Application of a dynamic energy budget model to the Pacific oyster, *Crassostrea gigas*, reared under various environmental conditions

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Received 25 November 2005; accepted 20 March 2006
Available online 6 April 2006

Abstract

The Dynamic Energy Budget (DEB) model (Kooijman, S.A.L.M., 1986. Energy budgets can explain body size relations. J. Theor. Biol. 121, 269–282; Kooijman, S.A.L.M., 2000. Dynamic Energy and Mass Budgets in Biological Systems. Cambridge University Press, Cambridge, 424 pp.) has been adapted to describe the dynamics of growth and reproduction of the Pacific oyster (*Crassostrea gigas*) reared in different areas under conditions ranging from controlled to natural. The values of the model parameters were estimated from available physiological data and from published information. The sets of data used to validate the model came from three long-term growth experiments (>5 months) performed on Pacific oysters reared under different conditions of food and environment. The forcing variables were temperature and phytoplankton densities, the latter being assessed from in vivo fluorescence and chlorophyll-a concentration measurement. The successful validation of the model on the three data sets demonstrated its ability to capture the dynamics of the energy budget in the Pacific oyster in various environments with the same set of parameters. The only parameter that varied between simulations was the half-saturation coefficient (XK), because of a different diet composition between the three environments under test. The model successfully reproduced quantitatively the growth and reproduction and the timing of spawning. These first simulation data led us to propose several promising perspectives of application for this model in shellfish ecosystems.

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Keywords: *Crassostrea gigas*; Dynamic energy budget; Ecophysiology; Growth; Reproduction; Reproductive effort

1. Introduction

Marine bivalves, and especially the Pacific oyster *Crassostrea gigas*, are economically important in French aquaculture. Exceeding 109 million kg in 2001 (Girard et al., 2001), the production of this species has become a major industry on the French coasts. As a consequence, oysters are often dominant in terms of biomass in several shellfish areas and form an integral part of the ecosystem in which they occur. These constraints have prompted the necessity for tools to
understand ecological processes in shellfish ecosystems and to help management of the oyster farming. Understanding of the interaction between this species and its environment could be facilitated through the development of ecological models (e.g. Héral, 1991).

The last fifteen years have seen the development of numerous energetic models that explain the growth of molluscs according to their environment, i.e. temperature and food supply. Most of them are net-production models based on the Scope for Growth concept (Bayne, 1976). They use a detailed empirical sequence of steps for nutrition and resource allocation, based on allometric relationships, and assume that assimilated energy is immediately available for maintenance, the rest is used for growth or stored as reserves (e.g. Bacher et al., 1991; Powell et al., 1992; Schneider, 1992; Raillard et al., 1993; Barillé et al., 1997; Grant and Bacher, 1998; Scholten and Smaal, 1998; Ren and Ross, 2001). Some of the models developed for bivalves are more mechanistic (Ross and Nisbet, 1990; Van Haren and Kooijman, 1993; Cardoso et al., 2001; Ren and Ross, in press). They are based on the dynamic energy budget or DEB theory proposed by Kooijman (1986) and extensively discussed in Kooijman (2000). DEB models differ from net-production models in several aspects. They assume that assimilated energy is first stored in reserves, and reserves are utilised to fuel other metabolic processes (maintenance, growth, development and reproduction). DEB models do not use empirical allometric relationships, but simply state that feeding is proportional to surface area whereas maintenance scales to structural body volume. More generally, DEB theory aims for a generic theory of energy budgets that assumes common physiological processes across species and life stages via a set of common DEB parameters, the only difference between species lying in the value of these parameters. These promising considerations led us to conduct investigations to apply the DEB model proposed by Kooijman (2000) to catch and simulate the life history (namely growth and reproduction) of C. gigas under different environmental conditions from controlled to natural ones.

The first problem in building such a model lies in the estimation of the DEB parameters. Most of them were previously assessed for the Pacific oyster by Van der Veer et al. (2006) independent of this study. Our contribution was aimed at checking the generic property of these parameters to determine whether their assessment of DEB parameters was sufficient to model oyster growth in various environments and for different populations. We also wondered whether the intra-specific differences are so great that the DEB parameters need to be recalculated for each new population and/or new environment.

A second problem lies in the diversity of the sources of food (phytoplankton, protozoa, micro-zooplankton, bacterial aggregates, detritical organic matter etc.) as well as its dilution in seston by mineral particles. The exact determination of ingestion fluxes is, thus, very hazardous because of the difficulty to monitor food and ascertain its origin. Energy allocation can be prejudicially affected by this lack of information. To overcome these problems and develop a generic model for C. gigas, we have designed a DEB model and we have tested it on several populations of oysters reared under conditions clearly identified through daily or weekly measurements of water temperature, salinity, oxygen concentration as well as food quality and phytoplankton concentration. This paper is focused on oysters after metamorphosis, i.e. juvenile and adult stages; embryonic and larval stages are not considered.

2. Material and methods

2.1. DEB model

The dynamic energy budget model used in this study is developed on the basis of DEB theory (Kooijman, 1986, 2000) and is depicted in Fig. 1. It includes some specific extra parameters needed to model the bioenergetics of the Pacific oyster. According to Kooijman (2000), the dynamics of growth and reproduction can be fully described by three differential equations: the first one specifies the growth of the structural body volume, $V$, the second one describes the dynamics of the energy reserves, $E$, and the third one deals with the storage and use of the energy allocated to development and reproduction, $E_R$.

Food uptake is assumed to be: (i) follow a type-II Holling function response depending on food density $X$ (expressed in µg chl-a l$^{-1}$ in this study) and (ii) be proportional to the surface area of the structural body volume ($V$; cm$^3$); thus, the ingestion rate $J_X$ (mg d$^{-1}$) can be written as:

$$J_X = \left\{J_{Xm} \right\} \cdot f \cdot V^{2/3} \text{ with } f = \left(\frac{X}{X + X_K}\right)^\theta$$

(1)

where $f$ is the scaled functional response (dimensionless), $X_K$ is the saturation coefficient or Michaelis-Menten constant (µg chl-a l$^{-1}$) and $\{J_{Xm}\}$ the area-specific maximum ingestion rate, expressed in mg d$^{-1}$ cm$^{-2}$. As a first approximation, the absorption efficiency ($ae$, dimensionless) and the food-energy conversion
\( \mu_X \) (J mg\(^{-1}\)) are assumed to be constant, and consequently the assimilation energy rate, \( \dot{p}_A \), i.e. the total energy input per individual, becomes:

\[
\dot{p}_A = a \epsilon \mu_X \cdot \dot{J}_X = a \epsilon \mu_X \cdot \left\{ \dot{J}_{Xm} \right\} \cdot f \cdot V^{2/3}
\]

where \( \left\{ \dot{J}_{Xm} \right\} \) is defined as the area-specific maximum assimilation rate and is expressed in J d\(^{-1}\) cm\(^{-2}\).

Because of the energy conservation law, the dynamics of the reserve can be written as:

\[
\frac{dE}{dt} = \dot{p}_A - \dot{p}_C
\]

(3)

where \( \dot{p}_C \) denotes the energy consumed (fixed and dissipated) by the body tissues; it is called the catabolic power or utilisation rate. Kooijman (2000, chapter 3.4) showed that \( \dot{p}_C \) can be written as:

\[
\dot{p}_C = \frac{[E]}{[E] + \kappa \cdot [E]} \left( \frac{[E_G] \cdot [\dot{J}_{Xm}] \cdot V^{2/3}}{[E_m]} + [\dot{p}_M] \cdot V \right)
\]

(4)

When combined with Eqs. (2) and (4), Eq. (3) fully describes the dynamics of the reserve, \( E \), necessary to establish this model. In formula (4), \([E]\) corresponds to the energy density in an organism. It is defined as \( E/V \) and expressed in J cm\(^{-3}\); according to the food density in the environment it may vary between 0 J cm\(^{-3}\) and the maximum energy density \([E_m]\). The parameter \( \kappa \) corresponds to a fixed fraction of the utilisation rate, \( \dot{p}_C \), which is spent on growth plus maintenance, with maintenance having priority (the rest, \( 1-\kappa \), is allocated to development (maturity) and reproduction (gametes) plus maturity maintenance). \([E_G]\) denotes the volume-specific cost for growth (J cm\(^{-3}\)), a constant for structural mass including all types of overheads, and not only the costs of biosynthesis. \([\dot{p}_M]\) denotes the volume-specific maintenance rate (J cm\(^{-3}\) d\(^{-1}\)).

Maintenance \( \dot{p}_M \) (J d\(^{-1}\)) stands for a collection of processes necessary to ‘stay alive’. For example, in the case of the Pacific oyster, it includes the maintenance of concentration gradients across membranes, the osmo-regulation, the turnover of structural body proteins, a certain level of muscle tension and movement for shell closure, a continuous production of shell and mucus. Maintenance cost is mainly scaled with volume: \( \dot{p}_M = [\dot{p}_M] \cdot V \). Then, the dynamics for the
structural body volume $V$ is deduced from $\dot{p}_C$ and $\dot{p}_M$ according to the $\kappa$ rule:

$$\frac{dV}{dt} = \frac{\dot{p}_G}{[E_G]} = \frac{\kappa \cdot \dot{p}_C - \dot{p}_M}{[E_G]}$$

(5)

Under prolonged starvation and when reserve density drops below the non-growth barrier ($\kappa \cdot \dot{p}_C < \dot{p}_M$), the maintenance costs are first paid by using energy stored in the reproduction buffer $E_R$ (see below). When $E_R$ is totally emptied, maintenance is then paid by direct shrinking of structural volume.

Growth and development are parallel processes in the DEB model. So, similarly to somatic allocation, the energy allocated to development plus reproduction is equal to $(1-\kappa)\dot{p}_C$ and is also split into two sub-fluxes denoted $\dot{p}_R$ and $\dot{p}_G$; the former is scaled with $dV/dt$ whereas the latter does it with $\dot{p}_M$ and corresponds to maturity maintenance costs (at a given level of complexity). Kooijman (2000, chapter 3) demonstrated that $\dot{p}_G$ can be defined as:

$$\dot{p}_G = \left(\frac{1-\kappa}{\kappa}\right) \cdot \text{Min}(V, \dot{p}_F) \cdot \dot{p}_M$$

(6)

where $V_F$ corresponds to the volume at sexual maturity. Once an individual has reached $V_F$, the dynamics for energy allocated to reproduction buffer $E_R$ is then:

$$\frac{dE_R}{dt} = (1-\kappa) \cdot \dot{p}_C - \dot{p}_J.$$  

(7)

In autumn and winter, the Pacific oyster stores glycogen in specialised cells named vesicular cells (e.g. Berthelin et al., 2000; Li et al., 2000). In the model, we assume that this storage period corresponds to an increase in $E_R$. In spring and summer, the previously stored energy and new inputs of energy in $E_R$ are converted into gametes (ovocyte or spermatozoid). Similarly to the cost for structure ($[E_G]$), the energy allocated to reproduction buffer $E_R$ is fixed into the cells (vesicular cells, spermatozoid and ovocyte) with some efficiency denoted $\kappa_R$; the rest $1-\kappa_R$ is dissipated as overhead in structure building. This conversion constitutes a significant loss of energy whose value should be very similar to the loss of the energy dissipated for structural volume synthesis.

Once enough energy has been accumulated in the reproduction buffer, i.e. once a certain gonado-somatic index ($GI$, %) has been reached, and if external temperature is above 20 °C, the buffer is completely emptied and further accumulation becomes possible. The number of gametes (spermatozoid or oocyte) $\dot{R}$ produced per individual during one spawning is:

$$\dot{R} = \frac{\text{GDW}}{w_g}$$

(8)

where $w_g$ is the dry mass of a spermatozoid or an oocyte of *C. gigas* and CDW is the dry weight of gonad.

Physiological rates (in the model, assimilation and maintenance) depend on the body temperature. This dependency is usually well-described by the Arrhenius relation within a species-specific tolerance range of temperatures. The lower and upper boundaries of the tolerance range are named $T_L$ and $T_H$, respectively. Within this range, all the physiological rates follow the relation: $\dot{k}(T) = k_1 \exp\left(\frac{T - T_H}{T_{AH}}\right)$ where $\dot{k}(T)$ is the value of the physiological rate at ambient temperature $T$ (in K), $k_1$ is the value of the physiological rate at a chosen reference temperature $T_r$, and $T_A$ is the so-called Arrhenius temperature (in K).

At temperatures lower than $T_L$, the true rate is generally lower than expected from the standard Arrhenius formula, because organisms are in a condition similar to a resting phase. At temperatures above $T_H$, the rate can also be lower than expected because organisms approach a condition of rapid death. To take into account both boundaries, the basic formula described above becomes:

$$\dot{k}(T) = k_1 \exp\left(\frac{T_L - T}{T_H - T_L}\right) \left(1 + \exp\left(\frac{T_H - T}{T_H - T_L}\right) + \exp\left(\frac{T_H - T}{T_L - T_H}\right)\right)^{-1}$$

(9)

where $T_{AL}$ and $T_{AH}$ are the Arrhenius temperatures (in K) for the rate of decrease at both boundaries.

2.2. Experimental data

The data sets used to test the model came from three independent and long-term growth experiments (>5 months) performed on Pacific oysters under different conditions of food and environment: (i) in experiment A, the oysters were placed in experimental facilities and reared at two contrasted food density levels; (ii) in experiment B, they were placed in an oyster pond and reared at a fluctuating food density, and (iii) in experiment C they were reared in a natural environment (Thau lagoon) over a complete annual cycle.

Experiment A was conducted over a 130-d period extending from April to August 2004 (see Bourles, 2004, for details). The oysters in this experiment were collected as spat in the bay of Arcachon (south-western France) in August 2003, and in March 2004 transferred to holding facilities within the IFREMER shellfish
laboratory located at Argenton (Brittany, France). After an acclimation period, the bivalves were randomly split into two groups. The first group was fed ad libitum (‘fed group’) with a mixture of three cultivated micro-algae (25% Chaetoceros calcitrans, 25% Skeletonema costatum and 50% Isochrysis galbana named T-iso) distributed at a daily ration per oyster of 12% (dry mass algae/dry mass oyster); phytoplankton density around the fed oysters generally exceeded 15 μg chl-a 1\(^{-1}\). The second group was fed with only a 2% daily ration (‘lean group’) of the same mixture of algae, and phytoplankton density was always below 5 μg chl-a 1\(^{-1}\). Throughout experiment A, the oysters were stacked in 300-L raceways supplied with 5-μm-filtered running seawater at a mean salinity of 34.5. The water temperature was regulated every day to mimic the mean seasonal cycle of seawater temperature within the Marennes-Oléron Bay considered as the reference site (e.g. Deslous-Paoli and Héral, 1988). The tanks were periodically washed.

Experiment B lasted from June to October 2002. Oysters were cultivated in a 600-m\(^3\) pond as part of an integrated mariculture system located on Oléron island (described extensively in Lefebvre et al., 2004). They were fed with pure phytoplankton (mainly diatoms). Biometry (flesh and shell mass) was conducted at the start and end of the experiment. In situ oxygen, temperature and in vivo chlorophyll-a were monitored daily.

Experiment C consisted of an annual growth survey conducted in the Thau lagoon (southern France). This study was carried out between September 2000 and October 2001 as described in Gangnery et al. (2003). Briefly, oysters were installed on ropes in late September 2000 at one site located in the northwestern part of the lagoon. In compliance with the culture methods in use in this lagoon, 27 groups of 3 oysters were glued on 3-m-long ropes with cement, and density on the ropes was adjusted to 34 individuals per metre of rope; water depth was 4 m at the study site. The potential food consisted of natural phytoplankton and growth was followed monthly over a year. Temperature, salinity and chlorophyll-a were determined once a week during the growth period and every month outside this period.

The methods used to assess the growth of oysters over these three experiments were similar. Under each condition, oysters (n>12) were randomly collected twice a month in experiments A and C, and at the start and end of experiment B. They were cleaned and weighed after draining. Individual total mass (TW, g) was recorded. Then, the oysters were opened, and their flesh was removed and drained prior to weighing. The wet mass of total soft tissues per oyster was termed WW. In some cases, the dry mass of soft tissues was determined after freeze-drying and termed DW.

### 2.3. Model simulations

The model was implemented in STELLA 8.0 software (High Performance Systems, Hannover, NH, USA). Most of the model parameters used in this study came from Van der Veer et al. (2006). Otherwise, they were estimated according to the literature or unpublished IFREMER data (see Table 1). The state variables and processes expressed in energy were converted into the appropriate units by using: (i) for structural volume: density=1 g cm\(^{-3}\) and 1 g wet mass=0.15 g dry mass=0.17 g ash-free dry mass (Whyte et al., 1990); (ii) for energy reserve (mainly glycogen): 1 mg ash free dry mass (AFDM)=17 J (e.g. Brody, 1945); (iii) for respiration rate (proportional to \(p_C\)): 1 mg O\(_2\)=13.8 J (Bayne and Newell, 1983), (iv) for gametes production: 1 spermatozoid=161 picogDW and 1 oocyte=93000 picogDW (Ernande et al., 2004).

Table 2 lists the initial value of the state variables for each experiment. Structural volume was calculated with regard to the length by using \(\delta\), the shape correction: \(V=(\delta L)^3\). For each simulation, the initial values for energy storage \(E\) and for the reproduction buffer \(E_R\) were then deduced to obtain not only the correct and initial total dry mass (DW) but also realistic initial values for GI index and energy density [E].

For each of the three experiments (A, B and C), the forcing variables used to run the model were the temperature and food density relative to the experiment concerned. They are shown in Fig. 2.

The model outputs, e.g. not only the total dry mass and potential spawning, but also the absorption and respiration rates, were compared to the growth and ecophysiology data obtained in these three experiments, respectively. The goodness-of-fit between prediction (Y) and observation (X) was tested according to the R\(^2\) value of the regression Y=X. The only parameter that
had a different value between the various simulations was $X_K$, the half-saturation coefficient because of differences in diet composition between experiments (see Kooijman, 2006-this issue).

3. Results

3.1. Model simulations

3.1.1. Experiment A

$X_K = 17 \mu g \text{chl-a} \, \text{L}^{-1}$ produced the best fit between observation and simulation by giving a very good agreement ($R^2 = 0.98$, $n=14$, $p<0.0001$) between the model-predicted growth and the experimental one from the start to the end of the experiment (April to August) whatever the food density (Fig. 3a). A more thorough analysis not only confirmed the very good simulation of somatic growth (reserve and structure) under both (‘lean’ and ‘fed’) conditions, but also highlighted, with a rather high reliability, the reproduction of a spawning event in the latter. On the other hand, under the low-food density, as predicted by the model, no spawning was observed. The model also calculated the assimilation and oxygen consumption rates, which had both been continuously measured throughout the experiment. Fig. 3b and c illustrate the comparison of model-simulated and recorded assimilation and respiration rates under both feeding conditions. Apart from some discrepancies in July (around the spawning period), the model showed a high correlation between simulations and observations for assimilation and respiration ($R^2 = 0.77$, $n=198$, Table 1

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Symbol</th>
<th>Units</th>
<th>Value</th>
<th>References</th>
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<td>Arrhenius temperature</td>
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<td>K</td>
<td>5800</td>
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<td>Half saturation coefficient</td>
<td>$X_K$</td>
<td>$\mu g \text{chl-a} , \text{L}^{-1}$</td>
<td>3.5-8-17</td>
<td>Free-fitting (see Kooijman, 2006-this issue)</td>
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<td>Max. surf. area-specific ingestion rate</td>
<td>${\eta_{Xm} }$</td>
<td>$\text{J cm}^{-2} , \text{d}^{-1}$</td>
<td>560</td>
<td>Van der Veer et al. (2006)</td>
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<td>Assimilation efficiency</td>
<td>$ae$</td>
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<td>0.75</td>
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<td>Volume-specific maintenance costs</td>
<td>$[\rho_v]$</td>
<td>$\text{J cm}^{-3} , \text{d}^{-1}$</td>
<td>24</td>
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<td>Maximum storage density</td>
<td>$[E_M]$</td>
<td>$\text{J cm}^{-3}$</td>
<td>2295</td>
<td>Van der Veer et al. (2006)</td>
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<td>$\text{J cm}^{-3}$</td>
<td>1900</td>
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<td>Structural volume at sexual maturity</td>
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<td>$\text{cm}^3$</td>
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<td>Fraction of $p_C$ spent on maintenance plus growth</td>
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<td>0.45</td>
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<td>Fraction of reproduction energy fixed in eggs</td>
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<td>0.175</td>
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Additional parameters:

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<td>Rate of decrease at upper boundary</td>
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<td>Energy content of reserves (in ash-free dry mass)</td>
<td>$\mu_E$</td>
<td>$\text{J mg}^{-1}$</td>
<td>17.5</td>
<td>Deslous-Paoli and Héral (1988)</td>
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<td>%</td>
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Table 2

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<th>Length L (cm)</th>
<th>Structure V (cm$^3$)</th>
<th>Storage E (J)</th>
<th>Reproduction buffer E$_R$ (J)</th>
<th>Total dry mass (g)</th>
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Experiment B

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<th>Length L (cm)</th>
<th>Structure V (cm$^3$)</th>
<th>Storage E (J)</th>
<th>Reproduction buffer E$_R$ (J)</th>
<th>Total dry mass (g)</th>
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<tr>
<td>2</td>
<td>7.9</td>
<td>2.6</td>
<td>500</td>
<td>0</td>
<td>0.55**</td>
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<tr>
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<td>8.3</td>
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<td>3500</td>
<td>8500</td>
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<td>4</td>
<td>4.7</td>
<td>1*</td>
<td>500</td>
<td>500</td>
<td>0.25</td>
</tr>
</tbody>
</table>

* Calculated with a shape coefficient $\delta = 0.2$ specific to suspended culture in the Thau lagoon.

** The low value of initial dry mass according to length and season (summer) indicates a possible spawning of oysters ($[E]$ low and $E_A$ set to zero) prior to the experiment.
p<0.0001 and $R^2=0.96$, n=192, p<0.0001, respectively) after pooling both feeding conditions.

3.1.2. Experiment B

The aim of experiment B was to test the model in a more fluctuating environment and on several populations of oysters from various origins. For this environment, the $X_K$ value was set equal to 8 $\mu$g chl-a l$^{-1}$. Comparison of the model-predicted growth with observed growth during experiment B (Fig. 4a) showed a good fit for the three populations of oysters. After pooling of all the data, the overall correlation coefficient between observation and simulation was $R^2=0.81$ (n=8, p<0.002). Final masses were very well predicted by the model in the three populations (Fig. 4a). In ‘batch 1’, oysters were transferred to the pond early enough in the season to allow continuation and completion of their gametogenesis in summer and the timing and magnitude of the spawning indicated by the mass loss observed in mid-September were clearly predicted by the model. The other two batches of oysters showed no sign of such an event.

3.1.3. Experiment C

In experiment C the model was applied under typical field conditions and over a complete annual cycle. The best fit between observation and simulation was obtained with $X_K=3.5$ $\mu$g chl-a l$^{-1}$ (Fig. 4b). An overall analysis of the prediction against observation indicated a goodness-of-fit: $R^2$ of 0.92 (n=24, p<0.0001). The model simulated not only oyster growth over a complete annual cycle, but also the gametogenesis and spawning periods in the Thau lagoon. In agreement with experimental data on dry flesh mass, the model showed two sharp drops: at the end of June and August. It anticipated slightly the first period of spawning, whereas the second one was predicted at the correct time. The quantities of
gametes released during the first and second spawning were 0.2 and 0.5 g DW, respectively, in agreement with observations. However, a more thorough analysis showed some discrepancies between the model and data with a slight underestimation of growth in spring and a small overestimation in summer.

3.2. Analysis of the model internal functioning

The simulations in the Thau lagoon (experiment C) were used to obtain clues as to how the model treats physiological responses.

One of the internal properties of the DEB model is that the energy utilisation rate $\dot{p}_C$ varied so that the scaled energy density ($e = [E]/[E_m]$) tends to reach the value of the scaled functional response $f$. Fig. 5a clearly illustrates this internal property in the Thau lagoon conditions: $f$ varied according to food densities, and after a short delay the scaled energy density $e$ follows exactly the same trend, but with a smoothing due to the storage compartment.

According to the assimilation values, food was limiting in winter, and the assimilation rate was just sufficient to meet the maintenance costs (Fig. 5b): in December, the assimilation rate of a 6 to 8-mo-old oyster was about 27 J d$^{-1}$, and maintenance costs reached the same value (27 J d$^{-1}$). At the other extreme, a 1-y-old oyster assimilated more than 700 J d$^{-1}$ in summer with maintenance rates accounting for 202 J d$^{-1}$; the resulting positive energy budget allows rapid growth and active gametogenesis.

Finally, the model was run over a 10-y period by setting the temperature and food density measured in Thau lagoon as forcing variables. At the end of the simulation, the dry mass (outside the spawning period)
had reached about 8 g corresponding to a maximum length of about 18 cm.

4. Discussion

Over the last decade, modelling approaches have gained popularity in studies on shellfish energetics (e.g. Bacher et al., 1991; Powell et al., 1992; Schneider, 1992; Raillard et al., 1993; Van Haren and Kooijman, 1993; Barillé et al., 1997; Grant and Bacher, 1998; Scholten and Smaal, 1998; Ren and Ross, 2001, 2005) especially in coastal management where carrying capacity and environmental changes are essential. Concerning the Pacific oyster, the model presented in Barillé et al. (1997) uses the widely known ‘scope for growth’ concept. It simulates the temporal evolution of the somatic and storage-gonad compartments according to several environmental variables (total particulate matter, particulate organic matter, particulate inorganic matter, chlorophyll-a, phaeopigments, proteins, lipids and carbohydrates). This highly parameterised model successfully reproduced the growth and spawning of oysters reared in the Bay of Marennes Oléron, but showed its limits when applied to other conditions. Ren and Ross (2001) also developed a bioenergetic model for the Pacific oyster. Though their model uses some aspects of the theory developed by Kooijman (2000) by distinguishing structure from reserve, it relies less on mechanics and, thus, differs from DEBs in two fundamentals aspects: (i) the use of allometric functions relying on an empirical basis (Kooijman, 2000, Chaps. 1 and 2), and (ii) the direct subtraction of respiration from assimilation before energy allocation. Our study is the first application of the generic DEB model developed by Kooijman (2000) to the Pacific oyster. It highlights the good agreement between model-based simulations and real observations, even though it constitutes only the first step of our research program. Such a concordance indicates that the DEB theory, developed by Kooijman (1986) for all kinds of animals, is an efficient tool for capturing the bioenergetics and physiology of molluscs, especially the Pacific oyster. It also demonstrates that: (i) the accuracy on the measurements of the estimates used here for the forcing variables and DEB parameters was sufficient, (ii) the food sources selected in this study were highly decisive for growth and reproduction, and (iii) the reproductive processes had been clearly formulated at this first stage.

Most of the estimates used for the DEB parameters in this study were taken from Van der Veer et al. (2006). However, the very small number of data used to determine some of the estimates together with their calculation from relationships with other parameters had caused these authors to question the quality of their estimates. Even the estimation procedure itself is a source of uncertainty: for example, Van der Meer (2006-this issue) illustrated clearly that simultaneous regressions on combined sets of data on the blue mussel, Mytilus edulis (i.e. weighted non-linear least squares regression) gave more reliable estimates than simple regressions on isolated data sets as done in Van Haren and Kooijman (1993). Nevertheless, the proven agreement between the simulation results produced by the model and observations indicates that, despite the lack of calibration, most of the estimates can be considered fairly reliable. The quality of a parameter value on the global output of the model can be tested by performing a sensitivity analysis. Such an analysis was performed on our model by Bacher and Gangnery (2006-this issue). They showed that parameters governing food consumption, i.e. \( \{p_{Am}\} \) and \( X_k \), had most effect on growth: for example a 10% increase in the parameter \( X_k \) induced a variation of ca. 10% in the tissue mass. This result indicates that more precise laboratory and field experiments are required to gain more insight into especially these two parameters.

As mentioned, in the three experiments analysed in this study, the great concordance between observation...
and simulation data suggested that growth and reproduction were both largely determined by phytoplankton dynamics and seasonal cycle of temperatures in the environments tested here. Indeed, each experiment relied on a good knowledge of the quantity (daily in vivo fluorescence or weekly chlorophyll-a measurements) and quality (cultured phytoplankton, monospecific blooms or natural suspended matter rich in phytoplankton) of potential food sources. Under such ideal conditions, the simple type-II feeding function seems to be sufficient to quantitatively reproduce ingestion rate by using chlorophyll-a as a quantifier for food. Under more complex field conditions with many sources of food often diluted with a high mineral seston load, this simplistic form of the feeding function would probably require further improvements (e.g. Kooijman, 2006-this issue). The effect of diet composition on ingestion rate is poorly known in the Pacific oyster (e.g. Barillé et al., 1997). Furthermore, many species are known to modify their diet in the course of development or reproductive cycle, but to our knowledge the literature presents no information on such behaviour in Crassostrea gigas.

Concerning ingestion rate assessment, another problem is the choice of the correct quantifier for food. As mentioned, in this study we used chlorophyll-a for two reasons: (i) the food supplied to the oysters consisted mainly, but not exclusively, of phytoplankton, and (ii) chlorophyll-a is often used as a proxy for phytoplankton biomass. The simulations indicated that this quantifier was quite good in the three experiments, but the half-saturation coefficient ($X_K$) expressed in µg chl-a l$^{-1}$ showed variations according to experiment. Under cultured algae conditions, $X_K$ was higher than under natural conditions (17 vs 3 µg chl-a l$^{-1}$ in experiments A and C, respectively). We therefore wonder whether this variation results from a bad quantification of phytoplankton abundance by chlorophyll-a and whether the use of another quantifier for food (total volume of phytoplankton or total amount of carbon for example) would reduce it. The former assumption is supported by Zonneveld (1998), who clearly demonstrated huge variations in phytoplankton Chl-a-to-carbon ratio according to environmental conditions. Further investigations are, therefore, needed to find a suitable generic quantifier for food, likely POC, and to develop a more elaborated equation to describe the effect of food composition and quality on the half-saturation coefficient (see Kooijman, 2006-this issue). Differences between sites in $X_K$ but also in $\langle \hat{p}_{Am} \rangle$ values may also be due to phenotypic adaptation in the clearance and selection capacities of oysters. It has been shown that these capacities depend on the size of gills and palps (e.g. Barillé et al., 2000; Honkoop et al., 2003) and individuals can adapt these organs according to local food conditions (e.g. Essink et al., 1989). Consequently, we assume that potential plasticity in ingestion capacity could partly explain the differences we found in $X_K$ values among experiments. And more generally, adaptive mechanisms within a species could potentially increase the variability in some DEB parameters.

If food sources and selection efficiency are often the origin of discrepancies in the modelling of mollusc growth, reproductive processes (gametogenesis and spawning) are also complex processes that need special attention to be properly implemented into a model. The amount of energy invested in reproduction usually accounts for a significant part of the energy budget in bivalves, especially in the Pacific oyster (e.g. Deslouis-Paoli and Héral, 1988) as demonstrated in the present study by the low $\kappa$-value (0.45) for this species. Furthermore, the sensitivity analysis performed by Bacher and Gangnery (2006-this issue) on the present model showed that parameter $\kappa$ also had a significant effect on the growth simulation. Therefore, particular attention was paid to the formulation of reproductive processes in our model. Most of this formulation has already been described by Kooijman (2000) but we needed to add some species-specific aspects. The reproductive cycle of a bivalve can be viewed as a two-phase process: the first one is devoted to storage accumulation (generally glycogen in bivalves), and the second one, which is fuelled by accumulated stores (e.g. Li et al., 2000) and/or directly available food (Enriquez-Diaz, 2004), is dedicated to gametogenesis. This suggests that the energy used for gametogenesis includes both recently assimilated and previously stored reserves. Our model directly reproduces this connection between storage accumulation and gamete synthesis, since the state variable, $E_R$, considers storage and gametes to be in the same compartment.

In autumn and winter, the Pacific oyster stores glycogen in specialised cells, called vesicular cells (e.g. Berthelin et al., 2000; Li et al., 2000). In spring and summer, the previously stored energy and the new energy input are converted into gametes (oocytes or spermatozoa). Consequently, in our model, throughout the year, the energy allocated to the reproduction buffer, $E_R$, is fixed (within vesicular cells, spermatozoa and oocyte) with a certain efficiency called $\kappa_R$, the rest ($1-\kappa_R$) is dissipated as overheads for structure building. This conversion constitutes a significant loss of energy corresponding to the cost of gametogenesis. This cost should be almost equal to the loss of energy dissipated
over structural volume synthesis (integrated in \([E_C]\)); this is why \(\kappa_R\) was set equal to 0.7. This cost should also be expected to differ with sex (male or female). As oysters can, however, change sex during their life cycle with no quantitative change in their growth or gonad mass, we first assumed that \(\kappa_R\) was exactly the same for males and females, but these assumptions have to be confirmed or refuted by further studies. Moreover, Ren and Ross (2001) have already stressed the strong need for quantitative investigation on the energetics associated with reproduction.

The spawning process was formulated in a simplistic way in the model by assuming that, once enough energy has been accumulated in the reproduction buffer, i.e. once a certain gonado-somatic index \((GI, \%)\) has been reached, provided that external temperature is above 20 °C, spawning can occur, and then the buffer is completely emptied. This kind of formulation for a spawning trigger in bivalves has been used in previous models (e.g. Pouvreau et al., 2000). For the moment, it seems to constitute a suitable way to formulate this process: for example the model predicted two spawning periods in Thau lagoon. Both predictions were validated in quantity and timing by the observation of significant losses in total dry mass, but also by histological observations performed on this population of oysters (Pouvreau, pers. comm., 2002). Further field testing of the model in various environments should indicate whether this simplistic formulation is sufficient or not.

We extended the basic model to include the possibility of using the energy stored in \(E_R\) to sustain maintenance under starvation conditions; knowledge on this issue is very limited. The observation in the field, in autumn and winter, of decrease in soft tissue mass (Deslous-Paoli and Héral, 1988) might indicate that this shrinking results mainly from a reduction of the energy reserve, \(E\), and to a lesser extent from a decrease in the energy stored in the reproduction buffer, \(E_R\). In autumn \(E_R\) can be either totally emptied (after a total spawning) or filled partially with a new storage of glycogen in vesicular cells for the next reproduction cycle or filled partially with un-spawned gametes. Unfortunately, few studies have dealt with the latter case, i.e. the use of \(E_R\) to sustain maintenance under condition of starvation, a process known as gametic degeneration, resorption or atresia. The process of resorption in \(C.\ gigas\) has often been reported (e.g. Steele and Mulcahy, 1999; Enríquez-Díaz, 2004); it is considered to be a ‘self-cleaning’ stage that prepares the gonads for a new sexual cycle and is accompanied by a progressive autumnal reduction in gonad mass. The formulation used in our model to take into account the resorption process is presumably too simple and probably requires further refinements.

In conclusion, by demonstrating its rather good ability to mimic growth and reproduction under various controlled conditions, this DEB model appears to be generally suitable for simulation of bioenergetics of oysters in the field. Nevertheless, for use in a generic approach, the sources of food and selection efficiency are likely to need further refinements as well as the formulation of reproductive physiology. For our objective (the development of a species-specific model) addition of some extra parameters to the original model of Kooijman (2000) may be required. However, it is a delicate step that needs proper justification (Kooijman, 2000), and for the moment does not seem to be required. By being appropriate for general questions and interspecific comparisons, the DEB model developed by Kooijman (2000) provides a satisfactory fit without needing any modification. The next step will be to investigate the suitability of this model to simulate growth and reproduction in the field under environmental conditions more complex than those handled in this study.

Acknowledgements

The authors are very grateful to Prof. S.A.L.M. Kooijman (Department of Theoretical Biology, Vrije Universiteit, Amsterdam) for the time he devoted to thoroughly explaining the DEB theory and for his helpful comments on the manuscript. Our thanks also to Dr Marie-Paule Friocourt and Dr Helen Boudry for improving the English. This study was supported by the MOREST national project funded by IFREMER, by the Conseil Général du Calvados, by the Régions of Basse-Normandie, Bretagne, Pays de la Loire and Poitou-Charentes and by IFOP from European Union.

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