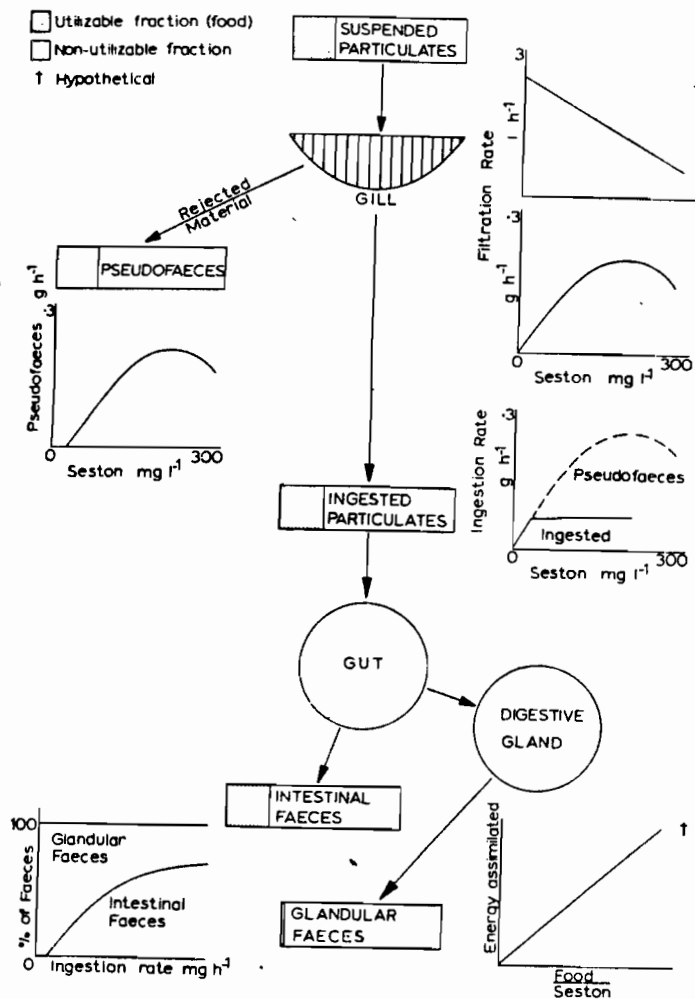
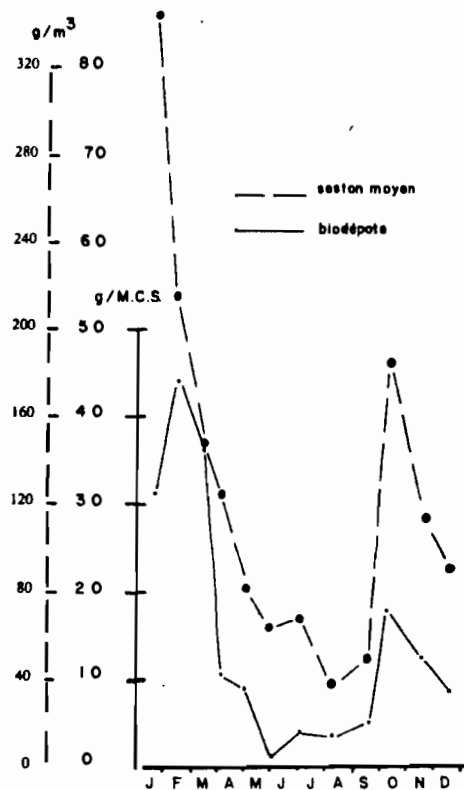


Figure 14 : *Mytilus edulis*. Schematic diagram summarising effect of particle concentration on feeding and digestive system (from Widdows et al., 1979a).

Figure 15 : Seasonal evolution of biodeposit product by *Crassostrea gigas* (g/g dry flesh weight) and of average seston (g/m^3) (from Sornin et al., 1983).



and pseudofeces can represent up to 98 % of the consumed energy in winter with high seston concentration and only 9 % during spring. In this study, the values of consumption are underestimated because urine and mucus was neglected. It reveals the importance of the seasonal availability and quality of food on the absorption efficiency of molluscs, but also of the grazing system (radula or not) between species.

If it is possible to estimate directly on the field the production P and the total biodeposition (F) and their fluctuations due to the environmental variations, laboratory experiments are necessary to quantify the losses due to heat metabolism (R) and excretion (U) and the actual input of food through the filtration (C) and ingestion (I) rate of individuals.

3.2. Laboratory experiments

3.2.1. Energy intake

There is no doubt that filtration and retention rate are related to the dry body weight (See Bayne and Newell, 1983 for a synthesis), to the flow rate (Møhlenberg and Røsgård, 1979), to the particulate concentration in sea water (Epifanio and Edward, 1977 ; Wisley and Reid, 1978 ; Winter, 1978 ; Widdows et al., 1979a ; Palmer and Williams, 1980 ; Lee and Chew, 1981 ; Fiala Medioni and Copello, 1985) (fig. 14), and to the size or volume of cells and particles used as food in laboratory study (Kusuki, 1977 ; Wisely and Reid, 1978 ; Jorgensen et al., 1984) (fig.16).

In contrary, diurnal and tidal rhythms of filtration are not really defined and depend on species. Some authors have found them (Salan-ky, 1966 ; Morton, 1971 ; Palmer, 1980a) and some other not (Winter, 1978 ; Higgins, 1980). In the same way it is still difficult to control the size or quality of particle selection ability. At high seston concentration, particle selection occurs when the threshold of pseudofeces production is over (Kiorboe and Møhlenberg, 1981) and will be performed by the labial palps (Bernard, 1974 ; Thiesen, 1977). Therefore a relative enrichment of energy in the ingested food is observed in front of energy of filtrate particulate matter (Haven and Morales-Alamo, 1966 ; Kiorboe et al., 1981 ; Newell and Jordan, 1983). At low seston concentration, the retention efficiency increases (Palmer and Williams, 1980 ; Fiala Médioni and Copello, 1985) (table 4) for the

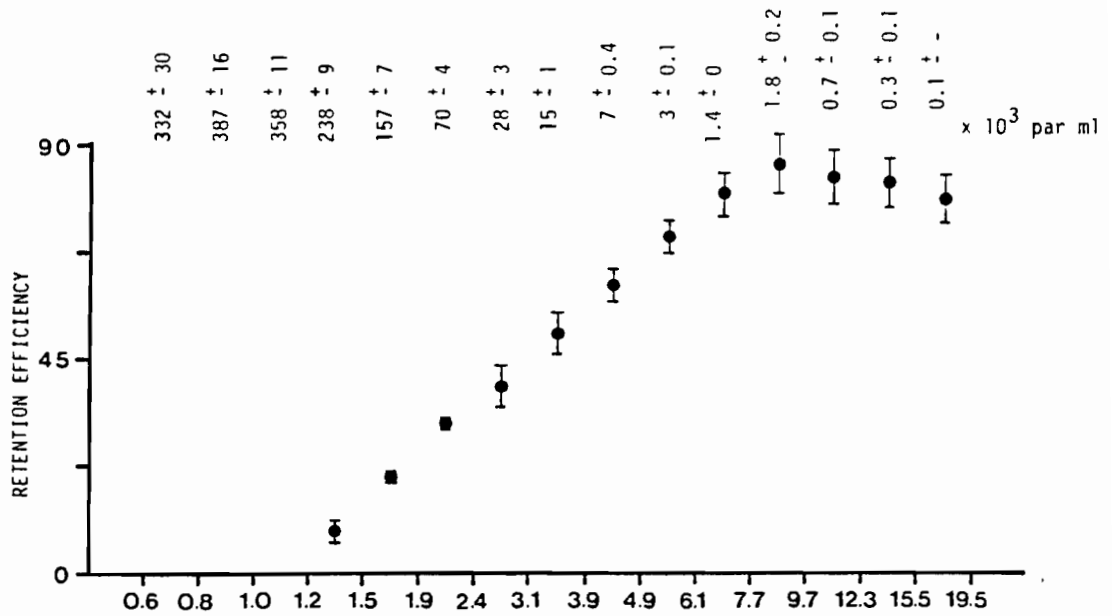


Figure 16 : Efficiency of particule retention by *Crassostrea gigas* with natura food in may, values are means \pm standard deviation. Values on the top are means of particule concentration in seston ($\times 10^3$ par ml) (Deslous-Paoli and Heral unpublsh data).

Table 4 : Efficiency of particle retention of *Crassostrea gigas* in front of high natural seston (20/2/84 ; 19/3/84 ; 14/5/84) and low natural seston (27/2/84 ; 27/3/84 ; 22/5/84) in relation with temperature. () : standard deviation. (Deslous-Paoli and Heral, unpublished data).

Date	20/2/84		27/2/84		19/3/84		27/3/84		14/5/84		22/5/84	
	réten-tion %	nb particules $\times 10^3 - ml^{-1}$	réten-tion %	nb particules $\times 10^3 - ml^{-1}$	réten-tion %	nb particules $\times 10^3 - ml^{-1}$	réten-tion %	nb particules $\times 10^3 - ml^{-1}$	réten-tion %	nb particules $\times 10^3 - ml^{-1}$	réten-tion %	nb particules $\times 10^3 - ml^{-1}$
0.6-0.8	0	-	0	556 (20)	0	291 (13)	7.4 (1.8)	829 (31)	0	332 (30)	0	745 (23)
0.8-1.0	0	-	1.2 (6.7)	207 (18)	0	360 (8)	6.7 (2.5)	322 (41)	0	387 (16)	14.4 (7.5)	343 (23)
1.0-1.2	0	60 (3)	7.4 (1.7)	91 (8)	0.9 (1.4)	350 (5)	6.5 (8.9)	70 (11)	0	358 (11)	18.3 (12.5)	123 (24)
1.2-1.5	0	74.5 (2.6)	6.4 (8.9)	53 (4)	6.3 (4)	221 (7)	8.3 (10.3)	22 (3)	8.6 (2.2)	238 (9)	24.2 (18)	45 (17)
1.5-1.9	1 (2)	80 (1)	14 (5.9)	28 (3.3)	13.6 (9.6)	159 (7)	15.3 (12.1)	12 (1.5)	20.3 (1.5)	157 (5)	29.2 (24)	19 (2)
1.9-2.4	16 (3)	56 (1.6)	22.5 (9.4)	10 (2.4)	19.5 (14)	73 (5)	26.4 (12.5)	6 (0.7)	31.2 (1.5)	70 (4)	37 (23)	11 (1)
2.4-3.1	29 (3)	32 (1.6)	32.4 (10)	4.2 (0.8)	26.9 (5.2)	36 (1.4)	41.6 (12)	3 (0.3)	39.1 (5.0)	28 (2.5)	49.6 (19)	6 (0.7)
3.1-3.9	39 (3)	14 (1)	42.9 (9.5)	2.4 (0.3)	39.2 (5.5)	17 (1)	41.3 (7.3)	3 (0.3)	50.1 (4.4)	15 (1.2)	65.5 (14)	3 (0.3)
3.9-4.9	50 (1)	5.5 (0.4)	53.1 (10)	1.2 (0.1)	51.7 (6.7)	7 (0.5)	48.7 (6.4)	1.1 (0.2)	60.1 (3.8)	7 (0.4)	76.1 (12)	1.6 (0.1)
4.9-6.1	65 (2)	2 (0.2)	62.1 (11.8)	0.6 (0.1)	62.3 (5.3)	2.7 (0.2)	58.5 (15.6)	0.3 (0.1)	70.4 (3.7)	3 (0.1)	84.9 (9.1)	1.1 (0.1)
6.1-7.7	76 (4)	0.8 (0)	64.6 (11.9)	0.3 (0)	71.8 (5.2)	1 (0.1)	64.8 (12.5)	0.2 (0)	79.9 (4.8)	1.4 (0.1)	89.5 (7.7)	0.8 (0.1)
7.7-9.7	78 (8)	0.2 (0)	64.1 (9.3)	0.2 (0)	78.9 (7.1)	0.6 (0)	72.2 (9.4)	0.2 (0)	85.7 (6.2)	1.8 (0.2)	82.4 (9.0)	0.2 (0)
9.7-12.3	-	-	-	-	74.4 (10.5)	0.2 (0)	66.3 (17.3)	0.1 (0)	83.2 (5.8)	0.7 (0.1)	-	-
12.3-15.5	-	-	-	-	67.6 (11.6)	0.1 (0)	51.2 (31.8)	0.02 (0)	81.6 (5.1)	0.3 (0.1)	-	-
15.5-19.5	-	-	-	-	69.1 (6.4)	0.1 (0)	-	-	78.9 (5.2)	0.1 (0)	-	-
seston $mg l^{-1}$	-	10	-	4	-	7.56	-	2.93	-	8.16	-	2.07
température °C	8°C		5°C		11°C		10,5°C		14°C		17°C	

finer particles, either with an hypersecretory of mucus on the gills (Palmer and Williams, 1980) or with a variation of the diameter of the gill ostia by changes of the blood pressure in the gill filaments (Elsay, 1935) or by muscular action (Dral, 1968).

The table 4 show an increased variance when the retention efficiency increases for smaller particles in *Crassostrea gigas* (Deslous-Paoli and Héral, unpublished data) *Cerastoderma edule* (Vahl, 1973) and *Crassostrea virginica* (Palmer and Williams, 1980 ; Palmer, 1980a), even though this efficiency is nearly constant with *Argopecten irradians*. This mechanisms may serve to maintain an optimum of ingested material (Davenport and Woolmington, 1982) and a continuous digestion (Palmer, 1980b). Figure 17 gives schematic aspects of the relationship between filtration, ingestion and assimilation rate (Navarro and Winter, 1982 ; Wilson, 1983) for *Mytilus chilensis* where B is the food density at which an optimum amount of food is ingested.

Assimilation efficiency is usually not dependent of body size and the main factor affecting it is undoubtedly the quantity and nature of ingested food (Griffiths and King, 1979a ; Gerdes, 1983a). For *Crassostrea gigas* the assimilation rate remains constant over a wide range of food concentration when the filtration rate decreases (Gerdes, 1983a) as well as *Crassostrea virginica* (Langefors and Maurer, 1975) *Mytilus chilensis* (Navarro and Winter, 1982) *Modiolus modiolus* and *Artica islandica* (Winter, 1969) (fig. 17). But if the filtration rate remains constant, the assimilation efficiency is still dependent on algal concentration, as for *Mytilus edulis* (Widdows, 1978) and *Aulocomya ater* (Griffiths and King, 1979a) (fig. 18)

But some differences appear between assimilation efficiency measured for *Perna perna* on the field (42 %) and in laboratory (61 %) (Berry and Schleyer, 1983). Nevertheless, Hawkins et al. (1985) find that the absence of resuspended bottom material, which has been found to stimulate rates of both absorption and growth (Winter, 1976, 1978 ; Kiorboe et al., 1981) does not affect the bioenergetic steady-state evident among mussels. These findings conform with those of Riisgard and Randlov (1981) who reported that a "restricted" diet of *Phaeodactylum tricornutum* enables *M. edulis* from Denmark to grow at rates comparable with those found in nature. But for *Crassostrea virginica*, Urban and Laigton (1984) suggest than kaolinite may improved oyster growth by increasing digestion efficiency.

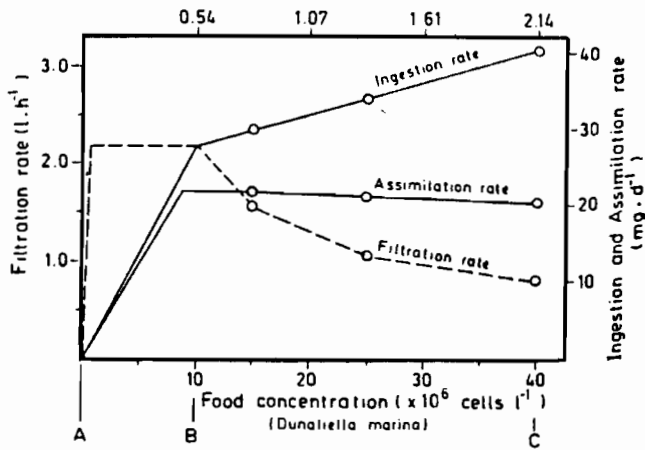
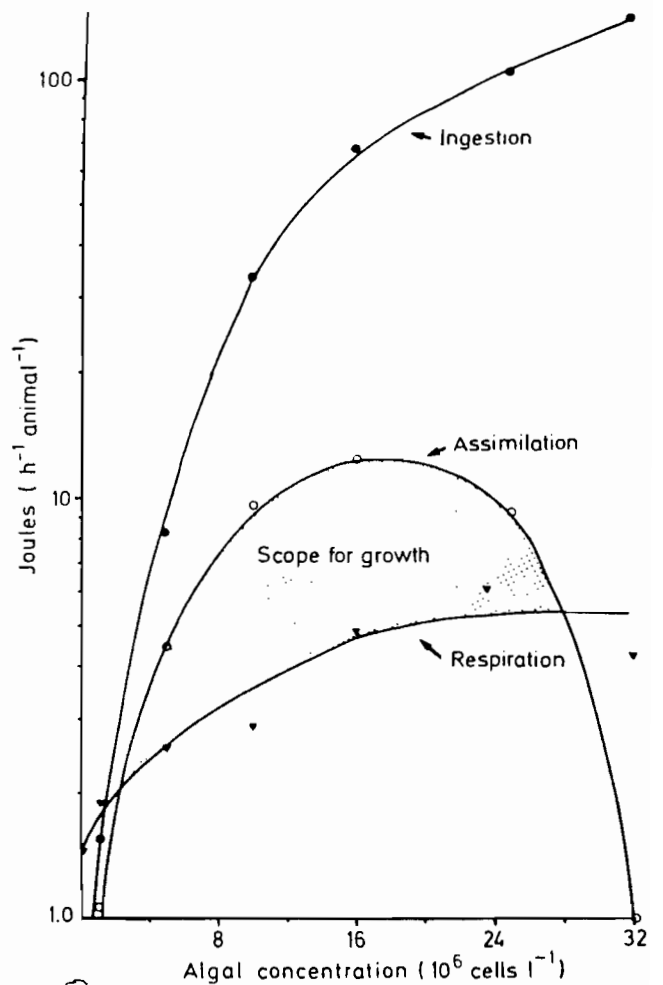


Figure 17 : *Mytilus edulis*, Concept of the interrelationships existing ^{between} filtration rate, assimilation rate, and food concentration (from Navarro and Winter, 1982)

Figure 18 : *Aulacomya ater*. Ingestion rate, assimilation rate, oxygen consumption and scope for growth in 50 mm mussels, expressed as functions of food concentrations (from Griffiths and King, 1979a).



3.2.2. Metabolic costs

Energetic costs of metabolism can be calculated from the consumed oxygen (Gnaiger and Forstner, 1983), from the released carbon dioxide, or from the produced heat. The energetic equivalent of oxygen consumption varies according to the substrate being used by the animal. Estimates of energy flow based on oxygen consumption generally assume a mean oxycaloric equivalent of 20.08 J/ml O₂. For a review on the oxygen consumption in oysters see Shumway (1982). Metabolic energy expenditure is affected by a large range of endogenous factors (body size, gametogenic stage, activity) as well as by environmental factors (temperature, salinity, oxygen availability, exposure to air, food availability) (Bayne, 1976 ; Widdows, 1978 ; Newell and Branch, 1980 ; Bayne and Newell, 1983).

For *Crassostrea gigas*, the metabolic rate is related to body size by an allometric equation (Lee and Chew, 1981 ; Gerdes, 1983b)(fig. 19) as well as for the others suspension and deposit feeders (Jorgensen, 1976 ; Newell et al., 1977 ; Rodhouse, 1978 ; Navarro and Winter, 1982 ; Hamburger et al., 1983). The average relationship defined from suspension and deposit feeders, is $Y = 0.5 X^{0.73}$ (Bayne and Newell, 1983) where Y is the oxygen consumption and X the body size. But, in order to compare the metabolic rate of organisms, the consumption of O₂ is related to the unit of body weight. It shows that energy flow through small individuals or species may be much greater than might otherwise be supposed on the basis of their biomass alone.

An increase in oxygen uptake associated with reproduction has been found in *Mytilus edulis* (De Vooy, 1976) as well as in *Chlamys islandica* (Vahl, 1978). Hawkin and al. (1985) have correlated the fluctuations in oxygen consumption with the reproductive cycle and use of stored reserves for *Mytilus edulis*. Mori (1968) has studied the relationship between tissues and oxygen consumption during sexual maturation and spawning for *Crassostrea gigas* and has suggested that carbohydrates are more efficient as an energy source than fats in gill, digestive diverticula and pallial margin.

Experiments on rate of oxygen consumption are difficult to compare because some concern active or routine rates with fed organisms and some others are performed on starved organism and concern basal or standard metabolic rates. The standard rates of oxygen consumption represent approximately

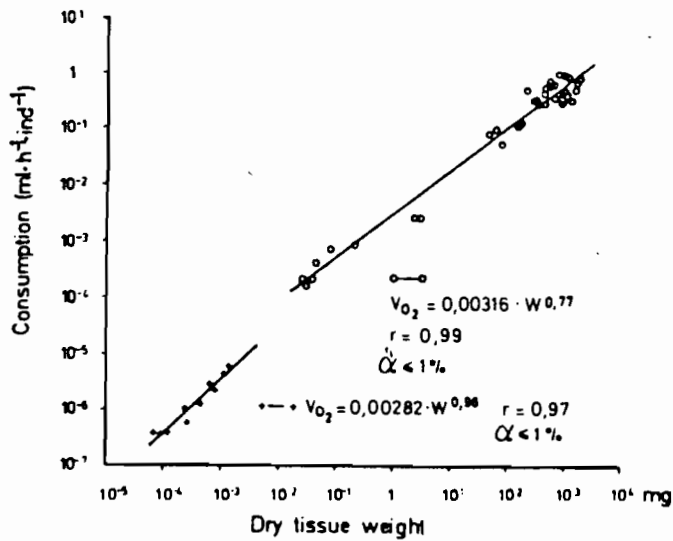
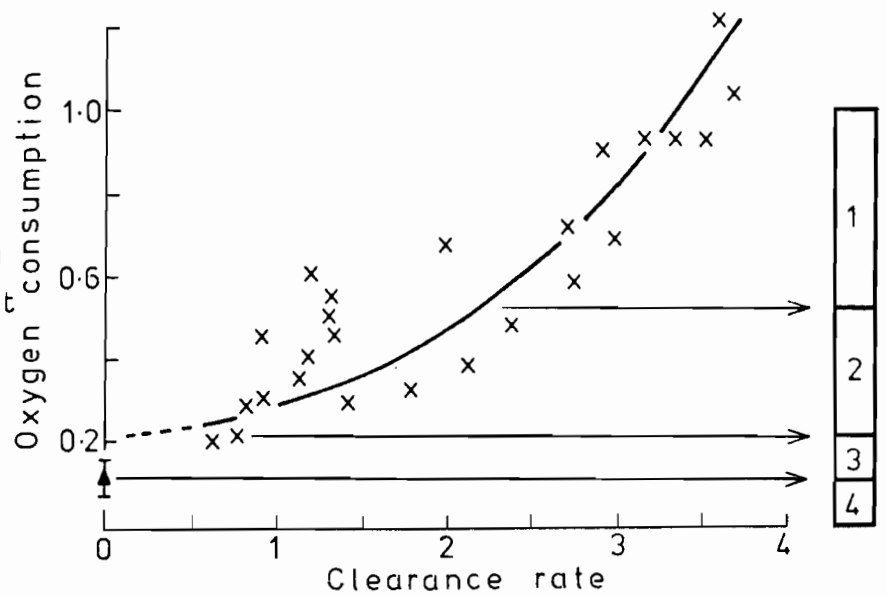


Figure 19 : *C. gigas* : relationship of oxygen consumption and body size (dry tissue weight) in oysters and oyster larvae. (from Gerdes, 1983b).

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Figure 20 : A relationship between the rate of oxygen consumption ($\text{ml O}_2 \text{ h}^{-1}$) and clearance rate (l h^{-1}) for *Mytilus californianus* (from Bayne et al., 1975). 1 : Net energy gain. 2 : Costs associated with feeding. 3 : Costs of digestion. 4 : Basal metabolic costs. (from Bayne, 1985).



half of the active rate (Dame, 1972 ; Bayne et al., 1976 ; Shumway and Koehn, 1982). For a given species, the rate of oxygen consumption also varies according to the temperatures within its thermal tolerance. Studies on the effect of temperature on oxygen consumption of oysters (Dame, 1972 ; Newell et al., 1977 ; Kim, 1980) show either a limited capability or no possibility for adaptation or acclimation, as for *Mytilus edulis* (Griffiths, 1980). Identical results were found for temperature salinity combinations (Shumway and Koehn, 1982). Energy losses from metabolism are compensated by changes in the feeding rates (Hughes, 1980 ; Fiala Medioni and Copello, 1985). For *Crepidula fornicata*, Newell and Branch (1980) have suggested that an adjustment of feeding rate and metabolic energy expenditure can occur in response to environmental temperature change.

For oysters and mussels, some relationships between oxygen consumption and feeding activity have been found by Collier (1959); Thompson and Bayne (1974) ; Bayne et al (1976) ; Griffiths and King (1979a) Navarro and Winter (1982). Bayne (1985) summarises the different levels of the metabolic costs in figure 20. The energetic costs of feeding activity are associated with filtration activity, movements and energetic requirement of ingestion and absorption (Jorgensen, 1976) and Jorgensen (1982) shows that for *Mytilus edulis*, the energy of dissolved amino acids absorbed by the gills which are practically only epidermal structures, correspond to 1.5 times the metabolic requirement of beating cilia. Such a cost has been defined for *Mytilus chilensis* as a function of body weight (Navarro and Winter, 1982) (table 5). For *Mytilus edulis*, the physiological costs of feeding represents 24 % of the ingested ration (Bayne and Scullard, 1977) whereas digestion and assimilation can be performed after filtration for only 4.6 % of the value of the ingested ration. Oxygen consumption in *Choromytilus meridionalis* is not influenced by ration level (Griffiths, 1980), *Mytilus edulis* has been shown to maintain a constant metabolic rate up to concentration of $280 \text{ mg seston.l}^{-1}$ by increasing the percentage of extraction efficiency to 25 %. This increasing of oxygen efficiency consumption equilibre the decreasing of ventilatory rate (Widdows et al., 1979). In *Crassostrea gigas*, metabolic rates are affected by the ration up to a threshold in food concentration for feeding, over this threshold routine rate remains constant (Fiala Medioni and Copello, 1985). Widdows (1985) shows that mussels subjected to a fluctuating salinity regime maintained a relative constant rate of respiration and feeding between 30 and 20 ‰. Below 19 ‰ there is partial valve closure, feeding cease and respiration

Table 5 : *Mytilus edulis*. Respiration rate (12°C) in relation to body and size different metabolic conditions (Values calculated from regression equations) (from Navarro and Winter, 1982).

Body size		Oxygen consumption			Energy used in routine metabolism (= 100%)						
Dry-tissue weight	Shell length	Stand. metab.	Stand. metab. + digestion.	Stand. metab. + digestion + feeding (= rout. metab.)	Stand. metab.	Feeding	Digestion	Rout. metab.			
(mg)	(mm)	(ml·h ⁻¹)	(ml·h ⁻¹)	(ml·h ⁻¹)	(cal·h ⁻¹) (%)	(cal·h ⁻¹) (%)	(cal·h ⁻¹) (%)	(cal·h ⁻¹)			
20	13.3	0.0137	0.0196	0.0202	0.0651	67.81	0.0029	3.02	0.0280	29.17	0.0960
50	18.4	0.0274	0.0383	0.0398	0.1302	68.85	0.0071	3.75	0.0518	27.39	0.1891
250	32.6	0.0931	0.1240	0.1308	0.4422	71.17	0.0323	5.20	0.1468	23.63	0.6213
500	41.7	0.1577	0.2056	0.2185	0.7491	72.17	0.0613	5.91	0.2275	21.92	1.0379
1 000	53.4	0.2670	0.3410	0.3650	1.2683	73.15	0.1140	6.58	0.3515	20.27	1.7338
1 500	61.6	0.3634	0.4585	0.4927	1.7262	73.76	0.1625	6.94	0.4517	19.30	2.3403
2 000	68.2	0.4522	0.5656	0.6096	2.1480	74.18	0.2090	7.22	0.5387	18.60	2.8956
2 500	71.8	0.5357	0.6657	0.7191	2.5446	74.50	0.2537	7.43	0.6175	18.08	3.4157
3 000	78.8	0.6154	0.7604	0.8229	2.9232	74.79	0.2969	7.60	0.6888	17.62	3.9088

Table 6 : Nitrogenous excretory products of some bivalve molluscs (from Bayne et al., 1976).

Species	Excreted components as % of total measured nitrogen (N)				Authority
	NH ₄ -N	Urea-N	amino-N	uric acid-N	
<i>Modiolus demissus</i>	62-75	0	25-38	—	Lum & Hammen (1964)
	66	0	34	—	Hammen (1968)
<i>Crassostrea virginica</i>	65	13	5	—	Hammen et al. (1966)
	68	8	21	3	Hammen (1968)
<i>Mercenaria mercenaria</i>	66	0	30	4	Hammen (1968)
<i>Solemya velum</i>	70	0	27	3	Hammen (1968)
<i>Donax variabilis</i>	75	0	24	1	Hammen (1968)
<i>Tagellus plebius</i>	50	0	31	19	Hammen (1968)
<i>Mya arenaria</i>	94	6	—	—	Allen & Garrett (1971b)
<i>Mytilus edulis</i>	41	4	55	—	Bayne (1973a): winter
<i>Mytilus edulis</i>	67	5	28	—	Bayne (1973a): summer

—, signifies that this component was not measured.

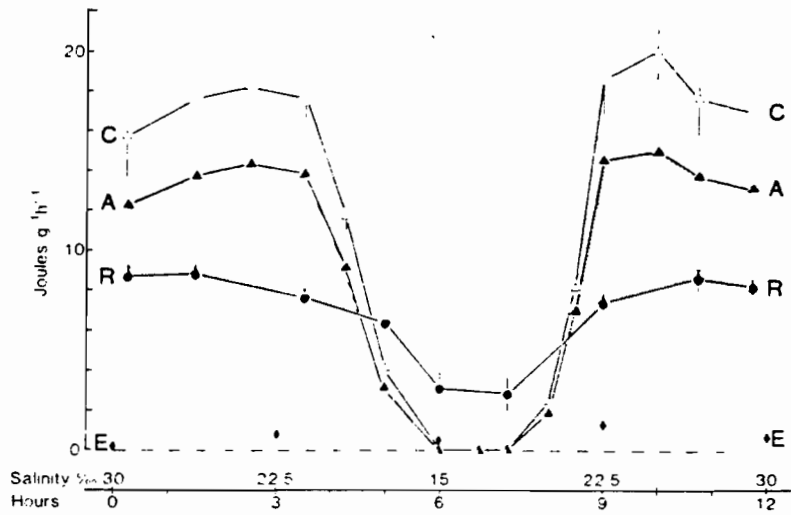


Figure 21 : Effect of fluctuating salinity between 30 and 15‰ on the food energy consumed (C, open triangles), energy absorbed (A, closed triangles), energy respired (R, closed circles) and the energy excreted (E, diamonds) by *Mytilus edulis*. Scope for growth ($A - (R + E)$) is represented by the shaded area. (from Widdows, 1985).

is reduced (fig. 21). But there is no acclimation to the fluctuating salinity regime over 21 days. The metabolic expenditure of marine filter feeders responds also to change in oxygen tension (Newell et al., 1977 ; Bayne and Livingstone, 1977; Shumway and Koehn, 1982) and aerial exposure (Widdows et al., 1979b; Griffiths, 1981). In such case anaerobic metabolism can replace aerial metabolism (see De Zwann, 1977 for bibliographic review ; Widdows et al., 1979 b, Ahmad and Chaplin, 1979 ; De Vooy, 1979 - 1980 ; Kluytmans et al., 1980). Bayne and Newell (1983), Famme et al. (1981) and Shick et al. (1983) have established both by direct and indirect calorimetry (Hammen, 1979), that processes of anaerobic metabolism may account for less than 5 % of total heat loss by *Mytilus edulis* under normoxic conditions. At reimmersion, after exposure to air, *Mytilus edulis* show a typical "oxygen debts" (fig. 22) (Widdows et al., 1979 b; De Vooy and De Zwann, 1979 ; Shick and Widdows, 1981). Estimations of metabolism losses by oxygen consumption are correlates quite closely with energy requirements as assessed through direct calorimetry, for *Mya arenaria* and *Crassostrea virginica*. But for *Mytilus edulis* oxygen consumption measurements could underestimate energy requirements by about 40 % (Hammen, 1979). Furthermore, oxygen consumption is not a relevant measure of energy metabolism during periods of anoxia such as the ones caused by tidal fluctuations.

3.2.3. Excretory losses

This parameter of the energy balance is often ignored, or just estimated by subtraction.

As in *Mytilus edulis* (Bayne and Scullard, 1977 ; Bayne et al., 1979 ; Bayne and Newell, 1983 ; Hawkins et al., 1985) *Crassostrea gigas* and *Ruditapes philippinarum* shows seasonal variations in both the rates of nitrogen excretion and the ration between ammonia and organic nitrogen as amino acids or urea (Robert and Vincendeau, 1985). This seasonal variation can be related to changes in the biological conditions (gametogenic for exemple) of the animals and in the level and nature of endogenous energy reserves (Mann and Glomb, 1978 ; Bayne and Newell, 1983 ; Riva and Masse, 1985).

Table 6 shows that ammonia is the main excretory product of bivalvia (Bayne et al., 1976). But in *Mytilus edulis*, the excretion of amino acids accounts for 0 to 63 % of total nitrogen (Bayne and Scullard, 1977). For

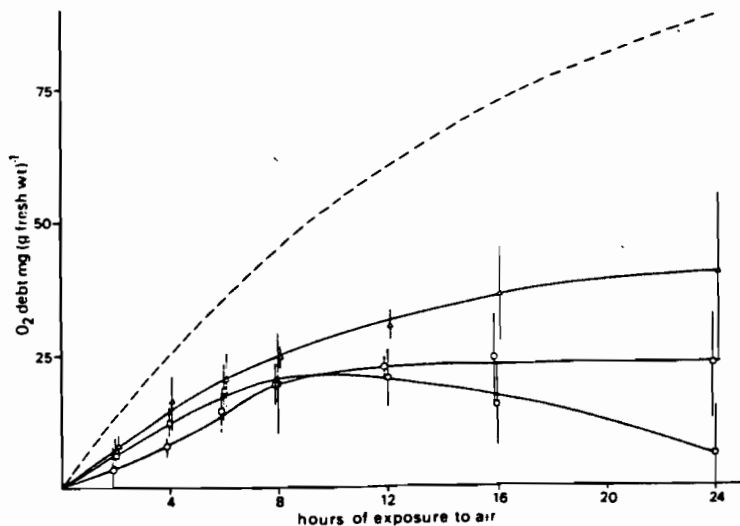
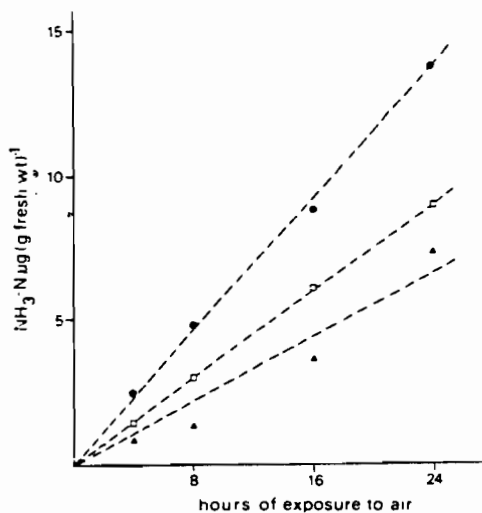


Figure 22 : The extra oxygen uptake (oxygen debt), after re-immersion in seawater, as a function of the duration of the preceding exposure period to air. Δ sub-littoral, 45-65 mm ; \circ littoral, 30-50 mm ; \square littoral, 45-65 mm. Values plotted are means \pm standard deviation. The dashed curve represents the calculated oxygen equivalent at complete oxidation of the accumulated succinate plus propionate

as a function of the exposure time in sub-littoral mussels with a length of 45-65 mm (after data from Kluytmans and de Zwaan, 1976, and Kluytmans et al., 1977, 1978). (from De Voys and De Zwaan, 1978).

Figure 23 : The extra ammonia excretion after re-immersion in seawater as a function of the duration of the preceding exposure period to air, \blacktriangle littoral, 30-50 mm ; \square sub-littoral 45-65 mm ; \bullet littoral 45-65 mm. (from De Voys and De Zwaan, 1978).



Crassostrea gigas, Robert et al. (1982) show that during summer the urea represents from 30 to 80 % of total nitrogen excretion. Robert and Vincendeau (1985) have measured the seasonal variation in all the components of nitrogen excretion for *Crassostrea gigas* and *Ruditapes philippinarum* (table 7). During summer the excretion rate are highest than during winter, but starvation produces an increase in nitrogen excretion in winter^{and} a fall in summer (Bayne and Scullard, 1977), because the proportional contribution of protein to total catabolism substrats is considerably higher during winter (33 to 67 %) than during summer (6 to 19 %) (Hawkins et al., 1985).

The contribution of ammonia excretion to energy losses in the energy budget may normally be between 1 and 10 % for *Mytilus edulis* (Bayne and Newell, 1983). Thompson (1984a) measured higher ammoniac excretion in non estuarine subarctic mussels (17 to 32 % of respiratory energy loss) than Bayne and Widdows (1978) for a lynher population (1 to 12 % of respiratory energy loss), and Srna and Baggley (1976) and Robert and Vincendeau (1985) show an higher excretion for clams (*Mercenaria mercenaria*, *Ruditapes philippinarum*) than for oysters (*Crassostrea virginica*, *Crassostrea gigas*).

As for oxygen consumption, a debt existes for ammonia excretion after tidal exposur to air (De Vooy and De Zwaan, 1978)(fig.23). This ammonia debt may reflect the ammonia release into the mantle cavity fluid during exposure (Bayne et al.. 1976) and/or may be caused by an active deamination of the end product of anaerobic metabolism.

Table 7 : Seasonal excretory product by *Crassostrea gigas* and *Ruditapes philippinarum*
(from Robert and Vincendeau, 1985).

<i>Crassostrea gigas</i>		December	February	April	June	August	October
N.NH ₄	%	12	8.1	28.8	85.4	8.8	73.7
Urea	%	15.5	91.8	19.2	4.7	9.7	26.2
Amino acids	%	-	-	51.9	5.2	6.2	-
unidentified	%	72.4	-	-	4.5	85.3	-
Total nitrogen $\mu\text{gat.g}^{-1}.\text{l}^{-1}$		6.46	2.32	2.48	2.10	2.36	0.86

<i>Ruditapes philippinarum</i>		December	February	April	June	August	October
N.NH ₄	%	48.5	1.2	52	100	57.2	61.2
Urea	%	3.3	-	8.2	-	6.9	38.8
Amino acids	%	-	-	0.8	-	22.7	-
unidentified	%	48.2	98.8	85.7	-	-	-
Total nitrogen $\mu\text{gat.g}^{-1}.\text{l}^{-1}$		1.58	16.15	10.92	6.36	2.06	1.51

Conclusion

As it has been said before, two complementary approaches of the energy balance are possible. The first, ecological one concerns the resource allocation between productions (Pg. Pr. Ps. Pe) of natural or cultivated populations, and their seasonal variations. The second, physiological one defines by experimental studies the main causes of variability in the physiological processes of production.

First, the analysis of energy allocation between the secretory products, somatic growth and reproduction related with body size and age is fundamental, but not always easy. If the assessment of energy allocation for *Crassostrea gigas*, *Ruditapes philippinarum*, *Chlamys varia* etc.. between somatic growth and reproduction is not really difficult, for *Mytilus edulis*, *Crepidula fornicata* etc..., the diffuse reproductive organs and/or successive and partial spawnings can induce, an underestimation of the reproductive effort. In the same way, natural biodeposition has to be assessed in relation to quantity and nature of potentially used seston by molluscs. By such approach, it will be possible to estimate not only the energy which is consumed, ingested and absorbed on the field (by separation and analyse of feces and pseudofeces), but also the impact of molluscs on the fixed food which can be either resuspended and reused, or can reduce the sediment under the cultures.

Secondly, as Bayne and Newell (1985) argue, the extrapolation of laboratory studies to the field may induce many problems. Environmental and trophic conditions of experimental studies rarely reproduce natural variabilities on the field. In addition of the stress due to acclimation and handling, the results obtained with organisms starved or feed with monospecific phytoplakton culture can induce insuitable data for environmental studies. Therefore now, the need for more experimental work under natural, field conditions is well recognized, particularly in situations for intertidal molluscs as changeable as in an estuary.

Assessment of actual metabolic losses, especially for tidal molluscs which present an anaerobic metabolism during exposure to air, should be approached by direct calorimetric measures to complement the studies on oxygen

consumption. Furthermore, some components of the energy budget are rarely estimated. Mucus produced by gastropods, for locomotion or feeding, can reach more than 30 per cent of the consumed energy. But there is available assessment for mucus production of filter feeders. A part of this mucus production is ingested with filtered particles, but another one is lost with pseudofeces production. The losses due to excretion are often ignored or estimated only with ammoniacal products, during laboratory experiments. To assess the magnitude of this potential error in the energy budget, the nature and the seasonal amounts of the all nitrogenous and products must be known. But filter feeders feed not only on particulate food as we have seen, but also on carbonate and nitrogenous dissolved substances. In energy budget nothing is known about the total intake of dissolved substances which, as amino acids, can be either used or excreted by filter feeders.

In the near future, if we want to deal with the integrated studies of a shell fish ecosystem and its modelisation it is mandatory to study altogether the biochemical, physiological and dynamical parameter not only for individuals but also for populations level as well as the quantity and nature of potential food consumed by molluscs.

Furthermore, a knowledge of seasonality of energy budgets could allow a better understanding of organisms tolerance and sensitivity to external stresses such as illness or man-induced pollutants.

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