International Seminar for Research on Planning and Development aids to the
shellfish industry

EVALUATION OF THE CARRYING CAPACITY OF
MOLLUSCAN SHELLFISH ECOSYSTEMS

EVALUATION DE LA CAPACITE BIOTIQUE
DES ECOSYSTEMES CONCHYLICOLES

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ABSTRACT

     Growth of molluscs raised in coastal zones, where the water exchange
rate is low, appears to be limited, once a certain biomass level is attained,
by the availability of food, making it necessary to determine as accurately
as possible the trophic capacity of an ecosystem. This paper analyses the
various sources of food for molluscs. It would appear that dissolved orga-
nic substances play a major role, providing up to half the energy necessary
for their metabolism. Particulate material is filtered by molluscs in pro-
portion to their size, with optimum filtration rates varying with species.
The negative effect on meat production of high mineral seston rates is demon-
strated, and an analysis provided of the respective role of each component
of organic matter. The trophic inflow represented by bacteria and organic
detritus is discussed, and phytoplankton rations described. A method inte-
grating current factors is proposed for calculating flows of food, and per-
centages of phytoplankton retained by molluscs raised in various shellfish-
culture ecosystems are presented.

Introduction

     As a preliminary, it might be asked why we should study the carrying
capacity of waters, i.e. the quantity of food available for molluscs, either
in shellfish farms or in some form of intensive culture. From a basin-
planning standpoint, it is possible to develop production models for the
populations under culture that are derived from models used in halieutics.
Such an approach would accordingly not take into consideration the limiting
effect of available food quantities, and yet the shellfish industry has
developed in estuaries, bays, ponds and relatively closed basins characterized
by a high degree of confinement and low water renewal rates. Cloern (1982)
demonstrated that, in San Francisco Bay, biomasses of filter-feeding bivalves
are large enough to filter a daily volume of water equivalent to the volume
of the bay, thus controlling the development of phytoplankton. In the
Marennes–Oléron basin, biomasses of oyster and cultivated mussel populations,
along with other molluscs, can filter over half the water volume of the
basin every day, bearing in mind the standing time for water masses. Table
1 shows that this same volume of water is filtered several times by molluscs.

     This could explain the relatively low rates ($5\mu g/l^{-1}$ of chlorophyll a) of
phytoplankton biomass found in these basins, which are nevertheless very
rich in nutrients (Conomos et al., 1979; Héral et al, 1984).

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Oyster biomass	Mussel biomass	Biomass other molluscs	Total biomass	Biomass dry weight	Filtration	Daily rate at neap tide	Water volume per tide cycle	Recycling time
70,000 t	3,600 t	5,000 t	80,000 t	2,400 t	$240 \times 10^5\,m^3/h$	$576 \times 10^6\,m^3/d$	$800 \times 10^6\,m^3$	4-9 days

Table 1: Water volume filtered by molluscs in the Marennes-Oléron basin

It is possible that an overall philosophy could be developed to guide planning in these cultivation zones. An empirical approach, i.e. a gradual increase in loads, might show that, past a certain point, production begins to decline, making it necessary to revert to an equilibrium position, although this production-biomass equilibrium can only be determined if the other parameters are constant. The decline in production may, of course, be due to overloading of culture biomass, but also to changes in the cultivation ecosystem involving such things as:

- a rise in bottom levels, causing a slowdown in current and thus of food inflow,

- changes in mineral salt inflows (due to drought, estuary dams, etc.),

- perturbation of phytoplankton growth by pollutants, which also upset mollusc physiology (this is the case, for example, with the organic salt of TBT (Alzieu and Héral, 1985),

- deterioration of shellfish beds through accumulation of organic matter (faeces and pseudofaeces) causing anoxic phases (Kusuki, 1984).

The above elements militate in favour of the overall study of shellfish ecosystems as integrated units. For the purposes of this seminar, we have arbitrarily chosen the following aspect: the food available for molluscs, which is dealt with in this document, i.e. the quantity of food molluscs need to cover their energy, metabolism, growth and reproduction requirements (Deslous-Paoli, 1985), and then the model-building phase, which will enable us to establish relationships between primary and secondary elements (Bacher, 1985).

Many authors have given experimental demonstrations of the role played by various parameters on mollusc nutrition and production. It must nevertheless be admitted (cf. Epifanio et al., 1975, and Dame et al., 1980) that laboratory results are difficult to extrapolate to natural or divergent environments. A study of the carrying capacity of an ecosystem can, however, only take into consideration a certain number of parameters. Initially, therefore, we will attempt to determine relationships observed in the literature in situ between various parameters and filter-feeding mollusc production, in order to propose a list of factors that it appears necessary to study further. We will pay particular attention to the spatio-temporal research procedures which must be developed, in particular for seas characterized by tides.

Relations between biotic and non-biotic water parameters
and the production of molluscs observed in situ

    A great many authors have demonstrated the influence of temperature.
Temperature controls the onset of gametogenesis (Lubet et al., 1981; Héral,
1985) but also its evolution (Mann, 1979). Temperature is also an extremely
important parameter which controls all phenomena in mollusc physiology:
filtering activity, metabolism and thus respiration and excretion, thus rep-
resenting a close link with growth in terms of size and weight. This impor-
tant influence of temperature has made it possible to develop mollusc growth
models on the basis of equations by Von Bertalanffy or Gompertz by integra-
ting temperature variations and thus building models of season growth fluc-
tuations: Bachelet (1984) for *Scrobicularia plana*, Bodoy (1982) for *Donax
trunculus*, Hamon (1983) for *Mytilus galloprovincialis* (Fig. 1), and Rodhouse
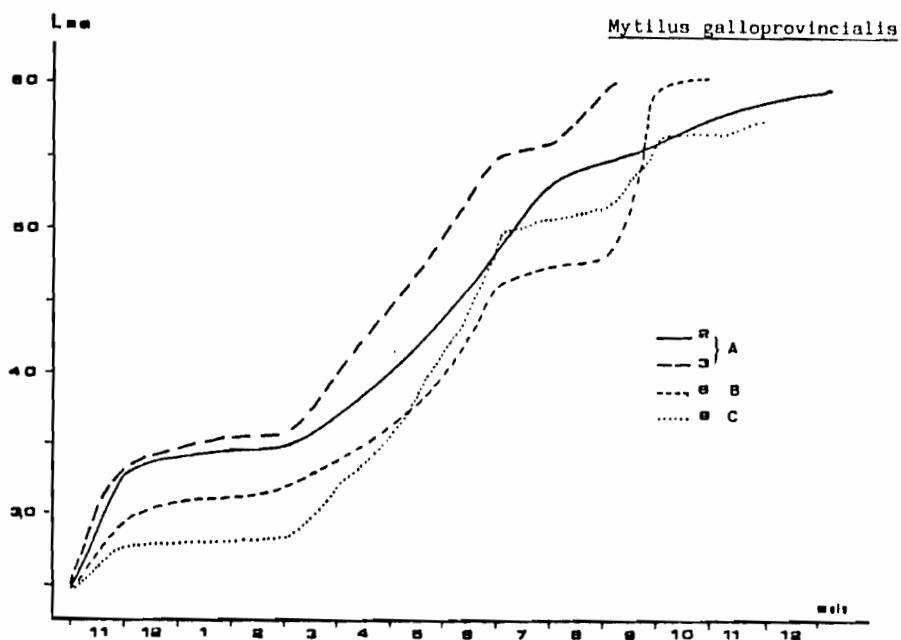et al. (1984) for *Mytilus edulis*.

Figure 1: Size-age curves obtained after incorporating temperature
and nitrates (Hamon, 1983)

    Héral et al. (1984) also demonstrated that, if the egg-laying period is
excluded, temperature is the primary explanatory factor for shell growth
and the third explanatory factor for meat production. This indicates that
other factors play a vital role in meat production. These authors also
showed a close link with dissolved carbonated and nitrogenated organic sub-
stances as well as with phytoplankton, whether deteriorated (phaeopigments)
or in live form (chlorophyll a) in the water or the water-sediment inter-
face (Fig. 2).

    Similarly, Lelong and Riva (1976) demonstrated in situ the action of
phytoplankton, temperature and salinity on the growth of *Ruditapes decussatus*.
A link between benthic biomass and the quantity of chlorophyll was estab-
lished by Hargrave and Peer (1973), while a logarythmic relationship between
ATP content based on current and filter-feeding mollusc production was demons-
trated by Wildish et al. (1981). The connection between phytoplankton biomass
and weight increase in the oyster *C. gigas* has been confirmed (Deslous-Paoli
et al., 1981), as well as a strong correlation between primary production

		T.	Sea	Ses.O	ATP	Chla	Phaeo	Prot	Carbh	Fat	C	N	Bact C	A Cl	A.A.	N Org
													dia hum dia			
meat	P	0,84	-0,32	-0,41	0,03	-0,25	0,85	-0,19	0,58	0,05	-0,24	-0,25	-0,76 0,98	-0,16	0,21	0,37 0,5?
	G	0,28	-0,41	0,06	0,36	0,31	0,58	0,03	0,25	0,05	0,34	0,40	-0,26 0,15	-0,03	0,51	0,72 0,39
shell	P	0,77	-0,38	-0,30	0,19	-0,30	0,31	-0,41	0,20	-0,17	-0,46	-0,47	0,45 0,77	-0,33	-0,04	0,12 0,5?
	G	0,87	-0,50	-0,14	0,05	-0,25	0,55	-0,04	0,29	-0,14	-0,28	0,35	-0,09 0,27	-0,72	-0,11	0,5? 0,57
Prot.	P	0,69	-0,35	-0,36	0,05	-0,28	0,89	-0,19	0,56	0,02	-0,70	-0,21	-0,23 0,92	-0,15	0,19	0,41 0,5?
	G	0,75	-0,37	0,70	0,35	0,32	0,48	-0,02	0,00	-0,05	0,46	0,55	-0,17 -0,13	-0,07	0,33	0,74 0,7?
Sugar.	P	0,55	-0,24	-0,45	0,05	-0,20	0,54	-0,21	0,52	0,09	-0,25	-0,36	-0,24 0,98	-0,19	0,73	0,16 0,3?
	G	0,19	0,02	-0,34	0,19	-0,02	0,24	0,08	0,59	0,29	-0,28	-0,48	-0,19 0,83	-0,16	0,36	-0,23 0,14
Carbh	P	0,54	-0,43	-0,45	-0,07	-0,27	0,58	-0,08	0,61	-0,05	-0,24	-0,15	-0,38 0,89	-0,05	0,23	0,45 0,5?
	G	0,20	-0,42	-0,12	-0,08	-0,06	0,43	0,04	0,18	-0,17	0,16	0,48	-0,31 -0,03	0,09	0,10	0,78 0,3?
Fats	P	0,59	-0,32	-0,49	0,01	-0,27	0,80	-0,20	0,55	0,03	-0,28	-0,25	-0,24 0,97	-0,17	0,19	0,37 0,46
	G	0,50	-0,51	-0,14	0,27	0,15	0,83	-0,13	0,39	-0,01	0,15	0,06	-0,26 0,54	-0,06	0,53	0,87 0,5?

		Chla	Phaeo	C	A Cl	Prot	Bact	Prot	Carboh	Fat
				dia hum dia						
meat	P	0,43	0,08	0,30 0,17	0,04	-0,03	-0,28	-0,16	0,57	-0,01
	G	0,71	0,45	0,39 0,80	-0,05	-0,29	-0,70	0,44	0,80	-0,44
shell	P	0,34	0,02	0,14 0,01	0,19	0,55	0,15	-0,03	0,47	-0,04
	G	0,75	0,68	0,02 0,16	-0,23	0,21	0,01	0,44	0,35	0,19
Prot.	P	0,53	0,15	0,28 0,22	0,06	0,00	-0,27	-0,11	0,56	-0,01
	G	0,75	0,64	0,24 0,75	-0,13	-0,22	-0,49	0,50	0,37	-0,37
Sugar	P	0,73	-0,10	0,32 0,10	0,03	-0,07	-0,24	-0,29	0,52	-0,05
	G	-0,21	-0,2?	0,37 0,00	0,10	-0,09	-0,32	-0,21	0,58	-0,08
Carbh	P	0,55	0,22	0,21 0,27	0,07	-0,10	-0,45	-0,05	0,61	-0,11
	G	0,73	0,70	0,02 0,47	-0,13	-0,28	-0,49	0,32	0,27	-0,31
Fats	P	0,31	0,03	0,27 0,14	0,02	-0,08	-0,31	-0,22	0,54	-0,12
	G	0,75	0,37	0,48 0,74	0,10	-0,17	-0,67	0,22	0,74	-0,37

Figure 2:

Correlation coefficients between water, water-sediment interface and oyster production. P = one-year oyster; G = two-year oyster. 0,6 = significant coefficient on the threshold of 95% r > 0.60

multiple correlations:

shell sm. oysters = 0.18 x water time - 11.45   r = 0.77
shell lg. oysters = 0.14 x chl a   in silt - 3.31 (2nd factor T)   r = 0.75
meat sm. oysters = 0.014 x dia.C + 0.017 phaeo. water - 2.98 (3rd factor T) r = 0.98
meat lg. oysters = 9.64 x hum silt C + 4.94 amino acids - 19.71 (3rd factor chl a) r = 0.97

and the energy content of *Ruditapes decussatus* (Bodoy and Plante-Cuny, 1983).
Kautsky (1982) showed good correlations in *Mytilus edulis* between shell growth
and temperature and between shell growth and chlorophyll content, if the
gametogenesis period is excluded. Shaffee and Lucas (1982) showed that pro--
duction yields are negative if chlorophyll and temperature levels are at a
minimum.

The harmful effect of excessive seston loads on flesh production was
shown by Vahl (1980). This was demonstrated in *Chlamys islandica* by Wildish
et al. (1981), for various lamellibranchs by Deslous-Paoli et al. (1981) and
by Héral et al. (1983) in adult *Crassostrea gigas*. The importance of bac-
teria (Prieur, 1981), often associated with particles, was mentioned by
Martin (1976) in *Ruditapes decussatus*, by Amouroux (1982) in *Venus veruscosa*
and by Mengus (1978).

Dissolved organic substances

Although experimental work by Péquignat (1973) demonstrated the nutri-
tional role of amino acids and sugars, the energy contribution they represent
has to date not been taken into account in determining mollusc energy balances.

The branchial epiderm of lamellibranchs is the site of high absorption
of dissolved organic molecules such as amino acids, sugars and fatty acids.
Numerous experimental studies have described these mechanisms, for instance
recent articles by Jorgensen (1982-1983, Wright and Stephen (1982), Gomme
(1982) and Neil et al. (1983). This absorption mainly takes place in the
gills, but also through the stomach and the middle intestine (Stewart and
Bomford, 1976; Bomford and Gingles, 1974). The kinetics of this absorption
is described using the Michaelis-Menten equation, the constants of which
depend on amino acid concentrations present in the ecosystem. Thus *Mytilus
edulis* can absorb half of the amino acids in water flowing through the
branchial cavity at concentrations of 1 μmole 1^{-1} (Jorgensen, 1983).
Jorgensen also shows that absorption of amino acids from natural sea water
may be sufficient to provide over twice the energy necessary for branchial
filtration. Similarly, Wright (1982) estimated that absorption of amino
acids contributes 6 to 60%, depending on concentrations available in the
water, of the oxydation requirements of metabolism exhausted by respiration.
This mechanism makes it possible to satisfy the requirements of 11 amino acids
necessary to *Mytilus caoifornianus*, principally L-methionine and L-lyzine-NCl
(Harrison, 1976), along with taurine, which represents 70% of the pool of
free intra-cellular amino acids in the gills (Zurburg and de Zwaan, 1981).
Conversely, Nell et al. (1983) showed that, although active absorption is
observed for glucose, the absorption resembles a sort of passive diffusion
that makes no major contribution to the carbohydrate requirements of oysters.

Similarly, a certain number of dissolved organic substances may be ab-
sorbed through the same metabolic channel and no longer play a role in energy
supply, but rather the role of a growth substance like choline chloride or
vitamins (Nell et al. 1983). Collier et al. (1953) also showed the very
beneficial effect of carbohydrates present in the marine environment on
pumping rates and the intervalval activity of oysters. These observations
led to the development of the early artificial diets based on sugars, fats
and vitamins (Castell and Trider, 1974; Trider and Castell, 1980; Nell and
Wisely, 1983).

In coastal waters, dissolved amino acid levels vary between 0.2 and 2
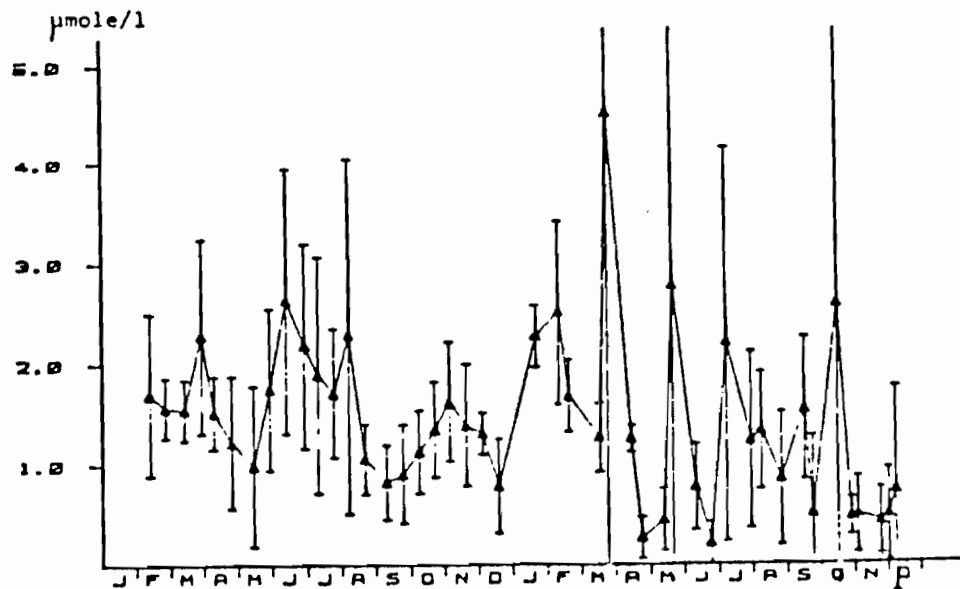μmole per litre (North, 1975). Jorgensen (1982) found variations in Isefjord

Figure 3: Variations in dissolved amino acid content of waters of the Marennes–Oléron basin (after Héral et al., unpublished)
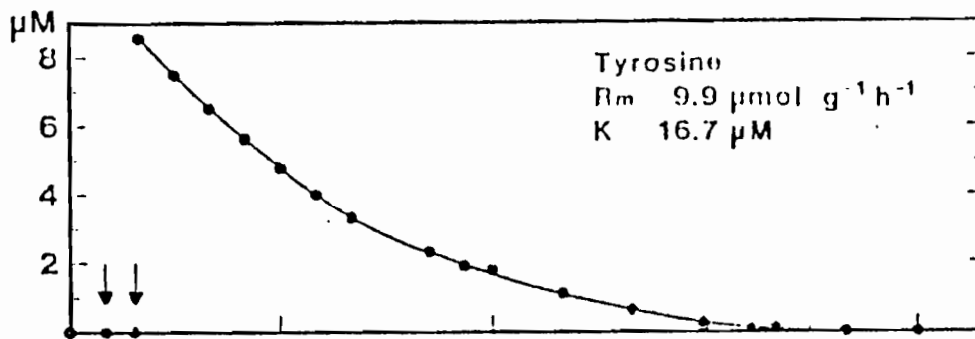

Figure 4: Uptake kinetics of amino acids in *Mytilus edulis* adapted to 50% artificial sea water at 14°C (after Jorgensen, 1983)

Amino acid	N	R_m $\mu mol\ g^{-1}\ h^{-1}$	K_u μM	R_m/K_u $l\ g^{-1}\ h^{-1}$	Uptake from $1\ \mu M$ $\mu mol\ g^{-1}\ h^{-1}$
Glycine	9	9.6 ± 1.1	4.2 ± 0.3	2.0 ± 0.3	1.8 ± 0.2
	4*	18.2 ± 2.0	3.9 ± 0.3	4.7 ± 0.7	3.8 ± 0.5
Glutamic acid	2*	9.6 (8.7, 10.5)	3.2 (3.1, 3.2)	3.1 (2.8, 3.3)	2.3 (2.1, 2.5)
Taurine	3	9.7 (7.4 – 12.5)	5.1 (3.3 – 8.3)	2.1 (1.5 – 2.5)	1.6 (1.3 – 1.9)
Glutamine	4	20.3 ± 3.0	10.4 ± 2.1	2.0 ± 0.2	1.8 ± 0.2
Tyrosine	2	9.9 (9.9, 9.9)	23 (17, 29)	0.5 (0.3, 0.6)	0.5 (0.3, 0.6)

between 0.4 and 2.5 $\mu mole\ l^{-1}$. In the Marennes–Oléron basin, Héral et al. (unpublished) found fluctuations between 0.2 and 10 $\mu mole\ l^{-1}$, but these showed no significant seasonal peaks, and daily variation during a given tidal cycle was greater than annual variation. The same was true for dissolved glucose or dissolved organic and inorganic carbon (Feuillet et al., 1979; Feuillet, pers. comm.). These wide variations may be due to the fact that measurements within the ecosystem are a synthesis of absorption and excretion by molluscs but also by phytoplankton and bacteria.

Suspended particulate matter

- Size consumed by filter-feeding molluscs

Recent use of particle meters (Coulter Counter, Luzex) has made it possible to determine the sizes trapped by the branchial filters of molluscs. It would appear that different species select different sizes. Fifty per cent of the particles retained by *Mytilus edulis* measured 1.5 µ (Silvester and Sleigh, 1984), and for *Cardium glaucum* 50% were 1 µ (Jorgensen et al., 1984), while for the anomia *Monia squarna* 50% were 3.5 µ (Jorgensen et al., 1984) and for *Crassostrea gigas* 50% were 3 µ (Kusuki, 1977; Deslous-Paoli and Héral, unpublished).

Optimum filtration for the oyster *C. gigas* takes place at 8-9 microns, while for *C. virginica* it is 5 microns (Palmer and Williams, 1980), and for mussels it is also 5 microns. These selection differences are not constant, however, and appear to depend on the seston load of the system. Deslous-Paoli and Héral (unpublished) show an increase in retention efficiency for waters with low turbidity for *C. gigas*, and Palmer and Williams (1980) demonstrate the same fluctuations for *C. virginica*. All particles larger than this size will then be trapped by the gills. The upper limit of ingestion is difficult to determine, but Paulmier (1972), examining stomach contents, indicates that particles smaller than 50 µ predominate, while those measuring 50 to 100 µ are frequently found, but particles of 100 to 150 µ are very rare.

It thus appears necessary, when studying particulate matter ingestible to molluscs, to take into account this size criterion and make biochemical analyses of the organic matter using differential filtration. This would yield a more accurate picture of the energy value of the fraction of this matter in estuary environments that can be utilized by molluscs. It has been observed in estuaries that the fraction ranging between 1 and 3 µ, of which only a small proportion is retained by the molluscs, may represent 50% of the total number of particles (Fig. 6). Conversely, nannoplankton smaller than 20 µ is directly related to growth of *Mytilus edulis* in the Gulf of Maine (Incze et al., 1980), while for the same species Rosenberg and Loo (1983), working in northwestern Sweden, found the same close link between nannoplankton and mussel weight increase.

- Seston

The mineral portion of seston may be significant in estuary environments during the winter period, when foreshore sediment is put back into suspension by strong tidal currents and storms, along with inflow from estuaries under high water conditions, allowing the silt plug to be expulsed. This high mineral load causes dilution of particulate organic matter and thus diminishes the energy value of suspended material. This causes molluscs to lose weight, since they must draw on their reserves in order to make up for the deficit. Vahl (1980) offers this explanation for variations in growth rates of *Chlamys islandica*. As well, Deslous-Paoli et al. (1981) and Héral et al. (1983) show the negative effect of seston contents higher than 100 mg l^{-1} on meat production in *C. gigas* and explain this negative production by the high rate of biodeposit mainly composed of pseudofaeces, causing larger amounts of energy to be used for sorting particles, mucus secretion and gill cleaning, at a time when phytoplankton biomass is in short supply.

- Bacteria

Counting aerobic heterotrophic bacteria populations, generally called total microflora, makes it possible to quantify bacteria biomasses, although
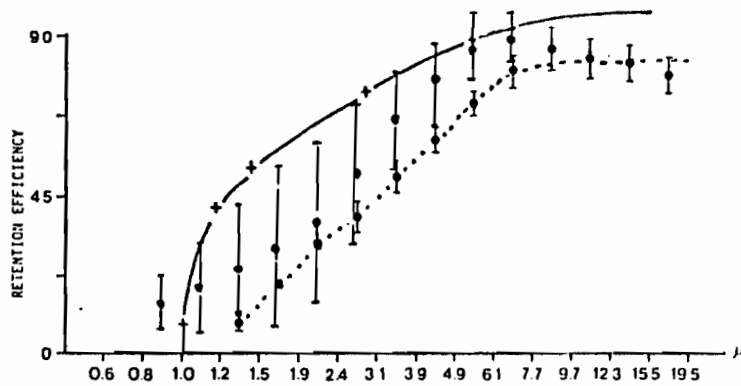
Figure 5: Retention efficiency based on particle size for *Mytilus edulis*+ according to Silvester and Sleigh (1984) and for *Crassostrea gigas* ‡ according to Deslous-Paoli and Héral (unpublished).

EVOLUTION OF DISTRIBUTION
IN NUMBER
OF PARTICLES 0.6 to 24.6 µ
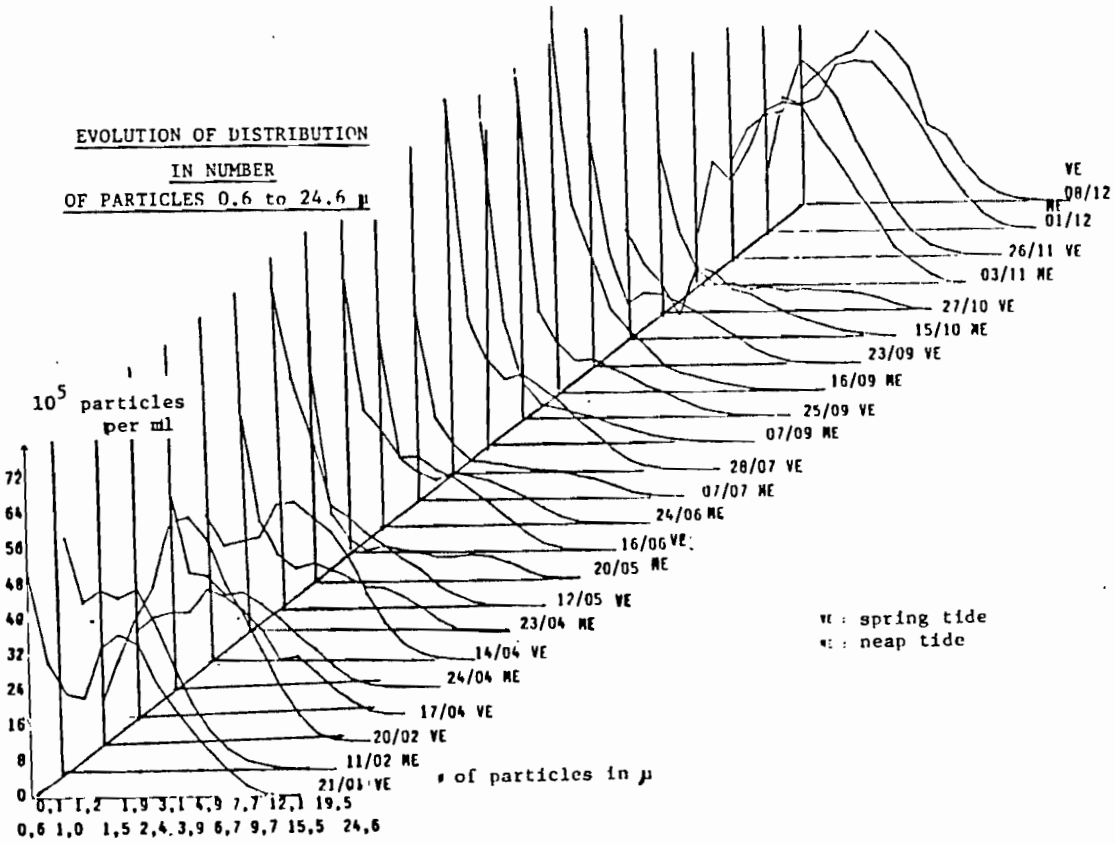
10^5 particles per ml

Figure 6: Number of particles according to size in the Marennes-Oléron basin (0.8 to 24.6 µ) (after Héral et al., unpublished)

it is necessary to convert these biomasses into their energy equivalent in order to compare their contribution with that of phytoplankton. Ferguson and Rublee (1976) estimate that, on the average, a bacterium corresponds to 7.8×10^{-5} g of carbon, and this value falls into the range given by Hamilton and Holm Hansen (1967). In the absence of a specific calorimetric coefficient for bacteria, that defined by Salonen et al. (1976) has been applied, i.e. 10.97 cal mg^{-1} of carbon for total aquatic invertebrates. Héral et al. (1983) and Deslous-Paoli and Héral (1984) showed that bacterial biomasses in a shellfish basin represent only a small part of the energy available to filter-feeding molluscs and that there is a high degree of variability between high and low water (Fig.7).
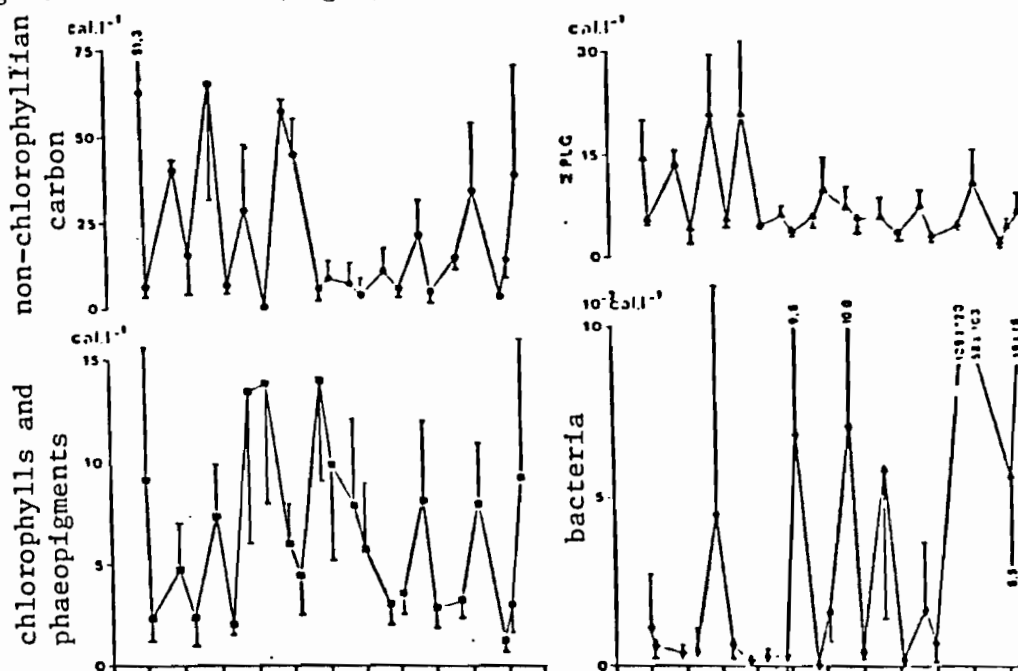

Figure 7: Energy values of bacteria compared to potential food (PLG), phytoplankton biomass (chl$a$ + phaeo) and non-chlorophyllian detritus (after Deslous-Paoli and Héral, 1984).

Zobell and Landon (1979), however, presented experimental results showing growth of adult *Mytilus californianus* on bacteria-based diets. Newell (1965) showed that *Macoma balthica* ingests and utilizes bacteria. Similarly Chakroun (1964) demonstrated that mussels concentrate the microflora in their environment. Martin (1978) pointed out that *Venerupis decussata* causes bacterial concentrations in a closed space to decrease by a factor of 7 in five hours, while phytoplankton is simultaneously consumed by a factor of 14. The capacity of bivalves to retain bacteria depends on their state in the natural milieu. Free bacteria are rare, and Sorokin (1981) showed that 30% to 40% of bacterial plankton form colonies of diameters greater than 4 μ and are thus more easily trapped by the branchial filters of filter-feeders, while the remaining bacteria are associated with suspended particles, particularly organic detritus. Lopez (1980), however, demonstrated the active role played by extracts from the crystalline style of *Mytilus edulis* in detaching bacteria from their substratum. Wiebe and Pomeroy (1972) estimate that 2.8×10^6 bacteria per ml would be required to support filter-feeder metabolisms, while Prieur (1981) found that the maintenance ration for a juvenile *Mytilus edulis* should be 1.33×10^6 cells per ml. Such figures may be found in estuaries

(Goulder, 1976; Héral and Prou, 1980), but they are neither constant nor current in natural environments (Prieur, 1981). For adult molluscs, therefore, bacteria appear to be only a complementary ration. The same is true for yeasts, and Epifania (1979), comparing diets with varying proportions of phytoplankton and yeasts, showed that juvenile *Argopecten irradians, Mercenaria mercenaria* and *Mytilus edulis* show good growth with a mixture containing 50% yeast. For *Crassostrea virginica*, on the contrary, any increase in the percentage of yeast in diets causes a drop in the growth of meat. Urban and Langdon (1984), working with the same species, confirm that growth in oysters fed with algae-yeast mixtures depends mainly on the quantity of phytoplankton.

Suspended organic matter

Non-living matter may be estimated on the basis of particulate carbon and nitrogen, from which has been subtracted the quantity of carbon and nitrogen of recent phytoplankton origin, as represented by the total amount of chlorophyll a and phaeopigments. The remainder thus obtained is multiplied by a caloric coefficient different from that of the plankton, which would overestimate the energy content (Héral et al., 1980). Bernard (1974) proposed 4 cal mg^{-1} of carbon, while Kenchington (1970) found a coefficient of 2.7 cal mg^{-1} of carbon for detritus, Parsons (1963) 5.8 cal mg^{-1} of carbon and Héral et al. (1980) a coefficient of 2.6 cal mg^{-1}. An estimate is thus obtained of the organic carbon of the non-chlorophyllian tripton representing detritus.

Accordingly to Widdows et al. (1979), the sum of the biochemical constituants of organic matter represents an estimate of the potential food for a filter-feeding mollusc. The resulting protides, fats and carbohydrates are multiplied by caloric conversion coefficients described by Brody (1945), which are 5.65 cal.mg^{-1}, 9.45 cal.mg^{-1} and 4.10 cal.mg^{-1} respectively. As for organic carbon content, Telek and Marshall (1974) showed that inorganic carbonates may produce an interference as great as 30% in CHN measuring when samples are rich in highly-carbonated mineral sestons. Héral et al. (1980) reported on the difference between the results of measuring organic carbon by combustion at 900°C and those for organic seston burned at 400°C. The same authors demonstrated that potential food (the sum of protides, fats and carbohydrates) represented only 2.6% of total seston, 16.6% of organic seston and 24.3% of organic matter as determined by CHN. This agrees with the results of several earlier studies (Menzel and Ryther, 1970; Holm-Hansen, 1972; Strickland, 1972; Widdows et al., 1979), which showed that a large proportion of particulate organic matter resists biochemical analysis, while molluscs apparently proportionately use only these reactive forms (Widdows et al., 1979). Notwithstanding the use of coefficients representing two times less energy than those for live plankton, potential food energy represents only an average of 50% of the calories calculated on the basis of organic carbon. The remaining 50% are linked to structural elements that are difficult to account for with biochemical analyses.

Use of detritus by molluscs may take place in two ways (Berry and Schleyer, 1983), either only the microorganisms attached to the detritus are digested and the non-digestible detritus rejected intact in the faeces and replaced in suspension where they may be recolonized by bacteria (Newell, 1965; Darnell, 1964; Odum, 1971), or part of the detritus is digested along with the associated bacteria (Adams and Angelovic, 1960), since the digestive enzymes of molluscs have the ability to utilize them (Bayne et al., 1976).

which will enable the phytoplankton fraction to be followed in connection with branchial-filter retention efficiency and mollusc growth. Incze et al. (1980) found a direct relationship between nannoplankton smaller than 20 μ and the growth of *Mytilus edulis*, whereas Lassus et al. (comm. pers.), working in the Leucate pond, proved that a chrysophyceae 2 to 3 μ long at 3.2×10^6 cells per litre caused oysters to lose weight and even starve to death.

Location	Chlorophyll a µg.l⁻¹		Phaeopigments µg.l⁻¹		Σ µg.l⁻¹	% chloro-phyll a
Brest Harbour Station 5 RNO	m	2.14	m	0.53	2.67	80.1
	max	9.17	max	0.78		
Gulf of Morbihan Station 4 RNO	m	1.10	m	1.47	2.57	42.8
	max	4.20	max	2.52		
Marennes-Oléron Station 3 RNO	m	2.35	m	4.25	6.60	35
	max	10.08	max	12.2		
Arcachon Station 3 RNO	m	1.04	m	2.04	3.08	33
	max	1.6	max	6.6		
Thau Station 3 RNO	m	1.19	m	0.77	1.98	60
	max	4.00	max	1.63		
Ria de Arosa Tenore & Gonzales (1976)	m	7.9				
	max	40				
Lynher Estuary Widdows et al. (1979)	m	1.4				
	max	4.0				
Natal, South Africa Schleyer (1981)	m	2.13				
	max	3.88				
oyster claires Robert (1982)	m	5.12	m	4	9.12	79
	max	20	max	0.98		

<u>Table 3</u>:   Phytoplankton biomass estimated according to chlorophyll a and phaeopigment contents in selected mollusc-rearing areas

A number of experimental studies of mollusc nutrition have been under-taken to get a better idea of the action of phytoplankton and the quantities of phytoplankton molluscs need for growth, reproduction and metabolism. Walne (1970) showed that a great many algae (19) may form the basis for feeding juveniles of *Ostreae*, *Mercenaria* and *Mytilus*. This author later demonstrated (Walne, 1974) that mollusc growth is obtained·more rapidly using a mixture of 3 algae rather than one or two algae alone. During a num-ber of experiments being carried out in hatcheries, it became apparent that some algae, when found alone, did not cause any growth. Epifanio (1979), working on 15 diets based on 4 algae, found that size and weight increase were not correlated with total chemical composition nor with amino acid com-position, but rather depended on the rate and speed of digestibility of an alga based on its anatomy (theca) as well as concentrations of it in sto-mach contents (Romberger and Epifanio, 1981). Epifanio et al. (1976) never-theless also showed that *Thalassomia pseudorona* alone can support growth of

If we compare the various energy values found by different authors (Table 2), we may observe a certain consistency in the caloric content found in different ecosystems.

False Bay S.A.	Griffith (1980)	6.1 KJ g^{-1} ash-free seston
Linher Estuary G.B.	Widdows et al. (1978)	23.6 KJ g^{-1} protides, lipids, glucides
Ori Reef S.A.	Berry and Schleyer (1983)	19 KJ g^{-1} ash-free seston
Marennes-Oléron	Héral et al. (1980)	0.5 KJ g^{-1} seston 3.6 KJ g^{-1} ash-free seston 21 KJ g^{-1} protides, lipides glucides

Table 2: Energy values of 1 g of seston in selected shellfish ecosystems

- Phytoplankton

Phytoplankton contents follow a seasonal cycle that depends on temperature and on factors that control phytoplankton growth, in particular nitrates and phosphates. Phytoplankton biomasses may be followed by measuring chlorophyll or ATP, as well as by counting the number of phytoplankton cells. The most commonly used data are chlorophyll counts. Biomasses vary from year to year at a given site, depending on inflow from estuaries, and may also vary from bay to bay (Table 3). It may be noted that areas of intenstive mollusc culture show high phaeopigment contents, only 30% of the chlorophyll being active. From a methodological standpoint, this grazing action by molluscs means that phaeopigments must be carefully separated from chlorophylls. It may also be seen that, in areas where mollusc-rearing is the most intensive (Marennes-Oléron, Ria de Arosa), the highest phytoplankton biomasses are found.

It should be borne in mind that, in these coastal environments, the microphytobenthic biomass is from 2 to 25 times greater than the phytoplankton biomass (Zanette, 1980; Robert, 1982), and that any strong tidal currents or severe weather conditions will replace this surface film in suspension, thus making it available to filter-feeding molluscs.

To translate phytoplankton biomass into the energy equivalent, most authors use the factor Organic C = 60 chlorophyll a (Strickland, 1960), and then apply the average K-factor of 11.4 cal.mg^{-1} of organic carbon (Platt and Irvin, 1973). The same type of conversion may be applied to phaeopigments, since, although they represent cells that are in the process of breaking down (Héral et al., 1983), they may have the same nutritive value. It is desirable to study these phytoplankton biomasses according to their size and separate nannoplankton, at 3 μ to 20 μ, from phytoplankton at 20-100 μ and 100-250 μ,

Mercenaria mercenaria, and Flaak and Epifanio (1978) again used this alga, produced in different cultural conditions, with varying sizes and biochemical composition. These authors showed that *Crassostrea virginica* grows more rapidly with a culture medium that is richer in carbohydrates than in proteins. In parallel with these nitrition studies, work was done on an approach to use by molluscs of natural phytoplankton populations, and Héral et al. (1982) showed evidence for consumption of natural populations by *Ruditapes philippinarum*, while Nedhif (1984) described the exhaustion of phytoplankton in basins where this clam was being reared. Zanette and Garnier (1981) gradually eliminated the phytoplankton in claires by increasing the density of cultivated *Crassostrea gigas*, with oyster growth depending on the quantity of phytoplankton consumed.

- Energy balance

If we wish to establish the relation between quantity of food, whether dissolved or particulate, and the energy requirements of mollscs, it must be borne in mind that water masses are in constant movement due to currents flowing over culture areas, and thus bring in a flow of food that will depend on the speed with which the water mass moves. Héral et al. (1983) used the following formula to express this:

$$X = \frac{\displaystyle\sum_{i=1}^{n} X_i \cdot C_i}{n} \cdot T \cdot h$$

where X is the quantity of energy per m^2 and per day of the water column
   X_i is the quantity of energy in Kcal or Kjoules per m^3 of a sampling from a tidal cycle
   C_i is the instantaneous current at sampling
   n is the number of the sample
   T is the immersion time of the oyster population
   h is the height of water

This formula considers that the mollusc population feeds in a permanent manner during immersion, but many physiological studies have shown that molluscs adapt to discontinuous feeding, either due to immersion or imposed by feeding and digestion cycles (Langton and Gabbott, 1974; Owen, 1974). Langton and McKay (1976) obtained growth in *Crassostrea gigas* by adding food discontinuously, with 6 hours with food and 6 hours without. Higgins (1980) showed that *Crassostrea virginica* seems to be able to detect food levels, and that the quantity of food filtered depends directly upon the time the oysters are exposed to the food. Similarly, Epifanio and Ewart (1977) demonstrated periods of active filtration and periods of quiescence in *Crassostrea virginica*. Copello (1982) observed *Crassostrea gigas* to have a filtration rhythm that was synchronized with the tidal cycle. According to Morton (1970, 1977, 1983) and Langton and Gabbott (1974), tidal rhythm controls the crystalline style of *Ostrea edulis* and *Crassostrea gigas*, causing the crystalline style to dissolve after arrival of food with the rising tide, the substances ingested being digested extra- and intra-cellularly in a cyclical manner depending on the various enzymatic activities related to digestion (Boucaud-Camou et al., 1985). The rhythmic character of digestion thus appears to be a fact, but filtration could remain constant during the period of immersion for intertidal populations. It must, however, be determine what happens during neap tide periods or in tide-less waters, and whether filtration activity is cyclical. If this is the case, the equation above must be modified using a factor based on the duration of feeding.

1 YR OYSTERS

1979

```
WATER COL. 0.1m                      CONSUMPTION

Total food  e  ○

32 947 030 Kcal  ─────────────────►  0.06 %

Potent.food  tielle  ②

10 592 579 Kcal  ─────────────────►  0.19 %

Phytoplankton
            ○

5 961 903 Kcal  ─────────────────►  0.34 %
```

```
              Repro.182 Kcal
              ②    0.89 %

OYSTERS

Metab     : 4 317 Kcal
          21.18 %
            ②

Shell     : 281 Kcal
          1.38 %
            ○

Meat : 567 Kcal
       2.70 %
         ②
```

not consumed

```
   99.83 %
   99.81 %
   99.79 %
```

```
Faeces and
pseudofaeces

② 15 035 Kcal 73.77 %
```

2 YR OYSTERS

1980

```
WATER COL.0.1 m                      CONSUMPTION

Total food  ①
29 926 051 Kcal  ─────────────────►  0.09 %

Potent.food   ○
14 877 061 Kcal  ────────────────►  0.19 %

Phytoplankton
            ①
5 764 693 Kcal  ─────────────────►  0.48 %
```

```
              Repro. 936 Kcal
              ②    3,4 %

OYSTERS

Metab     : 7 353 Kcal
          26,4 %
            ②

Shell     : 213 Kcal
          ·0,8 %
            ②

Meat:     45 Kcal
          ② 0,2 %
```

not consumed

```
   99.66 %
   99.86 %
   99.42 %
```

```
Faeces and
pseudofaeces

② 19 277 Kcal 69,3 %
```
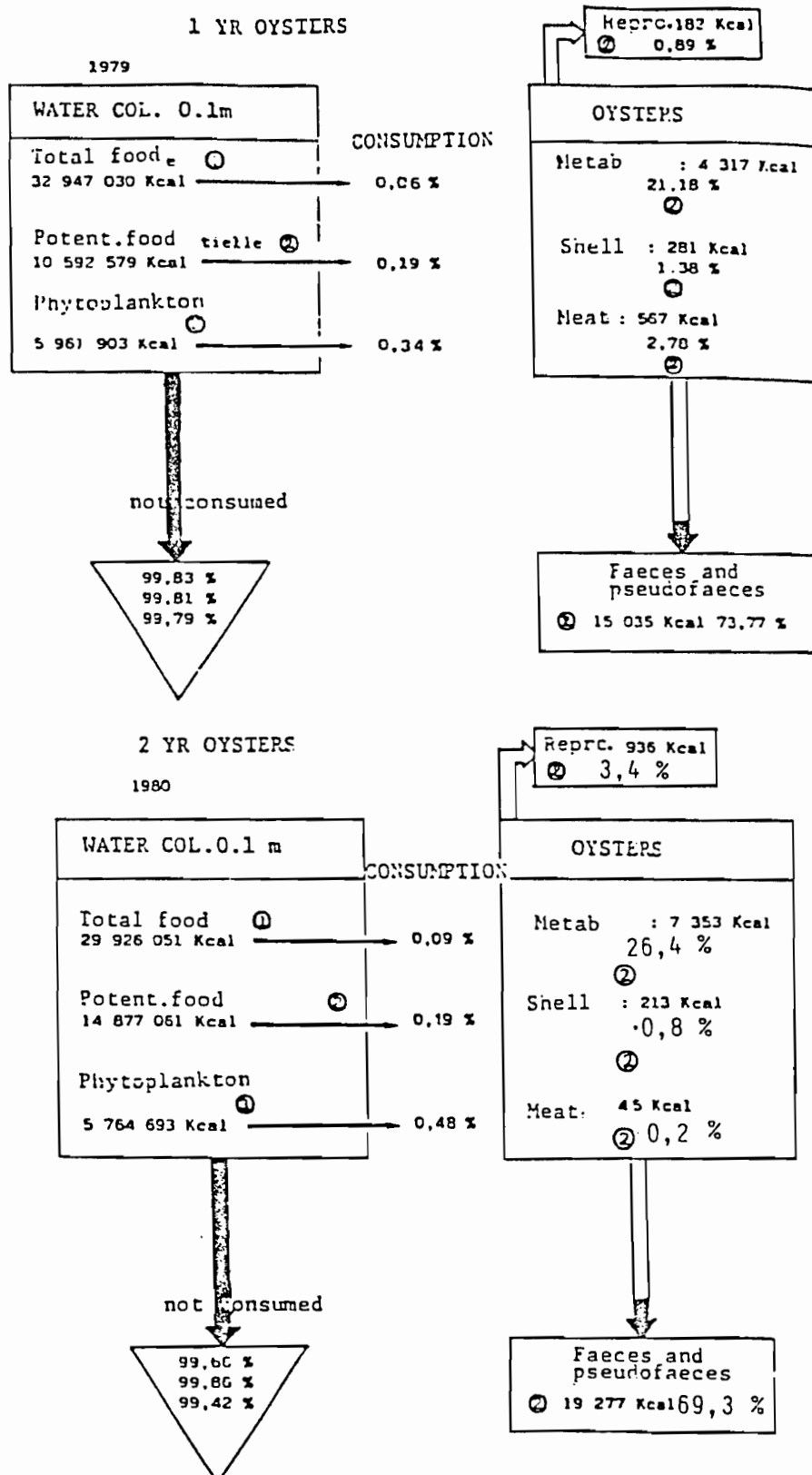
Figure 8: Annual energy flow between a 0.1 m water column transiting at a current of 0.3 m/s and a population of grown oysters at a density of 200 individuals/m^2 (after Héral et al., 1983, and Deslous-Paoli and Héral, 1984).

The relationship between this quantity of available energy and the energy balance of a population of *Crassostrea gigas* was established by Héral et al., 1983, and Deslous-Paoli and Héral, 1984). The energy flow between a water column and the energy balance of 1 m^2 of *Crassostrea gigas* under culture represents only 0.1% to 0.5% of the energy of the water column used by the oysters at an average current of 1 m s^{-1}. If we compare the percentage of phytoplankton use by bivalves at constant current for a constant biomass, it will be seen that, according to various authors, 13% to 90% of the chlorophyll a is filtered by the molluscs, depending mainly on the type of culture (on-ground or suspended).

The production capacity of a sector thus depends on the quantity of food available and mainly on current velocity (instantaneous velocity), but also on the general circulation of water masses in a basin, permitting the water volume used by the molluscs to be changed. This work, which includes a physical model of water mass circulation in a basin combined with a biological model of food consumption, has not yet been published.

authors + site	species biomass in dry weight per m^2	cultures distributed in water section of	% of chlorophyll a retained	current	% retention per m^2 for current of 1 m/s with dry biomass of 1 kg	% retention per m^3 for current of 1 m/s with dry biomass of 1 kg
Héral et al. (1983) Marennes-Oléron (France)	*C. gigas* adult 261 g	0.1 m	2.4%	0.7 m/s	13.1	1.31
Deslous-Paoli and Héral(1984) Marennes-Oléron (France)	*C. gigas* juvenile 65 g	0.1 m	1.5%	0.7 m/s	32.9	3.9
recalculated after Cabanas et al. (1979) Ria de Arosa (Spain)	*M. edulis* 2 yr. 13 250 g	8 m	60%	0.05 m/s	90.6	11.3
Recalculated after Rodhouse et al. (1985) Ireland	*M. edulis* 2 yr 20 000 g	10 m	47%	0.1 m/s	23.5	2.35

Table 4: Percentage of phytoplankton retained by oysters and mussels in selected ecosystems for 1 ms^{-1} current and dry biomass of 1 kg

Apart from the specific model-building problems involved, construction of this model brought with it a number of problems with respect to estimating the carrying capacity of ecosystems.

a) taking into account the food regeneration rate: primary phytoplankton and bacteria production during residual movement of water masses,

b) recycling and reutilization of organic matter from faeces and pseudo-faeces,

c) measurement of biomasses and production over the entire sector under study, which underlies an appropriate sampling strategy, with in particular constant measurements to the limits of the model of the phytoplankton biomass with variations according to day, tides and inflow from estuaries.

Data published to date on the carrying capacity of rearing basins are often more precise as concerns the energy requirements of molluscs, but are still somewhat sketchy with respect to the quantity of food available, with only a few stations normally being studied on a monthly basis. There is considerable trophic variability in these coastal environments, and daily variations in tidal seas is often greater than seasonal variation for a number of papameters. Sampling spread out over a large number of stations makes it possible to assigned to each bay sector a different nutritive value, which is of course well known to operators. Thus any general observations on trophic relations must be obtained through sampling of the characteristics of each bay over a period of time and at various locations.

To conclude this rapid overview of the state of research on determining the trophic value of ecosystems for mollusc production, we may propose the following recommendations:

- improve strategies for sampling nutrients,

- include in energy balance calculations the contribution of nitrogenated and carbonated dissolved organic substances,

- greatly increase the number of current measurements and the number of physical models of residual circulation of water masses,

- examine the recycling of bio-deposited organic matter by molluscs being cultivated,

- seek to develop continuous measurement of phytoplankton biomasses (fluorimeter) and primary production (DCMU)

- develop studies of phytoplankton biomasses according to particle size, with emphasis on nannoplankton,

- increase measurements of in situ consumption rates in ecosystems with weak current regimes.

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