



A dynamic energy budget model: parameterisation and application to the Pacific oyster *Crassostrea gigas* in New Zealand waters

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ABSTRACT

A dynamic energy budget (DEB) model was developed and applied to the Pacific oyster *Crassostrea gigas* in central New Zealand. The model was based on DEB theory and developed prior to empirical information according to a common mechanistic rule in organisms' physiology. Subsequently, both laboratory and field experiments were specifically designed to collect datasets for parameter estimation and testing of the model. This approach to the modelling aimed to reduce uncertainties in parameter estimates and hence improve the applicability of the model. A lab-based starvation experiment was done over 170 days. Changes in body flesh weight were monitored and the respiration rate was measured. Dry flesh weight and the oxygen consumption rate decreased by 63.4% and 44.0% respectively over the experiment. Ash free dry flesh weight was proportional to the dry flesh weight, with coefficients of 83.5% and 58.7% respectively at the beginning and late stages of the experiment. Field-based growth experiments were done on a marine farm at two depths over 150 days to obtain biological and environmental information. The growth rate of oysters at 8 m depth was significantly greater than at 32 m depth. Chlorophyll-*a* concentration was highly variable, both spatially and temporally. Variation between depths provided ideal information for validation of the DEB model. Estimates of model parameters were augmented from studies in a local population. In comparison with previous studies on the same species from other ecosystems in the world, intraspecific variation was apparent in some parameters including maximum surface area-specific assimilation rate, which governs the ability of an individual for energy acquisition, and the fraction of energy utilisation rate used for maintenance plus growth, which determines energy fluxes to different components. The maximum storage density and volume-specific cost for growth also showed considerable intraspecific variability. Application of the model developed here showed that it is capable of simulating energetics and growth of the oyster in the growing area of central New Zealand.

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1. Introduction

The Pacific oyster *Crassostrea gigas* is one of the most sought after shellfish worldwide and the culture of this species has increased markedly in the last couple of decades (e.g. Curtin, 1989; Grizel and Héral, 1991; Girard et al., 2001). As spaces for the culture of this species are filled, there may be a depression of individual growth rates caused by several factors associated with overstocking (Héral and Deslouis-Paoli, 1991; Curtin, 1989; Grizel and Héral, 1991). In New Zealand, the perception among oyster growers already suggests that decreasing conditions, manifested through poor growth and reduced "fatness" of oysters, have occurred within the Marlborough Sounds, the main aquaculture area, due to periodic shortages of food for oysters (Ren, 2001). To manage individual farms and the industry properly, there is an acute need to be aware of the impact of oyster aquaculture on the environment and estimate the ability of the

ecosystem to support oyster production. This has prompted the necessity for a tool to understand ecological processes in the culture ecosystem and manage oyster farming. Ecological models offer such a tool in understanding the interactions between cultured species and their environment, and energetic modelling of individuals is one of the most important components of an ecological model.

Over the past decade, several attempts have been made to model the energetics of cultured shellfish. The existing models of oysters can be classified into two categories: net production and κ -rule models. The former type of models have been widely used over a couple of decades (Raillard et al., 1993; Barillé et al., 1997; Kobayashi et al., 1997; Gangnery et al., 2003), while the latter has been increasingly popular recently (Bacher and Gangnery, 2006; Pouvreau et al., 2006). The main difference between the two types of models is the rule of energy allocation (see Kooijman, 2000; van der Meer, 2006). Although net production models can successfully simulate the growth and reproduction of targeted species after calibration, validation of such models is questionable, particularly their applications to different datasets (e.g. Kobayashi et al., 1997). This is presumably due to variation in both

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model structure and parameters. The recent development of dynamic energy budget (DEB) theory (Kooijman, 2000) offers considerable improvement and simplicity for energetic modelling. Based on this theory, an energetic model can be developed prior to empirical information. It assumes common physiological processes across species and the only difference is in parameter values.

Appropriate parameter values, however, are critical for applications of a DEB model. Most parameters can be estimated in the laboratory under varying environmental conditions, including temperature and food density. Although many physiological experiments have been done on *C. gigas* (e.g. Gerdes, 1983; Deslous-Paoli et al., 1992; Barillé et al., 1994; Bougrier et al., 1995), feeding and metabolic rates were greatly different among studies. This variation in physiological rates may have been due to genetic differences within the species from different populations (e.g., Ren et al., 2000). Therefore, direct application of a DEB model to a species in different ecosystems is not warranted without altering values of some or all parameters. Ideally, parameterisation of a DEB model should be based on datasets from local populations.

Physiological and biological studies on the Pacific oyster have been done in New Zealand (Ren et al., 2000, 2003), which provides empirical data for parameterisation of a DEB model for *C. gigas*. However, information is still needed to estimate some parameters, including maximum storage density [E_M], volume-specific cost for growth [E_C] and volume-specific maintenance cost [\dot{p}_M]. To our knowledge, studies for obtaining such information have not been reported in aquatic organisms. According to DEB theory, these parameters can be estimated from starvation experiments. We therefore designed and conducted laboratory experiments to collect datasets for estimates of these parameters. Furthermore, the model application requires datasets consisting of growth and environmental variables, which are not available for this species in New Zealand. Growth experiments were subsequently done for this purpose.

Table 1
Equations of the dynamic energy budget model

Equation	Definition
$k(T) = k_1 \cdot e^{\left(\frac{T_A - T}{T_A - T_H}\right)} \cdot \left[1 + e^{\left(\frac{T_H - T}{T_H - T_C}\right)} + e^{\left(\frac{T_H - T}{T_H - T_M}\right)} \right]^{-1}$	temperature dependence
$\dot{p}_C = k(T) \cdot \frac{[E]}{[E_C] + \kappa \cdot [E]} \cdot \left(\frac{[E_C] \cdot \{\dot{p}_{Am}\} \cdot V^{2/3}}{[E_M]} + [\dot{p}_M] \cdot V \right)$	catabolic rate
$\dot{p}_A = k(T) \cdot f \cdot \{\dot{p}_{Am}\} \cdot V^{2/3}$	assimilation rate
$f = \frac{F}{F + F_H}$	functional response
$\dot{p}_M = k(T) \cdot [\dot{p}_M] \cdot V$	maintenance rate
$\dot{p}_J = k(T) \cdot \min(V, V_p) \cdot [\dot{p}_M] \cdot \frac{1 - \kappa}{\kappa}$	maturity maintenance rate
$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	reserve dynamic
$\frac{dE_R}{dt} = (1 - \kappa) \cdot \dot{p}_C - \dot{p}_J$	reproductive reserve dynamic
$\frac{dV}{dt} = \kappa \cdot \dot{p}_C - \dot{p}_M$	biovolume growth
$DFW = \frac{E}{\mu_E} + \frac{k_R \cdot E_R}{\mu_E} + V \cdot \rho$	Dry flesh weight

The purpose of the study was to develop a DEB model, particularly applicable to the Pacific oyster in New Zealand waters. Several steps were taken to achieve this. First, we present a generic DEB model. The parameterisation of the model would then be based on experimental data from New Zealand. Second, because available information was not sufficient for estimates of all parameters, we obtained missing information. Laboratory experiments were designed to test the use of reserves by oysters during a period of starvation and measure respiration rates. Third, estimates of parameters were made on the basis of our experimental results and published empirical information of the oyster in New Zealand. Fourth, field experiments were done to obtain datasets for calibration and testing of the DEB model. Last, the model was tested using the growth datasets from this study.

2. The DEB model

DEB theory (Kooijman, 2000) describes energetic processes of an individual organism by the three state variables of structural volume (V), reserves (E) and reproductive reserves (E_R). It assumes that energy uptake from the environment is immediately incorporated into a reserve pool from which it is used for maintenance, growth, development and reproduction. Partitioning of energy use follows a κ -allocation rule, which assumes that a fixed proportion κ of the energy from the reserves goes to maintenance and growth, where maintenance always has priority over growth. The remaining fraction $1 - \kappa$ goes to development and reproduction. If energy use is less than the maintenance requirement, growth stops and the maintenance need is met from reducing reproduction. It also assumes that energy for reproduction in an adult equals that for development in its juvenile stage. A transition size (V_p) is introduced to separate the adult from the juvenile.

The model variables and equations are detailed in Table 1. The assimilated energy is incorporated into a reserve pool. The dynamics of the reserves in the pool are simply the difference between uptake from the environment (\dot{p}_A) and utilisation for physiological processes (\dot{p}_C). During starvation, no energy is built up in the pool and the dynamic of the reserves is simply a function of energy utilisation rate. The uptake rate depends on surface area of an individual, while maintenance rate depends on structural volume. According to the κ -rule, a fixed proportion of \dot{p}_C is used for maintenance and growth. The remaining portion of energy utilisation goes to development and reproduction. Maturity maintenance increases with structural size and becomes constant after the individual becomes an adult. This is based on the assumption that an individual does not become more complex after it reaches the size V_p . Once the individual reaches V_p , energy for reproduction is allocated into a reproduction buffer and emptied at spawning.

Physiological rates depend on temperature. Within a species-specific tolerance range of temperatures, the rates of processes can be described by the Arrhenius relationship using a single Arrhenius temperature. Because the enzymes would be less active beyond the tolerance range of temperatures, this equation is further extended to include a species-specific tolerance range for low and high temperatures. A schematic diagram of a DEB model can be found elsewhere (e.g. Pouvreau et al., 2006).

Parameterisation of the model requires comprehensive information about the physiology of an organism. Ideally, this information should be collected from experiments specially designed for the purpose of modelling. After parameterisation, the model should undergo calibration processes on datasets including environmental and growth information. One or more different datasets are required for testing and validation of the model.

3. Experimental methods

3.1. Laboratory experiments

Starvation experiments were done to obtain information for parameter estimations of the DEB model. Oysters were collected from a farm

in the Marlborough Sounds in central New Zealand (173°42′–46′E, 41°02′–05′S). Specimens were cleaned of epibionts and transported to the University of Canterbury Field Station in Kaikoura where they were kept in running seawater and acclimatised for 2 months prior to the starvation experiment. Seven hundred oysters ranging from 25 to 175 mm shell length were placed into a 500-litre tank containing 1 µm filtered seawater. Among these specimens, there were c. 300 oysters with a size of 100±10 mm, which were used for monitoring reserve utilisation by animals (see below). The water was re-circulated through a protein skimmer and cascaded to keep the oxygen concentration at a high level. Ammonia was monitored daily as a check for water quality and the temperature was kept at 18±2 °C. Oysters were checked daily and any dead animals were removed immediately.

For measurements of reserve utilisation, a sample of 10–15 similarly-sized oysters (100±10 mm) was removed from the tank at intervals of 1–3 weeks. Length, wet weight and volume were measured to the nearest mm, g and cm³. The body flesh of each oyster was carefully dissected from shells, drained on paper towels and stored in pre-weighed aluminium pans. They were dried at 60 °C for 72 h and weighed, ashed at 500 °C for 4 h and weighed again to obtain ash-free dry weight.

The experiment was terminated after 170 days when there was little storage of reserves in the animals. At that time, all remaining animals were harvested and processed as above. The storage of reserves can be distinguished from the structural tissue by a change in relative abundance if resource levels change (Kooijman, 2000). For the purposes of the present modelling, we define storage of reserves as the component of body weight that can be lost during starvation. In this study, storage was calculated as the difference of dry flesh weight (DFW) between the beginning and late stages of the starvation period. The structural weight is defined as the structural material of oyster flesh that either increases or remains constant (when energy allocation is less than the maintenance requirement). Because death may not occur immediately after all reserves are depleted due to possible degradation and utilisation of structural tissue, again for the purpose of present modelling the point at which reserves were used up was decided using the following criteria: 1) DFW remained constant (at the level of detection); 2) oxygen consumption rate would no longer decrease but remained constant (at the detection limitation); and 3) oysters progressively died daily. The structural weight was measured as DFW approached a constant value.

Oxygen consumption rates (ml O₂ h⁻¹) of oysters were measured at day 0 of the experiment, on day 90, and thereafter at intervals of 1–2 weeks. The oxygen consumption rate was measured in closed glass bottles of 500–1000 ml depending on the size of animals. The bottles were filled with the same seawater as in starvation tank and immersed in the tank to keep the temperature constant. The water was manually mixed using a syringe before sampling. One ml of the water sample was taken using a syringe at intervals of 5–10 minutes (depending on the rate of decrease in oxygen concentration in the bottles). There were 5–7 replicates. Oxygen consumption was calculated as the rate of decrease of oxygen concentration inside the bottles as recorded by an oxygen meter (Radiometer, model PHM 73). The averaged oxygen concentration rate from each of the replicate measurements was used in this paper.

3.2. Growth experiments

Growth experiments were done to collect datasets for testing of the DEB model. One site and two depths were selected for the experiments during 15 May – 12 October 1999 in Beatrix Bay of the Marlborough Sounds. Experimental oysters were collected from an oyster-farming site in the Marlborough Sounds and were initially attached to scallop shells as spat. These oysters were transplanted to the experimental site where they were suspended in the water column. To test biotic and abiotic effects on oyster growth, animals

were attached to a nylon rope and suspended at two depths (8 m and 32 m below the surface). Oysters were initially 78.7 mm in length (±7.3SD, n=25) and 1.18 g in dry flesh weight (±0.47SD, n=25).

Approximately 25 oysters from each depth were sampled at approximately monthly intervals. After sampling, the live oysters were transferred to the laboratory where all measurements were performed. Fouling organisms were carefully removed from each oyster with a scalpel. After measurements of wet weight (g) and length (mm), soft tissues were separated from the shell and placed into a tared aluminium weighing pan, dried at 60 °C to a constant weight and weighed. Shell valves were weighed after drying at 60 °C for 72 h.

At each depth, three duplicate water samples were taken at the same time of oyster sampling to measure chlorophyll-*a* (Chl: µg l⁻¹), particulate organic matter (POM: (mg l⁻¹) and total particulate matter (PTM: mg l⁻¹). The water samples were filtered onto 25-mm GF/F filters (Whatman) for chlorophyll-*a* analysis. The filters were put into plastic bags and stored in a dark box at -20 °C until analysis. Chlorophyll-*a* was measured according to standard procedures for acetone extraction and fluorometric analysis (excitation: 431 nm, emission: 670 nm) (Strickland and Parson, 1968). Water temperature was measured at the same time as the sampling of water.

4. Experimental results

4.1. Laboratory experiment

4.1.1. Changes in DFW

The change of the dry flesh weight during the experiment is presented in Fig. 1. Throughout the experiment, as the reserves declined, the DFW approached the asymptotic value of the structural weight. DFW decreased exponentially until day 113, after which little change was detected. This implies that the storage of body reserves had been depleted. Although progressive death of oysters did not occur until day 170, animals might have relied on decomposition of structural tissues for their maintenance needs. It is reasonable to assume that the somatic mass at day 113 consisted of only structural mass. At this time, the total DFW had decreased by 63.4%. Changes in reserves during the course of the experiment can be obtained by subtracting DFW at day 113 from DFW at day 0 (Fig. 1). This reflects changes of reserve density that approaches zero at day 113 from the maximum at the beginning of the experiment. The maximum ratio of structural mass to reserves was 1:1.73.

Ash free dry flesh weight (AFDFW) was measured, and it was proportional to DFW. AFDFW was 83.5% and 58.7% of the DFW respectively at the beginning and the late stages of the experiment. More AFDFW in non-starved oysters than in starved ones suggests that the carbon content of the flesh decreased with declining reserves.

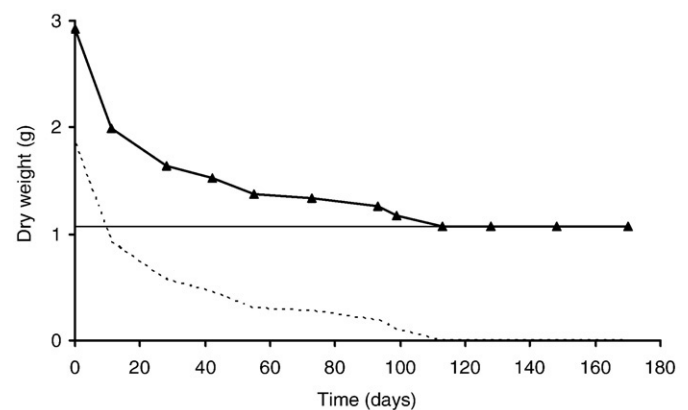


Fig. 1. The changes in dry flesh weight (solid line with filled diamonds) and storage of reserves (broken line) in the Pacific oyster during the starvation experiment, relative to the structural mass (horizontal solid line).

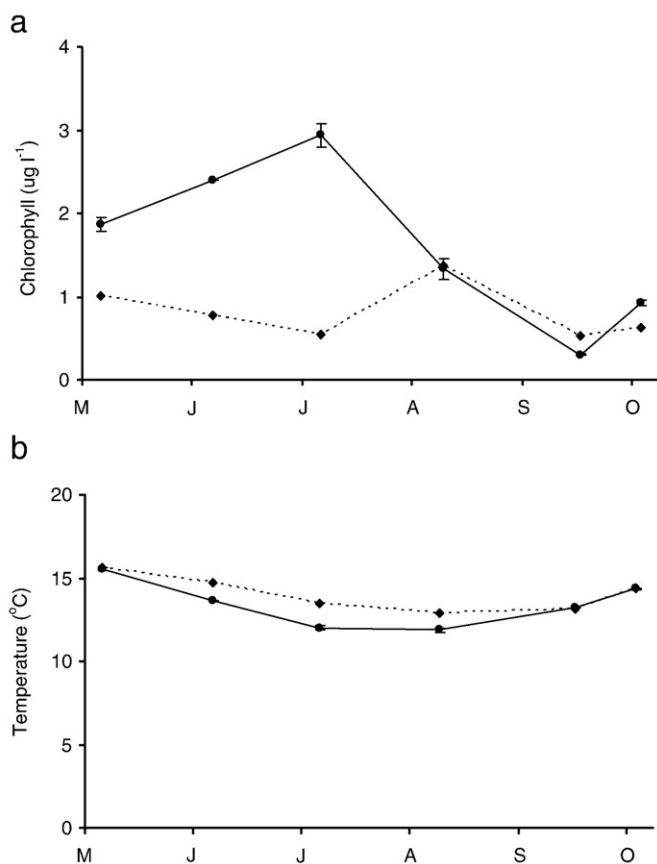


Fig. 2. Temporal and spatial variation in a) chlorophyll-*a* and b) temperature at depths of 8 m (solid lines) and 32 m (broken lines). Error bars are ± 1 standard error.

We did not measure the energy value of DFW, but this result suggests that the energy content of reserves is higher than that of structural tissues. Using above proportional coefficients between AFDW and DFW, ratio of structural mass to reserves, and a conversion factor of 23 kJ g^{-1} for AFDW to energy (van der Veer et al., 2006), the energy contents were 19.21, 13.5 and 22.49 kJ g^{-1} AFDW respectively for DFW, structural mass and reserves.

4.1.2. Oxygen consumption rate

Oxygen consumption rates were measured at day 0 and during the late stages of the experiment (from day 90 onwards). Because there were no differences among the rates during the late stages, only the rate at day 113 is presented here. The oxygen consumption rate increased allometrically with body length at day 0, which can be best described by $\text{O}_2 = 9.60 \times 10^{-4} L^{2.44}$ ($R^2 = 0.90$).

Similarly, the relationship between oxygen consumption rate and body length at day 113 can also be best described by $\text{O}_2 = 2.76 \times 10^{-3} L^{2.36}$ ($R^2 = 0.89$). Over oysters of all sizes, the average oxygen consumption rate at day 113 was 44.0% of that at day 0.

4.2. Growth experiments

The mean chlorophyll-*a* and temperature at each sampling date during the period of the experiment are shown in Fig. 2. For our purpose, information about particulate organic matter and total particulate matter concentrations is not presented here. Chlorophyll-*a* concentrations were considerably higher at 8 m than at 32 m in the first 2 months of the experiment, and remained low all the time at 32 m. However, variations in temperature were not obvious between depths, although it was generally higher at 32 m than at 8 m over the experimental period.

Dry flesh weight of oysters increased considerably at both depths after 5 months of growth (Fig. 3). For the present purpose, growth in length is not presented here. Considerable temporal and spatial variation in growth rates was recorded. Oysters tripled their DFW at 8 m between May and August, but only doubled their size at 32 m during this period. The mean daily growth rates of DFW were about 40% higher at 8 m than at 32 m.

5. Parameter estimation

The parameters of the DEB model were estimated from physiological and biological studies on *C. gigas* in New Zealand waters. The shape coefficient was estimated from the relationship between somatic mass and length. The ratio of dry flesh weight to wet somatic mass varied between 0.14–0.25. Using an average value of 0.2 would result in shape coefficient value of 0.21. The minimal length at first reproduction is 6 cm (Ren et al., 2003), which corresponds to a structural volume of 2.0 cm^3 .

Oxygen consumption rates are suitable for the determination of Arrhenius temperature and have been used in a few marine bivalves (van der Veer et al., 2006). Based on an experiment on oxygen consumption as a function of temperature within the range tested (Ren et al., 2000), the Arrhenius temperature was estimated to be 5900 K. According to van der Veer et al. (2006), the lower (T_L) and upper (T_H) boundaries of the tolerance range are the temperatures at which ln2% of the enzymes are active. This resulted in the Arrhenius temperatures for the rate of decrease at lower and upper boundaries being 13000 and 80000 K respectively for T_{AL} and T_{AH} .

Three parameters, ($[p_M]$, $[E_M]$ and $[E_G]$), were estimated from the starvation experiment in this study. Maintenance is defined as the energy requirement of an individual to stay alive, which excludes investments in the production processes of growth, reproduction and development (Kooijman, 2000). Therefore, the volume-specific maintenance cost $[p_M]$ can be estimated from the respiration rate of the experiment when reserves were depleted. In combination with the shape coefficient, the volume-specific oxygen consumption rate was measured as $0.91 \text{ ml O}_2 \text{ cm}^{-3} \text{ d}^{-1}$ at $18 \text{ }^{\circ}\text{C}$ or $18.5 \text{ J cm}^{-3} \text{ d}^{-1}$, which is regarded as the maintenance rate. The reserves were depleted at day 113 and the somatic mass roughly equalled the structural mass. In combination with the shape coefficient and energy content, the volume-specific energy content was estimated to be 2050 J cm^{-3} . According to van der Veer et al. (2006), the overhead cost for material synthesis was 40%. This would give about 2900 J cm^{-3} for the volume-specific costs for growth $[E_G]$. The difference in somatic mass at the beginning and late stages of the starvation experiment would be the mass of reserves. Using the shape coefficient and energy content,

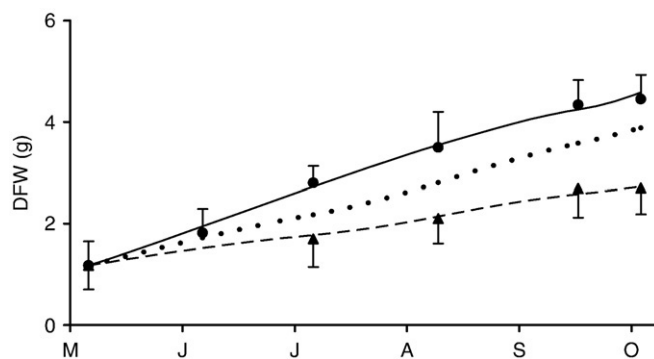


Fig. 3. Comparison of observed and simulated dry flesh weight (DFW) of the Pacific oyster. Dots and triangles are observed DFW at depth of 8 m and 32 m respectively. Solid and dot lines are simulated growth trajectories of DFW at depth of 8 m and 32 m respectively using the same F_h -value. The dashed line is the simulated growth trajectory of DFW at depth of 32 m with changed F_h -value to obtain the "best" match between model simulation and observation. Error bars are ± 1 standard error.

we estimated the maximum storage density [E_M] to be about 5 900 J cm⁻³.

The maximum surface area-specific assimilation rate, $\{\dot{p}_{Am}\}$, can be estimated from feeding experiments. From this method, the estimated $\{\dot{p}_{Am}\}$ showed large variability, which was ascribed to the change of food density during the course of measurements (van der Veer et al., 2006). Ideally, feeding experiments should be done at a constant food density. Although feeding experiments in New Zealand were conducted using variable food densities (Ren et al., 2000; Ren, 2001), in a number of the experimental runs, food density was kept constant. Using information of assimilation rates measured in POM concentration of 0.4–2.4 mg l⁻¹, the regression on surface area of the oyster and surface area-specific assimilation rate resulted in an estimate of $\{\dot{p}_{Am}\}$ about 356 J cm⁻² d⁻¹ at 12 °C or 550 J cm⁻² d⁻¹ at 18 °C.

Until now, we have estimated most model parameters except κ and F_h . There were no data to directly estimate the fraction of energy utilisation rate spent on maintenance plus growth (κ). According to van der Veer et al. (2006), it can be indirectly estimated from gonad index information, that is, the ratio of gonad to somatic mass. With a set of model parameters and a constant F_h -value, the DEB model was run by varying κ in a range of 0.1–0.9. Therefore, κ value can be determined when the simulated gonad index corresponds to the field-observed value before spawning. Seasonal variation in reproductive activity and biochemical composition has shown one spawning season in the Pacific oyster in the studied area (Ren et al., 2003), during late December and early January. According to this study, the variation of gonad-to-somatic ratio followed a regular seasonal cycle, with an average highest value of 0.66 in December and lowest value of 0.43. The difference between highest and lowest values (0.20–0.24) would be the ratio of energy for reproduction, which corresponds to a value for κ of about 0.65 Table 2.

Although physiological studies have been done to measure feeding and ingestion rates in the oyster (e.g. Ren et al., 2000), these measurements were made under controlled condition of a mixed diet of silt and a single phytoplankton species in the laboratory. From this information, we could not estimate the parameter of the half-saturation coefficient (F_h) to reflect field conditions. It was treated as “free-fitting” parameter and is discussed in the following section.

Table 2
Model parameters used in this study

Symbol	Value	Dimension	Definition	Sources
$[E_C]$	2 900	J cm ⁻³	volume-specific costs for structure	this study
$[E_M]$	5 900	J cm ⁻³	maximum storage density	this study
κ	0.65	–	fraction of catabolic flux to growth & maintenance	this study
κ_R	0.7	–	fraction of reproductive reserves fixed in eggs	van der Veer et al. (2006)
V_p	2.0	cm ³	structural body volume at puberty	Ren et al. (2003)
δ_m	0.21	–	shape coefficient	This study
$\{\dot{p}_{Am}\}$	550	J cm ⁻² d ⁻¹	maximum surface area-specific assimilation rate	Ren et al. (2000)
$[\dot{p}_M]$	18.5	J cm ⁻³ d ⁻¹	volume-specific maintenance rate	this study
T_I	291	K	reference temperature	this study
T_A	5 900	K	Arrhenius temperature	Ren et al. (2000)
T_L	283	K	Lower boundary temperature of the tolerance range	Ren et al. (2000)
T_H	303	K	Upper boundary temperature of the tolerance range	Ren et al. (2000)
T_{AL}	13 000	K	Arrhenius temperature for the rate of decrease at lower boundary	Ren et al. (2000)
T_{AH}	80 000	K	Arrhenius temperature for the rate of decrease at upper boundary	Ren et al. (2000)
k_1	1	–	reference physiological reaction rate at 291 K	this study
μ_E	22.49	J g ⁻¹	energy content of reserves	this study
ρ	0.2	g cm ⁻³	volume-specific dry flesh weight	this study

6. Model application

The model was tested on the growth data of *C. gigas* from this study. The driving forces are chlorophyll and temperature. The growth data were also used to obtain the “free-fitting” parameter (F_h). The model was run by varying F_h until the “best-fit” between the simulation and observation was achieved. The initial values of state variables were estimated according to length, dry flesh weight and gonad index. Because the gonad index follows a regular seasonal cycle, the value of reproductive reserves (E_R) at the time of simulation can be estimated accordingly. The resolution of the model is one day. The values of forcing inputs were linearly interpolated to obtain values at daily intervals to be consistent with the time step used in the model.

The model simulation showed that it can capture system behaviour, particularly phytoplankton supply (Fig. 3). The “best-fit” between model simulation and observation was achieved at $F_h = 1.0 \mu\text{g l}^{-1}$ chlorophyll for the oyster at a depth of 8 m. High growth rate in the first few months was predicted by the model, which corresponds with a high chlorophyll-*a* concentration. The slow growth in the last two months of the experiment resulted from a considerable decline in food concentration.

The same value of F_h could not generate the “best-fit” between model simulation and observation for the oyster at depth of 32 m, but a good agreement could still be obtained at $F_h = 1.9 \mu\text{g l}^{-1}$ (Fig. 3). Because the chlorophyll-*a* concentration was at all time low with little variation during the course of the experiment, the oyster grew at a considerably lower rate compared to that at a depth of 8 m. This difference in food supply was successfully predicted by the model. The different F_h -values between depths might reflect variation in energy values of phytoplankton (i.e., chlorophyll to carbon ratio). This is discussed below.

7. Discussion

A DEB model was applied to the Pacific oyster to simulate its energetics and growth in varying environmental conditions. Most parameters of the model were estimated from experimental studies on an oyster population in New Zealand. During the modelling exercise, both laboratory and field experiments were used to obtain information for parameterisation and testing of the model. Application of the model to datasets showed that the model is capable of reproducing system behaviour in the growing area of central New Zealand.

Parameterisation of a DEB model requires comprehensive datasets which ideally should be collected from factorially designed experiments under controlled conditions (van der Veer et al., 2006) but such datasets are not usually available. This is partly due to the paucity of work done on physiology and partly due to the fact that many physiological experiments have not been appropriately designed for the purpose of modelling (Ren and Ross, 2001). Consequently, parameters estimated from data in the literature have always showed a large variability (e.g. Ren and Ross, 2001; van der Veer et al., 2006). Alternatively, van der Veer et al. (2006) proposed to estimate individual parameters based on combining many published datasets by means of simultaneous regression. This would make some improvement over the estimation relying on a single dataset. However, the intraspecific variation in physiological rates has not been taken into account in their estimates.

Lack of information for parameterisation of the DEB model necessitated laboratory experiments to collect essential data. Unlike traditional starvation experiments to observe the change of body components (e.g. Riley, 1976; Gaffney and Diehl, 1986), our experiments were specially designed for the purpose of modelling. According to DEB theory (Kooijman, 2000), three parameters can only be estimated on data collected from physiological experiments under starvation, including maximum storage density [E_M], volume-

specific cost for growth [E_G] and the volume-specific maintenance cost [\dot{p}_M]. Although starvation experiments have been done on *C. gigas* (Riley, 1976; Whyte et al., 1990), data collected from these experiments were not appropriate for estimating the parameters for two reasons. First, these experiments were not appropriately designed for the purpose of developing energetic models and hence estimating these parameters from these data was not possible. Second, their experiments were done using oysters from ecosystems other than the present study area, and *a priori* our expectation was that there would be intraspecies variation in physiological rates. As expected, the present study showed that the values of some parameters differ considerably from the estimates of van der Veer et al. (2006). Most apparent parameters include maximum surface area-specific ingestion rate [\dot{p}_{MA}], fraction of energy utilisation rate on maintenance plus growth κ , maximum storage density [E_M] and volume-specific cost for growth [E_G]. Our estimated [\dot{p}_{MA}]-value was $550 \text{ J cm}^{-2} \text{ d}^{-1}$ at 18°C or $670 \text{ J cm}^{-2} \text{ d}^{-1}$ at 20°C , which is considerably higher than theirs, $560 \text{ J cm}^{-2} \text{ d}^{-1}$ at 20°C . Similarly, the κ -value from present study was 0.65 compared with 0.45 from their estimate. The values of [E_M] and [E_G] in the present study were over 250% and 60% times those from their estimation. This variation might be due largely to intraspecies variability in physiological characters resulting from differences in environmental conditions or/and genetics.

Genetic differences may be important in determining some of the biological and physiological characters. Many studies have found that gene flow is restricted between populations in marine bivalves (e.g. Koehn et al., 1976; Lassen and Turano, 1978; Hilbilish and Koehn, 1985; Kautsky et al., 1990) and population parameters including growth and mortality are genetically variable (Mallet and Haley, 1983; Dickie et al., 1984; Kautsky et al., 1990). A genetic difference between populations was also recorded in the New Zealand greenshell mussel *Perna canaliculus*, which was probably due to adaptation to different thermal environments (Smith, 1988). Adaptation to the prevailing environmental conditions would modify the physiological traits of mussels (Mallet et al., 1987; Camacho et al., 1995; Bayne et al., 1984, 1987). This is in agreement with Widdows et al. (1984) who found that the growth differences were the result of different environmental conditions in *Mytilus edulis*. These studies imply that variation in both genetics and environmental conditions can affect physiological rates of an organism. Although genetic differences between *C. gigas* populations remain to be investigated, environmental conditions in New Zealand differ from those in other ecosystems including Thau lagoon (France). For example, water temperature, chlorophyll-*a* and seston concentration are all lower with a small range of variation in New Zealand (Ren et al., 2000). This difference in environment alone would likely affect physiological processes of individuals. Differences in some other biological traits between populations might have also affected physiological rates. For example, there is only one annual spawning event of the oyster in the growing area, although there might be several small spawning events in some other areas in New Zealand, while an individual can spawn twice a year in Thau lagoon. The difference in κ -value reflects the differing allocation strategy of oysters investing significantly more energy for reproduction in Thau lagoon than in New Zealand waters.

The model simulation indicates that phytoplankton is the main driving force for the growth of the oyster. Particulate organic matter (POM) has little contribution to the growth (data not shown), and the presence of a high concentration of non-phytoplankton particulate (e.g. detritus, bacteria) does not support rapid growth of the oyster (Ren, 2001). This is in agreement with other modelling studies in which growth of bivalves can be predicted by a single food source of phytoplankton but which failed to predict growth trajectories with the inclusion of POM (Ren and Ross, 2001, 2005). Similarly, growth experiments have shown that non-phytoplankton food resulted in poor growth of *M. edulis* (Winter, 1978; Williams, 1981). The present modelling exercise used chlorophyll-*a* as an indicator of phytoplank-

ton. Despite good agreement between the model simulation and observations, the half-saturation coefficient F_h showed variation relating to environmental conditions. The calibrated model using data from 8 m depth failed to simulate the growth trajectory of the oyster at 32 m depth without altering the value of F_h . However, the growth trajectory at depth 32 m can still be reproduced by increasing the F_h -value. This environment-specific variability in F_h -value was also found in other modelling studies (Bacher and Gangnery, 2006; Pouvreau et al., 2006). Pouvreau et al. (2006) postulated that differences in the F_h -value were due to variation in adaptive mechanisms within a species. However, this explanation cannot be applied to the present case because experimental oysters were collected from the same source and it is unlikely there was genetic variation due to areas sampled. Furthermore, growing depth might have some effect, but which could not be assessed from available information. Variability might have largely related to the choice for the indicator of food availability. Temporal and spatial variations in the chlorophyll-*a*: phytoplankton carbon ratio can be very large in many bivalve farming ecosystems, including those in New Zealand where the ratio varied between 25 and 500. Although we do not have information about the chlorophyll-*a*:phytoplankton carbon ratio, it would be reasonable to postulate that less light intensity resulted in less favourable conditions for phytoplankton growth in the lower water layer than in the upper layer. Consequently, the chlorophyll-*a*:phytoplankton carbon ratio was likely higher in the lower layer than in the upper layer.

Selective ingestion of phytoplankton species would be another uncertainty potentially affecting the variability in F_h -value. This selective ingestion is common in some bivalves (e.g. Kreeger and Newell, 1996; Wang and Fisher, 1996). The mussel *M. galloprovincialis* preferentially selects dinoflagellates rather than diatoms, and the digestion rate of the dinoflagellates may vary among species as well (Sidari et al., 1998). Similarly, assimilation efficiency of *P. canaliculus* depends on the phytoplankton genera and/or species (Ren et al., 2006). This variation was large and can exceed 50%. Temporal variation in species composition has been recorded in the studied area (Mackenzie et al., 1986), but information on spatial variation is lacking. Further improvement of the model would be based on the appropriate choice of food availability, which relies on our understanding of the variation in the chlorophyll-*a*:phytoplankton carbon ratio, phytoplankton species composition and species-specific assimilation efficiency in the oyster.

In conclusion, the DEB model was parameterised on datasets from physiological experiments on the Pacific oyster in a New Zealand ecosystem. Using an experimental approach in developing a DEB model greatly reduces uncertainties in parameter estimates and hence improves applicability of the model. This is probably the most desirable way to develop a DEB model, but few modelling exercises have followed this type of procedure (Ren, 2001). The present model is capable of simulating energetics and growth of the oyster in the growing area of central New Zealand. Nevertheless, the functional response of food needs further improvement to include the effect of food quantity and quality on the half-saturation coefficient as well as some refinement of parameters derived from the literature. In addition, further refinements of the model would rely on comprehensive datasets from sites with different environmental conditions.

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