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Simulating physiological responses of cockles (*Cerastoderma edule*) to variable conditions within estuarine media

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Abstract

A physiological model has been developed to provide a simulation of scope for growth responses of cockles *Cerastoderma edule* to environmental factors such as temperature and seston parameters. As in previous treatments, model structure consisted of a series of equations representing the various physiological processes which are integrated in the energy balance of filter-feeders. Unlike these treatments, however, the present model was designed to give account of the separate processing of phytoplankton and detritus, as components of suspended food that are submitted to differential selection and absorption. In this way, effect of quality indexes based on phytoplankton abundance on growth rates could be explored. Subsequently, we have applied this model to: (a) simulating scope for growth under conditions subjected to variation in the estuarine media, and (b) predicting growth variability as a function of food regime, by comparing two particular estuaries with contrasting seston characteristics.

Keywords: *Cerastoderma edule*, physiological model, scope for growth, phytoplankton, detritus, estuarine media.

Simulación de la respuesta fisiológica del berberecho Cerastoderma edule *frente a condiciones variables en el medio estuarino.*

Resumen

El presente trabajo desarrolla un modelo fisiológico susceptible de simular el crecimiento potencial del berberecho *Cerastoderma edule* sometido a condiciones variables de temperatura y composición del seston. A semejanza de otros tratamientos previos, la estructura del modelo incluye una serie de ecuaciones representativas de los diferentes procesos fisiológicos que se integran en el balance energético de los filtradores suspensívoros. Sin embargo, difiere de estos otros tratamientos en el hecho de haber sido diseñado para poder formalizar la utilización digestiva del fitoplancton y los detritos como procesos diferenciados, donde cada uno de estos componentes del alimento presenta sus propias eficiencias de selección y absorción. Esta característica permite establecer índices de calidad nutricional basados en la abundancia fitoplanctónica, tomando como referencia los efectos sobre el crecimiento. Se han desarrollado las siguientes aplicaciones concretas del modelo: (a) Simular valores de crecimiento potencial correspondientes a condiciones ambientales típicamente variables en los sistemas estuarinos. (b) Efectuar predicciones de crecimiento en dos estuarios concretos con características del seston altamente diferenciadas al objeto de elustrar el tipo de dependencia existente entre crecimiento y régimen nutricional.

Palabras clave: *Cerastoderma edule*, modelo fisiológico, crecimiento potencial, fitoplancton, medio estuarino.

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INTRODUCTION

This contribution come within the context of a multidisciplinary effort whose common objective is to establish some methodological principles to evaluate carrying capacity of estuaries where cultivation of suspension-feeding molluscs takes place. In dealing with these complex dynamic systems, the understanding of relationships between nutritional parameters of seston and associated physiological responses constitutes a basic requirement. Thus, physiological processes underlying the successive energy interchanges within the organism could be measured and arranged in a model of the bivalve's energy budget.

Available models of growth in bivalves have been generally based on a set of relationships accounting for rates and efficiencies of operations involved in the processing of particulate food (filtration, ingestion and absorption) and metabolic rates, as a function of temperature and food environment (Bacher *et al.*, 1996; Grant *et al.*, 1993; Herman *et al.*, 1993). Recent development in such ecophysiological modelling has taken advantage of extensive information concerning physiological behaviour of species of bivalves under natural food conditions linked with precise characterisation of seston. These attempts, undertaken by the TROPHEE group within the context of an EEC project (see Hawkins *et al.*, 1996; Iglesias *et al.*, 1996; Soletchnik *et al.*, 1996; Urrutia *et al.*, 1996), made evident the strong dependence of growth on food quality, a variable this scarcely taken into consideration. Commonly represented in its simplest form, as the organic content of food suspensions, it is our conviction that additional precision in growth predictions could be gained by applying more specific indices of quality.

In this respect, increasing evidence indicates different components of food, namely phytoplankton and organic detritus, can be selected and absorbed with different efficiencies. Consequently, we have developed a physiological model for cockles (*Cerastoderma edule*) leading to scope for growth estimates in which feeding and digestive processing of phytoplankton and detrital material have been independently considered. The output from this model was then used to simulate growth responses under different scenarios which consisted of particular combinations of environmental variables.

Present objectives do not include model calibration against factual growth data, but focus rather on providing growth trend-simulations, under variable values of specific factors naturally subjected to intense fluctuations in the estuarine media. According to the most recent improvements of the model, specific emphasis has been laid on exploring model responses to changing food quality, this defined in terms of chlorophyll abundance rather than organic content.

MATERIAL AND METHODS

Environmental parameters used as the input variables to the model are presented in Table 1.

The structure of the model consisted of a sequence of physiological equations accounting for the successive components of the energy budget in cockles (Table 1). When possible, the form of these relationships was based on theoretical considerations; alternatively, observed trends exhibited by data provided adequate design of the function. Coefficients were then obtained by statistical fitting of data with these equations, using least squares procedure. When required, data were size standardized to a 500 mg dry flesh weight using the appropriate allometric coefficients (Iglesias *et al.*, 1996).

Environmental effects on clearance rate were introduced in two steps:

– Temperature effects were entered by means of crt, and the corresponding expression relating clearance rate to temperature was obtained by fitting seasonal data taken from Larretxea (1995) with a semilogarithmic equation. To introduce these thermal effects under a relative form, crt was converted to an index (crr) representing the fraction of the clearance rate recorded with the optimum temperature (*i.e.* 1.2 litres per hour).

– Dependence of clearance rate on food parameters (as represented by cr) was treated as an exponential function of tpm and f. The expression resulted from fitting an extensive pool of data that has been already reported (Iglesias *et al.*, 1992, 1996; Urrutia *et al.*, 1996). The clearance rate corrected for temperature effects (*i.e.* cr × crr) was then applied to compute filtration rate.

The rejection rate has been shown to depend significantly on the filtration rate and the organic content of food (data set reported by Iglesias *et al.*, 1992, 1996; Urrutia *et al.*, 1996).

Specific experiments were performed to measure mucus losses associated with pseudofaeces rejection. Diets used were a mixture of ashed silt (inorganic particles) and phytoplankton, and organic enrichment due to mucus computed from comparing chlorophyll contents with organic content of pseudofaeces. These data (mucus) were subsequently related to the rejection rate by means of a power function.

Selection efficiency data were appropriately described as a polynomial function of food organic content. Differential expressions for selection of algal cells and detritus were obtained from specifically designed experiments. Selection efficiency of algae was explored by means of diets composed of phytoplankton and inorganic particles and efficiencies were computed, according to Navarro *et al.* (1992), from the chlorophyll contents in food and pseudofaeces. For selection efficiency of detritus, diets included detritus obtained from *Spartina* sp. and inorganic particles, and

Table 1. – Classification of parameters used in this study and equations considered in this model.

Definition	Units	Abbreviation
Environmental parameters		
Temperature	°C	t
Total particulate matter	mg.l^{-1}	tpm
Particulate organic matter	mg.l^{-1}	pom
Organic content of suspended food	–	f
Chlorophyll concentration	µg.l^{-1}	Chl.
pom of algal origin	mg.l^{-1}	poma
pom of detrital origin mg.l^{-1}	mg.l^{-1}	pomd
Equations		
$f = pom/tpm$		
$poma = 0.04\ Chl.$		
$pomd = pom - poma$		
Physiological parameters		
Clearance rate	l.h^{-1}	crt, cr
Filtration rate	mg.h^{-1}	fr
Rejection rate	mg.h^{-1}	rr
Mucus production	mg.h^{-1}	mucus
Ingestion rate	mg.h^{-1}	ir
Selection efficiency of algae	–	sea
Selection efficiency of detritus	–	sed
Organic filtration	mg.h^{-1}	of
Filtration of algae	mg.h^{-1}	af
Filtration of detritus	mg.h^{-1}	df
Ingestion of algae	mg.h^{-1}	ai
Ingestion of detritus	mg.h^{-1}	di
Organic ingestion	mg.h^{-1}	oi
Organic content of ingested food	–	i
Absorption efficiency of algae	–	aea
Absorption efficiency of detritus	–	aed
Absorption rate	mg.h^{-1}	ar
Absorption rate	mg.h^{-1}	nar
Net absorption rate	J.h^{-1}	r
Metabolic rate	J.h^{-1}	sfg
Scope for growth		
Equations		
$crt = -1.463 + 0.980\ t$		
$crr = crt / 1.2$		
$cr = e^{(0.216 + 1.743\ f + tpm\ (0.0254 - 0.306\ f))}$		
$fr = crr \times cr \times tpm$		
$rr = -2.002 + 1.033\ fr - 1.004 \times fr \times f$		
$mucus = 0.046\ rr^{0.817}$		
$ir = fr - rr$		
$sea = 0.925 - 0.304\ f - 0.712\ f^3$		
$sed = 0.579 - 0.595\ f - 1.644\ f^3$		
$of = fr \times f$		
$af = of \times (poma/pom)$		
$df = of \times (pomd/pom)$		
$ai = af \times sea + (1\text{-}sea) \times ir \times (af/fr)$		
$di = df \times sed + (1\text{-}sed) \times ir \times (df/fr)$		
$oi = ai + di$		
$i = oi/ir$		
$aea = 0.769 - (0.024/i)$		
$aed = 0.693 - (0.047/i)$		
$ar = ai \times aea + di \times aed$		
$nar = ar - mucus$		
$r = e^{(0.047 + 0.053\ t + 0.034\ nar)}$		
$sfg = 20\ nar - 1.1\ r$		

efficiencies were computed from the organic contents in food and pseudofaeces, then corrected for mucus production. Third order polynomials were then fitted to these data by multiple regression analysis.

The organic filtration is the organic fraction of filtered material, subsequently used to compute the filtration rates of phytoplankton and detritus from its corresponding fraction in the particulate organic matter.

Ingestion rates of both algae and detritus were computed from the corresponding filtration rates and selection efficiencies of both components, plus the ingestion: filtration ratio. Formulae were derived according to methods given in Iglesias *et al.* (1992). By adding both these components, ingestion rate of total organics was obtained, from which the organic content of ingested matter could be calculated as a quality index for the food incorporated into the digestive system.

Following theoretical considerations, absorption efficiency was defined as a hyperbolic function of this organic content of the ingested ration. Hyperbolic functions were thus used to fit absorption efficiency data for phytoplankton and detritus, which were obtained in the course of experiments with diets of variable organic content and where the sole organic component was either phytoplankton or detritus elaborated from *Spartina* sp. The absorption rate of algal and detrital components were obtained as products of the corresponding ingestion rate and absorption efficiency; both components summed together give the total absorption. Finally, net rate of absorption was calculated as absorption rate minus mucus production.

Metabolic rate was modelled as an exponential function of both temperature and the net rate of absorption by using an extensive set of data on oxygen consumption (Navarro *et al.*, 1994; Iglesias *et al.*, 1996). To compute total metabolic expenditures, a 10 % increment on r was considered to account for ammonia excretion (Bayne and Newell, 1983).

By assuming an energy conversion factor of 20 J per mg. organic matter, net absorption can be converted into Joules, and scope for growth computed as this absorbed energy minus total metabolic expenditures.

RESULTS

Simulating growth responses to variable conditions

The above physiological model was used to simulate growth responses of cockles to environmental conditions within the estuarine media. To achieve this, seston parameters (tpm, pom and Chl.) were considered to fluctuate along a tidal cycle according to a standard profile which was based on a combination of data from Marennes-Oleron Bay in France (Prou *et al.*, 1994) and Oosterschelde in Holland (Smaal *et al.*, 1986) to reproduce the time-course of turbidity induced by tidal currents. Organic contents of the seston and chlorophyll concentration values used in this simulation were taken from the last site, while total particle load was maintained at half the seston concentration of that rather turbid estuary.

The foregoing premises led to reference values (Table 2) upon which three sources of variation were assayed: temperature, chlorophyll abundance and tidal emersion.

– Temperature effects were measured at 7, 12 and 17 °C, which covers a central range in temperate estuaries.

– Effects of changing chlorophyll abundance were analysed by halving and doubling the chlorophyll concentration values given in Table 2, while maintaining tpm and pom. In this way we have simulated variable proportions of phytoplankton in total pom.

– Variable periods of tidal exposure (0, 25 and 50 % of the tidal cycle) were considered in order to explore the consequences of occupying different shore heights. In these computations we have assumed that seston parameters would depict the same tidal profile, irrespective of shore position, with changes lasting progressively less towards the upper shore. Under this assumption, assimilation would simply result a direct function of the immersion time. As for metabolism, we have considered, according to Iglesias and Navarro

Table 2. – Reference values for total particulate matter (tpm), particulate organic matter (pom) and chlorophyll concentration (Chl.) used to simulate physiological responses of cockles over a tidal cycle (see text for explanation).

Time (h)	tpm ($mg.l^{-1}$)	pom ($mg.l^{-1}$)	Chl. ($\mu g.l^{-1}$)
1	14.89	1.77	3.41
2	16.04	1.87	3.35
3	17.23	2.01	3.30
4	24.80	2.74	3.90
5	32.45	3.49	4.51
6	29.15	3.22	4.97
7	25.56	2.84	5.43
8	25.52	2.81	6.12
9	25.66	2.84	6.82
10	24.99	2.70	5.22
11	24.52	2.63	3.63
12	21.69	2.36	3.56

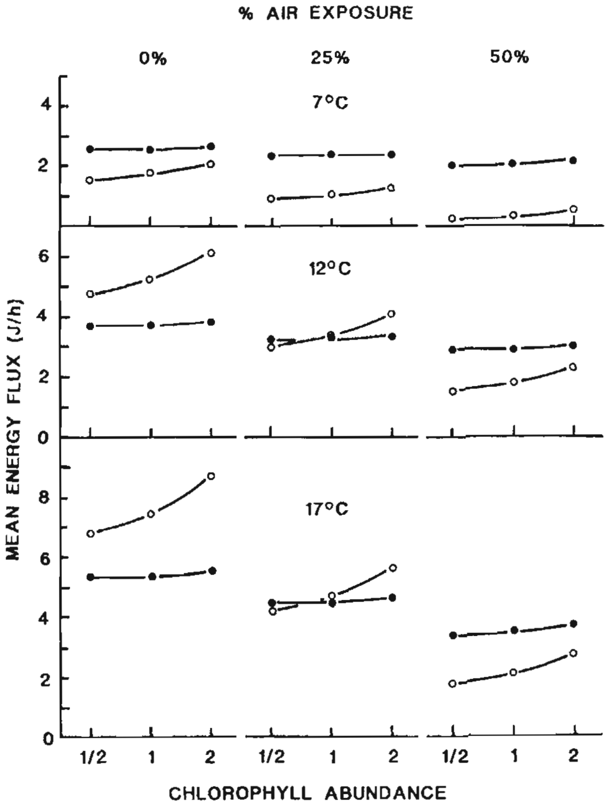

Figure 1. – Net absorption (hollow simbols) and metabolism (full simbols) of cockles (*Cerastoderma edule*), as a function of chlorophyll abundance, temperature and tidal exposure. Conditions for tidal simulation are represented by values given in Table 2.

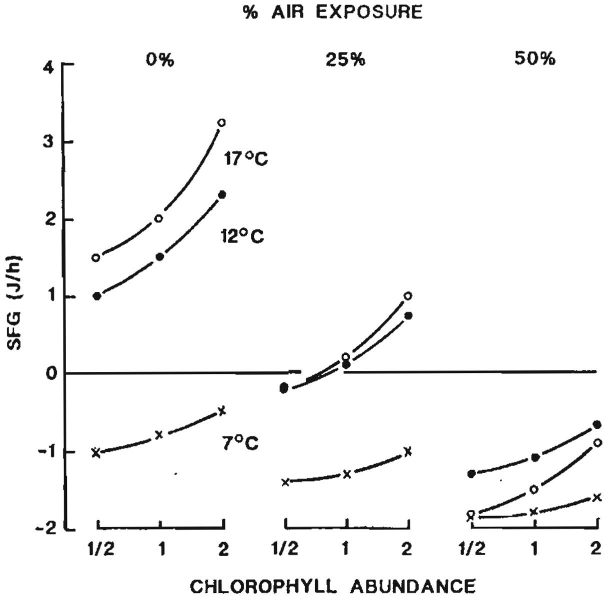

Figure 2. – Scope for growth of cockles (*Cerastoderma edule*) as a function of chlorophyll abundance, temperature and tidal exposure. Conditions as in Figure 1.

(1991), that tidal exposure reduces respiration to 0.7 the aquatic rate.

Figure 1 shows mean values of inward (absorption) and outward (metabolism) energy fluxes within the organism, as a function of chlorophyll abundance, temperature and percent air exposure. Scope for growth has been represented in Figure 2 as an integrated measurement of the balance between both these fluxes.

A case for application to particular estuaries

The physiological model was subsequently applied to predict growth under contrasting natural food regimes. To keep this simulation within realistic limits we have made use of seston data for a full tidal cycle recorded in two quite different estuaries: The Oosterschelde in Holland (Smaal *et al.*, 1986) and the Ría de Arosa in Spain (Nunes *et al.*, 1984 and own

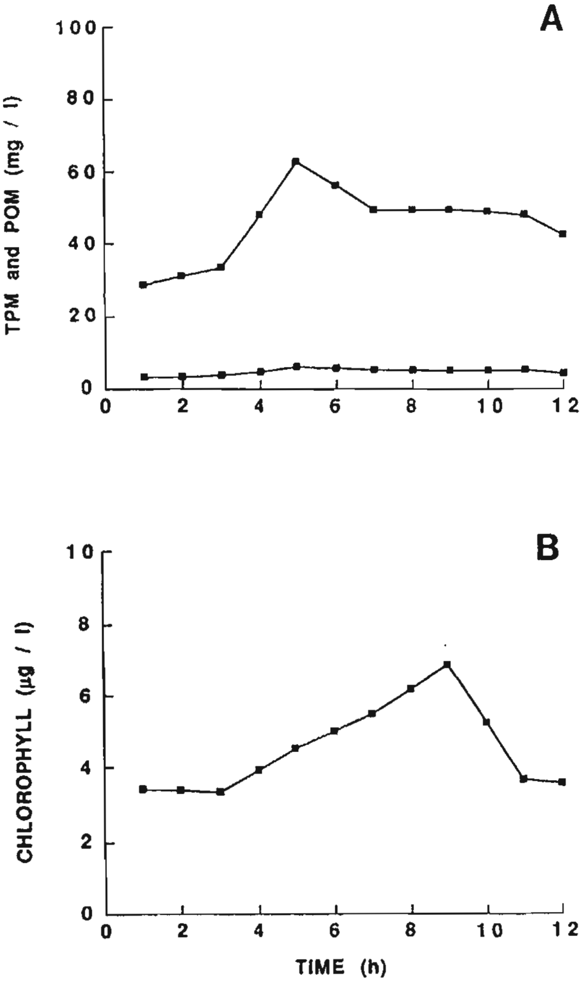

Figure 3. – Tidal variations of (A) total particulate matter (TPM) and particulate organic matter (POM) (upper and lower lines, respectively) and (B) Chlorophyll concentration, in the Oosterschelde estuary (The Netherlands). Data taken from Smaal *et al.* (1986).

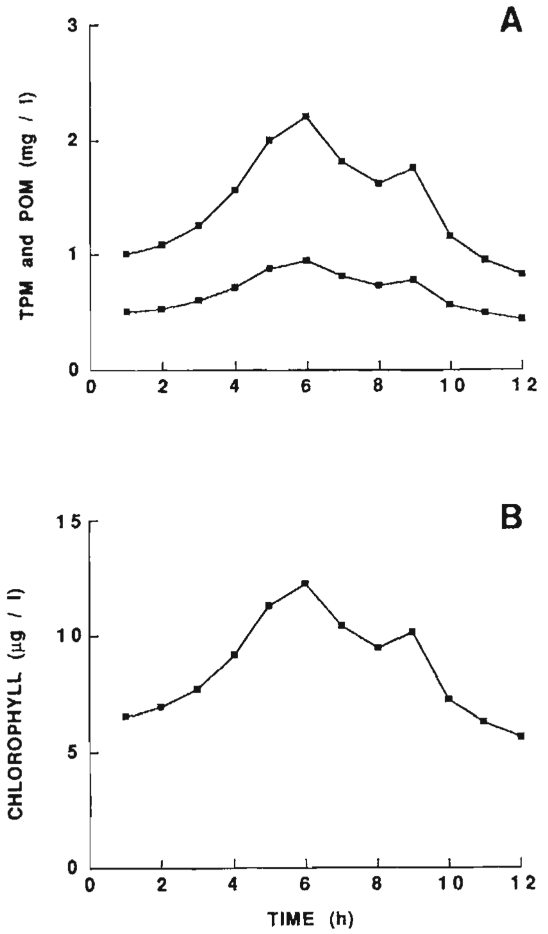

Figure 4. – Tidal variations of (A) total particulate matter (TPM) and particulate organic matter (POM) (upper and lower lines, respectively) and (B) Chlorophyll concentration, in the Ría de Arosa (Spain). Data taken from Nunes *et al.* (1984).

unpublished results). Differences are clearly shown by comparing seston data from Figures 3 and 4: tpm in Oosterschelde is some 30 to 50 times that in Arosa. Thus, in spite of much lower organic content in the former (mean 10 %, compared with 45 % in Arosa), total organic availability (pom) is about 7 times higher in Oosterschelde. However, phytoplankton availability (as computed from chlorophyll concentration) is as much as two times greater in Arosa, meaning that the proportion of phytoplankton in total pom is much higher in this estuary (52 %) than in Oosterschelde (3 % to 5 %). Tidal profiles for absorption and metabolism of cockles under the seston conditions prevailing in Osterschelde and Arosa are shown in Figures 5 and 6, respectively.

DISCUSSION

Beside the development of a novel physiological model suitable for growth computation in cockles, aims of the present work were:

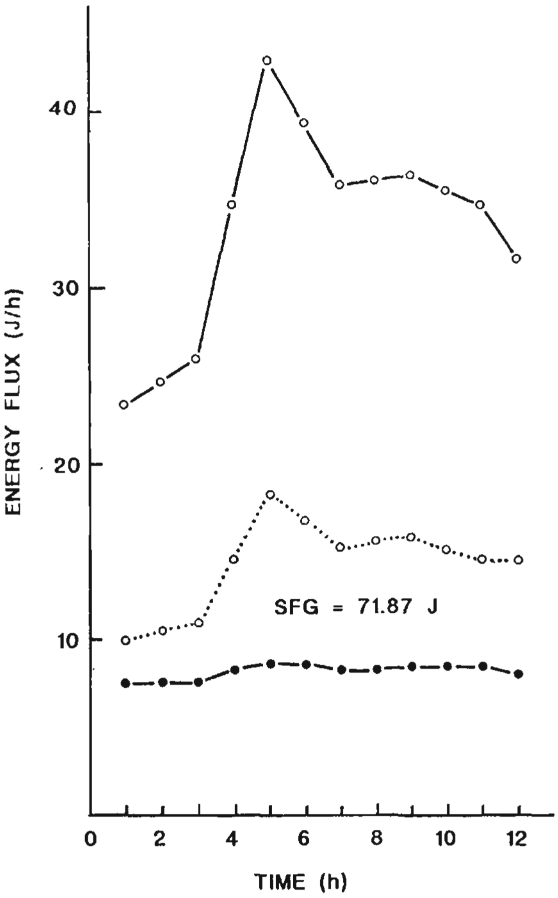

Figure 5. – Tidal variations of absorption (hollow simbols) and metabolism (full simbols) of cockles (*Cerastoderma edule*) under the conditions of Oosterschelde estuary. Continuous line: ar; dotted line: net absorption rate (nar) (*see* Material and methods).

a) To use the model as a tool for predicting the effects, in terms of growth rates, of those factors that are common sources of environmental variability in the estuarine media; namely, chlorophyll abundance, temperature and tidal air exposure.

b) To help understanding of the physiological basis underlying differences in growth rate among sites exposed to contrasting seston characteristics (*see* Smaal *et al.*, 1986 and Pérez-Camacho and Román, 1984)

With respect to the first aspect, a consideration of data presented in Figures 1 and 2 leads to the following conclusions:

1 – Strong positive effects on growth would be expected from an increment in the chlorophyll abundance. This might contribute to an explanation of the many instances in which outstandingly high rates of growth recorded in the spring cannot be accounted for by temperature or total organics' availability. Slopes of this relationship exhibit positive thermodependence, implying that temperature would tend to reinforce the beneficial effect of an increased

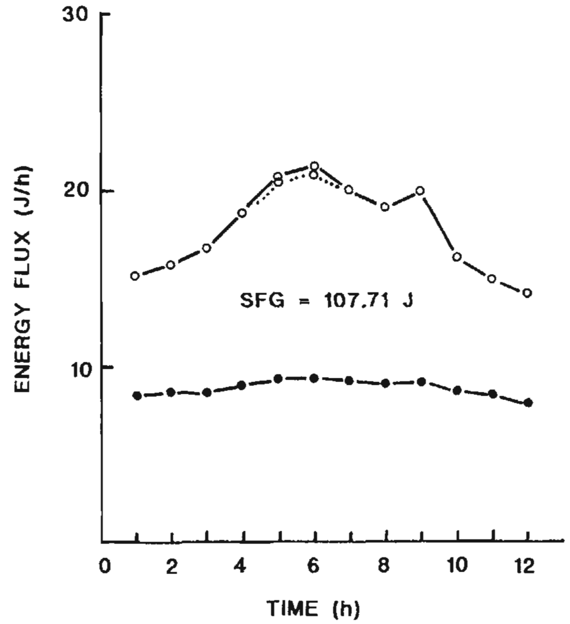

Figure 6. – Tidal variations of absorption (hollow simbols) and metabolism (full simbols) of cockles (*Cerastoderma edule*) under the conditions of Ría de Arosa. Continuous line: ar; dotted line: net absorption rate (nar) (*see* Material and methods).

proportion of phytoplankton in the diet, possibly through positive thermal effects on clearance rate.

2 – Through a direct reduction of assimilation, tidal exposure would cause growth to change from positive values for most temperatures, at 0 exposure, to negative at 50 % exposure, irrespective of temperature or chlorophyll abundance.

3 – In general, reduced temperatures would be growth limiting, but thermal effects have to be analysed in combination with assimilation rate. At high to moderate levels of assimilation (0 to 25 % air exposure), increasing temperature tends to increase growth potential. However, below a certain level of assimilation (as resulting from 50 % exposure in the present simulation), the optimum temperature would be reduced (from 17 to 12 °C, in this case). This kind of interaction between temperature and ration is a well known physiological trait of mussels (*Mytilus edulis*) under conditions of SFG determination in the laboratory (Thompson and Bayne, 1974).

As to the second aspect, a comparison of Figures 3 and 4 shows that the main differences between Oosterschelde and Ría de Arosa are those of a higher food availability in the former, but of a much lower quality, both in terms of organic content and phytoplankton abundance. Hence, comparison of growth rates predicted at these contrasting sites are of interest from the perspective of exploring sensitivity of the physiological components of growth to the main sources of variation encountered by bivalves in their food environment.

The two measurements of absorption provided by the model were plotted to illustrate the magnitude of endogenous energy losses involved in pseudofaecal production. Given its high seston loads, these mucous losses are quite large in Oosterschelde, becoming greater than net absorption rates (Fig. 5). Even if these losses are normally overcome by benefits of selection (otherwise, selection efficiency would be negative), we have considered it important to discuss this point in order to illustrate the enormous potential for saving energy which is inherent to any possibility of improving selection efficiency. This consideration would help to understand inter or intraspecific differences in selection efficiency, in the perspective of adaptation to turbid environments.

While preingestive selection for organics could fully compensate for reduced organic contents of seston recorded at Oosterschede, there is not such compensation for reduced phytoplankton abundance. Preingestive selection and absorption of phytoplankton occurs with increased efficiency as compared with detritus. From this behaviour derives a greater potential for growth improvement in media of high primary production. According to the present simulation, scope for growth values computed for Arosa would exceed by 50 % those in Oosterschelde, this difference being mainly caused by the fact that phytoplankton constitutes a greater proportion of POM in Arosa, rather than being the effect of a higher organic content of the seston.

As a conclusion, the separate consideration of phytoplankton and detritus as differentiated components of suspended organic matter, though introducing some additional complexity into physiologial formulations, would allow more precise account to be taken of differences in growth between sites with contrasting seston characteristics. Additionally, growth trends actually recorded appear well described by this approach (Parra, 1995), whose requirements in terms of environmental input are quite simple and commonly available from standard seston recording.

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