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A comparison of scope for growth (SFG) and dynamic energy budget (DEB) models applied to the blue mussel (*Mytilus edulis*)☆

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ABSTRACT

Growth of Mytilus edulis was simulated using individual based models following both Scope For Growth (SFG) and Dynamic Energy Budget (DEB) approaches. These models were parameterized using independent studies and calibrated for each dataset by adjusting the half-saturation coefficient of the food ingestion function term, X_K, a common parameter in both approaches related to feeding behavior. Auto-calibration was carried out using an optimization tool, which provides an objective way of tuning the model. Both approaches yielded similar performance, suggesting that although the basis for constructing the models is different, both can successfully reproduce *M. edulis* growth. The good performance of both models in different environments achieved by adjusting a single parameter, X_K, highlights the potential of these models for (1) producing prospective analysis of mussel growth and (2) investigating mussel feeding response in different ecosystems. Finally, we emphasize that the convergence of two different modeling approaches via calibration of X_K, indicates the importance of the feeding behavior and local trophic conditions for bivalve growth performance. Consequently, further investigations should be conducted to explore the relationship of X_K to environmental variables and/or to the sophistication of the functional response to food availability with the final objective of creating a general model that can be applied to different ecosystems without the need for calibration.

1. Introduction

Growth of bivalve species with economic value has been widely studied due to their role in aquaculture and other ecosystem services such as water filtration (Officer et al., 1982). The need to make growth predictions goal of creating tools to carry out prospective studies has promoted the development of individual bivalve growth models, which can be based on empirical (e.g. Hawkins et al., 2002; Gangnery et al. 2003), mechanistic (e.g. Willows, 1992; Kooijman, 2000) or mixed (e.g. Duarte et al., 2010) approaches. Two main approaches have been applied to model bivalve growth: Scope For Growth (SFG, Winberg, 1960) and Dynamic Energy Budget (DEB, Kooijman, 1986). The SFG approach is based on the measurement of the energetic balance of a "standard" organism, applying allometric curves to extrapolate the measurement to other animal sizes. The energetic balance is the difference between the energy absorbed from the food and the energy lost in respiration and excretion. If this balance is positive, the organism has energy available for growth and reproduction that is manifest as an increase in body weight. In contrast, a negative balance will result in a decrease in body weight as a consequence of the utilization of reserves. DEB theory describes the individual in terms of two state variables, structural body and reserves (van der Meer, 2006), describing energy flow through organisms from assimilation to allocation to growth, reproduction and maintenance. Therefore, in DEB theory the description of these energetic processes in an organism is a function of its state and the environment (Nisbet et al., 2000).

The main difference between these approaches is that SFG models assume assimilated energy is immediately available for catabolism (respiration and excretion) and the remainder is used for growth or stored as reserves. This assumption implies that energy from catabolism is lost. However, the energy from catabolism that has been reinvested in the anabolic processes of growth stays in the organism and is not subsequently lost, causing an imbalance according to the energy conservation rule. DEB theory is based on the assumption that assimilated energy is first stored in reserves, which in turn are utilized to fuel other metabolic processes (Pouvreau et al., 2006). Thus, reserves reflect the feeding history of the organisms and consequently the structural growth dynamics in a DEB model become different from the SFG model, particularly in situations with temporal fluctuations in energy supply. Another important assumption of the DEB model is the κ-rule which implies that a fixed proportion κ of the available energy is allocated to somatic

☆ All authors contributed in all the steps related to study design, analysis and writing.

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maintenance and growth, with priority for maintenance, and the remaining $1-\kappa$ is allocated to maturation and reproduction/maturity maintenance for juveniles and adults respectively. Recently, Brigolin et al. (2009) applied a variation of the κ-rule concept to an SFG model, fractionating the energy into two state variables: somatic structural tissue and reproductive tissue. Given the different energy allocation pathways and the influence of the internal state of the organism, DEB models are more suitable to predict reproduction, a function of the energy accumulated in reproductive tissue, and mortality, a function of the energy deficits in reserve tissue (Duarte et al., 2010). This aspect of DEB has been explored in bivalves, for example, spawning triggers related to gonado-somatic index and external temperature (Pouvreau et al., 2006; Bourlès et al., 2009) or preset spawning events based on observations at given times of the year (Rosland et al., 2009; Duarte et al., 2010).

The different energy allocation pathways in SFG and DEB are a direct consequence of the simplification adopted in SFG models, which studies organism physiology through the measurement of processes that are relatively easy to measure, and not because their relationship to body mass could be readily derived from first principles (van der Meer, 2006). Although this simplification violates the energy conservation rule, SFG modeling has been widely used because it is an easy way to empirically estimate growth and therefore can be useful in some applications. This shortcoming is not present in DEB modeling, which is based on more generic principals that assumes common physiological processes across species and life stages (Pouvreau et al., 2006). However, one of the challenges in DEB modeling is to estimate the basic parameter sets for different species (Pouvreau et al., 2006; van der Meer, 2006). Therefore both approaches, SFG and DEB, present advantages and disadvantages, and both have been successfully applied in individual bivalve growth models (e.g. SFG: Grant and Bacher, 1998; Hawkins et al., 2002; Brigolin et al., 2009; e.g. DEB: Bacher and Gangnery, 2006; van der Veer et al., 2006; Rosland et al., 2009) as well as submodels of complex ecological models (e.g. SFG: Pastres et al., 2001; Ferreira et al., 2008; Filgueira and Grant 2009; e.g. DEB: Grangeré et al., 2009; Maar et al., 2009, Ren et al., 2010).

A common function of both the SFG and DEB models applied in this study is the one describing food ingestion. This is based on a Michaelis-Menten term that regulates the amount of food that is ingested by the organism depending on the food concentration itself. Therefore, the half-saturation coefficient of the Michaelis-Menten term, X_K, is an important parameter for regulating the feeding response. The implications of X_K on the feeding behavior are not limited to filter feeders. For example, Gallegos (1989) used the same approach to describe the dynamics of microzooplankton grazing on phytoplankton. This author described the half-saturation coefficient as an indicator of the range of food levels over which maximal consumption rates are maintained and suggested a high correlation of its value with the initial concentration of

Table 1
Differential equations and parameters of both SFG and DEB models. See references for parameter values discussion.

Equation	Terms and parameters	
Scope For Growth (Grant et al., 1993[a], 2007[b]; Filgueira and Grant, 2009)		
$\frac{dM_w}{dt} = \varepsilon_m I - f_{mr}\beta_{mr} - \sigma_\gamma \varepsilon_m I$	M_w	Mussel weight (mg C)
	ε_m	Dimensionless phytoplankton assimilation efficiency[a,b]
	I	Ingestion rate (see text)
	f_{mr}	Dimensionless standard respiration function[a,b]
	β_{mr}	Standard respiration rate (d^{-1})[a,b]
	σ_γ	Dimensionless cost of growth coefficient[a,b]
$f_{mr} = C_{mr}\ \exp(Q_{mr}T)\left(\frac{M_w}{M_{wRef}}\right)^{b_{mr}}$	C_{mr}	Dimensionless scaling constant[a,b]
	Q_{mr}	Temperature rate constant for standard respiration ($°C^{-1}$)[a,b]
	T	Temperature (°C)
	M_{wRef}	Mussel reference weight (mg C)[a,b]
	b_{mr}	Dimensionless allometric exponent for respiration[a,b]
Dynamic Energy Budget (Pouvreau et al., 2006; Van der Veer et al., 2006[c]; Rosland et al., 2009[d])		
$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$	E	Energy storage (J)
	$\dot{p}_A$	Assimilation rate ($J\ d^{-1}$)
	$\dot{p}_C$	Mobilization rate of reserve energy ($J\ d^{-1}$)
$\dot{p}_A = \{\dot{p}_{Am}\} T_D f V^{2/3}$	$\{\dot{p}_{Am}\}$	Maximum surface-area-specific assimilation rate ($J\ cm^{-2}\ d^{-1}$)[c]
	f	Michaelis-Menten term (see text)
	V	Structural volume (see text)
	T_D	Arrhenius temperature function
$T_D = \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T_K}\right)\cdot\left(1 + \exp\left(\frac{T_{AL}}{T_K} - \frac{T_{AL}}{T_L}\right) + \exp\left(\frac{T_{AH}}{T_H} - \frac{T_{AH}}{T_K}\right)\right)^{-1}$	T_A	Arrhenius temperature[c]
	T_L	Lower boundary of tolerance range (K)[c]
	T_{AL}	Rate of decrease at lower boundary (K)[c]
	T_{AH}	Rate of decrease at upper boundary (K)[c]
	T_1	Reference temperature (K)[c]
	T_H	Upper boundary of tolerance range (K)[c]
	κ	Fraction of utilized energy to somatic maintenance and growth[d]
$\dot{p}_C = \frac{[E]}{[E_G] + \kappa[E]}\left(\frac{[E_G]\{\dot{p}_{Am}\}V^{2/3}}{[E_m]} + \dot{p}_M\right)$	$[E_G]$	Volume-specific costs for structure ($J\ cm^{-3}$)[c]
	$[E_m]$	Maximum storage density ($J\ cm^{-3}$)[c]
	$\dot{p}_M$	Maintenance rate ($J\ d^{-1}$)
$\dot{p}_M = [\dot{p}_M]\ V$	$[\dot{p}_M]$	Volume-specific maintenance costs ($J\ cm^{-3}\ d^{-1}$)[d]
$\frac{dV}{dt} = (\kappa\dot{p}_C - \dot{p}_M)/[E_G]$		
	E_R	Energy allocated to reproductive buffer (J)
$\frac{dE_R}{dt} = (1-\kappa)\dot{p}_C - \left(\frac{1-\kappa}{\kappa}\right)\cdot\ \min(V_P, V)\cdot[\dot{p}_M]$	V_p	Structural volume at sexual maturity (cm^{-3})[c]
$\frac{dE_R}{dt} = \kappa\dot{p}_C - \dot{p}_M \mid \kappa\dot{p}_C - \dot{p}_M < 0$		Reproductive buffer dynamics when energy storage is too low
$L = \frac{V^{1/3}}{\delta_M}$	L	Mussel length (cm)
	δ_M	Dimensionless shape coefficient[d]

chlorophyll. In the particular case of filter feeder modeling, several studies have highlighted the need to calibrate X_K according to local conditions (Kooijman, 2006; Pouvreau et al., 2006).

In the present study, two individual growth models for the blue mussel *Mytilus edulis* were applied using both approaches, SFG and DEB, with the aim of: (1) calibrating both models based on a single parameter, the half-saturation coefficient X_K, (2) validating a set of parameters for *M. edulis* using at field and laboratory data from Norway and France, and (3) comparing the results obtained with both approaches.

2. Material and methods

2.1. The SFG-model

The model is based on our earlier works (Grant et al., 1993; Grant et al., 2007; Filgueira and Grant, 2009), which are in turn based upon the Kremer & Nixon equations (Kremer and Nixon, 1978) and it was developed in Matlab® (http://www.mathworks.com). A brief description of the main equations is included in Table 1. The ingestion function has been slightly modified compared to our previous studies, where ingestion depended on both phytoplankton and detritus concentration. In the present study, ingestion depends exclusively on phytoplankton concentration. The mg of carbon ingested per day depends on the weight of the mussel:

$$I = I_m f_{mi} \left(\frac{M_w}{M_{wRef}} \right)^{b_{mi}} \tag{1a}$$

where I_m is the reference ingestion rate (d^{-1}), f_{mi} is the dimensionless mussel ingestion function, M_w is the weight of the mussel, M_{wRef} is the mussel reference weight and b_{mi} is the dimensionless allometric exponent for mussel ingestion. The f_{mi} function depends on water temperature and phytoplankton concentration (X) following a Michaelis-Menten term:

$$f_{mi} = C_{mi} \ \exp(Q_{mi} T) \left(\frac{X}{X + X_K} \right) \tag{1b}$$

where C_{mi} is the dimensionless scaling constant that assures a value of unity at a specified mussel reference mass, Q_{mi} is the temperature rate constant for mussel ingestion ($°C^{-1}$), T is temperature (°C) and X_K is the half-saturation coefficient (μg Chl a L^{-1}) which is the food concentration when ingestion rate reaches half the maximum rate.

2.2. The DEB-model

The model is identical to the DEB mussel model presented in Rosland et al. (2009) using the same set of parameter values and it was constructed in Matlab® (http://www.mathworks.com). A brief description of the model is presented in Table 1, and a more thorough presentation of the model and the equations is given in Pouvreau et al. (2006) and Rosland et al. (2009). In the same way as for the SFG-model, we limit the detailed description of the model to the formulation of the ingestion function. We have adapted the DEB symbols and notations from Kooijman (2000), where braces {} denote quantities expressed as per unit surface-area of the structural volume and first derivatives with respect to time are indicated with overdots. The energy ingestion rate $\dot{p}_X$ (J d^{-1}) is proportional to the surface area of the mussel:

$$\dot{p}_x = \{\dot{p}_{Xm}\} T_D f V^{2/3} \tag{2a}$$

where $\{\dot{p}_{Xm}\}$ is the maximum ingestion rate per unit surface area (J cm^{-2} d^{-1}), T_D is the Arrhenius temperature function and $V^{2/3}$ is proportional to the surface of the mussel expressed by the structural volume V. As for the SFG-model, f scales the ingestion rate to the food concentrations (X) following a Michaelis-Menten term:

$$f = \frac{X}{X + X_K} \tag{2b}$$

The maximum surface-area-specific assimilation rate ($\{p_{Am}\}$ in Table 2) is equal to the maximum surface-area-specific ingestion rate $\{p_{Xm}\}$ multiplied by an assimilation constant a of value 0.75 (van der Veer, 2006).

2.3. Calibration of the half-saturation (X_K) coefficient

The half-saturation X_K coefficient (Eq. 1b and Eq. 2b for SFG and DEB respectively) was used to calibrate the model. The auto-calibration used a non-linear optimization algorithm (Nelder–Mead) to search for the parameter value of X_K which yielded the best fit between model and observations. The best fit is defined as the smallest deviation between simulated and observed mussel flesh mass for each site, where the deviation (D) is calculated by:

$$D = \frac{1}{N} \sum_{n=1}^{N} \frac{|M_s(n) - M_o(n)|}{M_o(n)} \tag{3}$$

where n is the observation index, N is the total number of observations in each dataset, and M_s and M_o are simulated and observed mussel flesh mass, respectively.

2.4. Norwegian datasets

The data are from laboratory and in situ experiments and include a time series of size data (mussel shell length and dry flesh mass) and environmental data (chlorophyll concentrations and water temperature). The laboratory datasets are from Austevoll research station (August 2006–April 2007, D1 to D4, following the nomenclature used by Rosland et al., 2009 for the different datasets) while the in situ experiments in suspended culture are from Toskasundet (August 2006–April 2007, D5), Austevoll (February 2007–December 2007, D6) and Flødevigen (March 2007–November 2007, D7). The laboratory data involved serial dilution of low seston waters to examine mussel feeding under these conditions. A more thorough description of the mussel characteristics (weight, density, etc.), sampling scheme through time and forcing time series can be found in Rosland et al. (2009) and Strohmeier et al. (2009).

2.5. French datasets

These experiments were carried out in Pertuis Breton between February 1999 and February 2000, however, only the period between February 1999 and September 1999 was analyzed, in order to avoid the spawning event that occurs between September and October. Spawning events were not modeled in the present study. The time series include size data (mussel shell length and dry flesh mass) and environmental data (chlorophyll concentration and water temperature). One dataset corresponds to mussels that were grown in suspended long lines (D8) and the other to mussels that were grown in bouchots (D9 and D10, bouchots are wooden poles anchored perpendicularly to the marine floor), the latter exposed to air 26.5% of the time. Two simulations were carried out for mussels cultivated in bouchots, assuming 26.5% (D9) and 0% (D10) emersion time. Although emersion implies different metabolic pathways, no changes were made in the model given the shorter aerial exposure (maximum of 1.7 h) and in the interest of comparing X_K values of D9 and D10 datasets under the same modeling set up. A detailed description of the

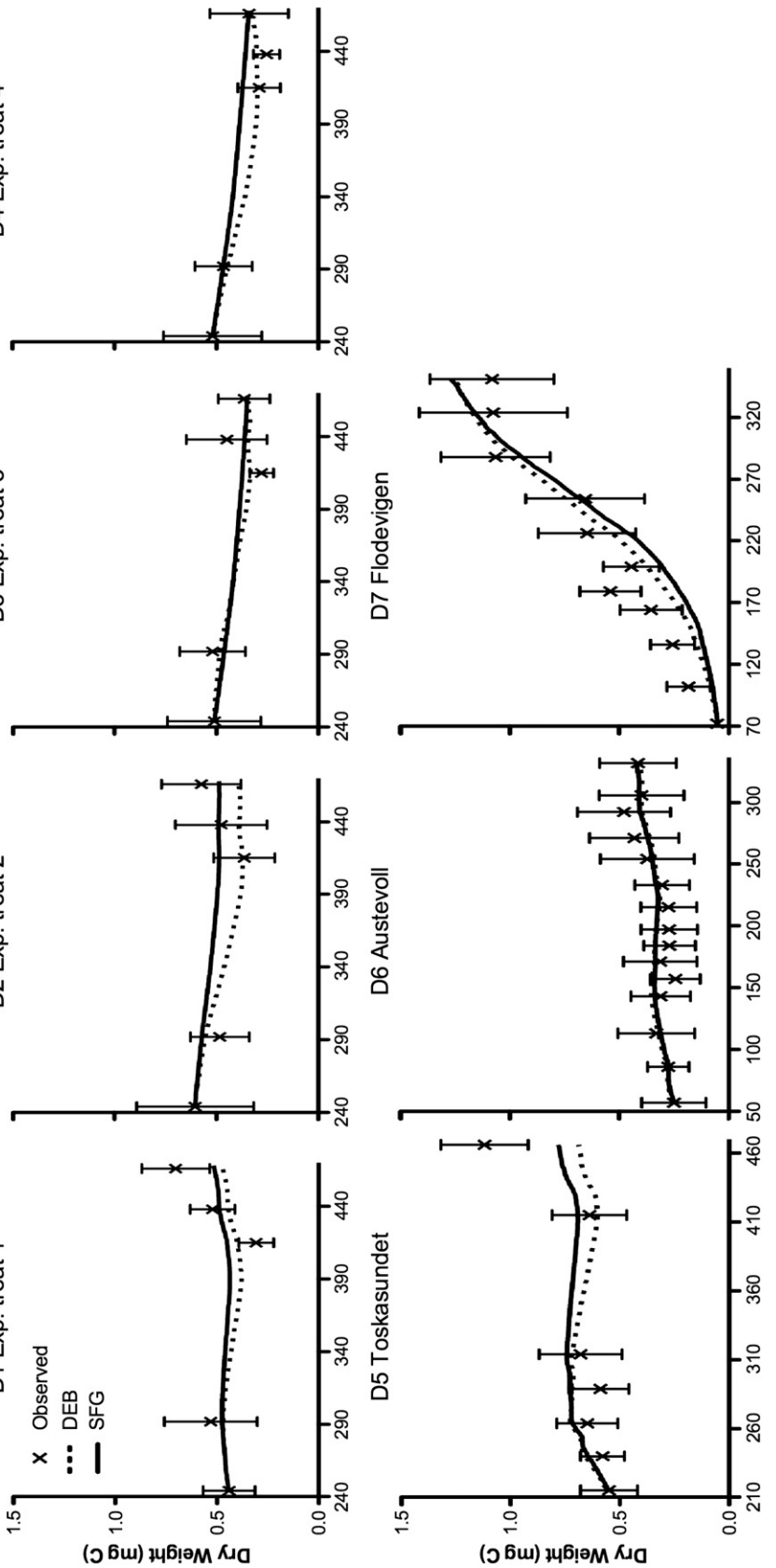

Fig. 1. Modeled (dashed and continuous lines for DEB and SFG, respectively) and observed (crosses with bars showing standard deviation) dry flesh mass (g) for the Norwegian datasets.

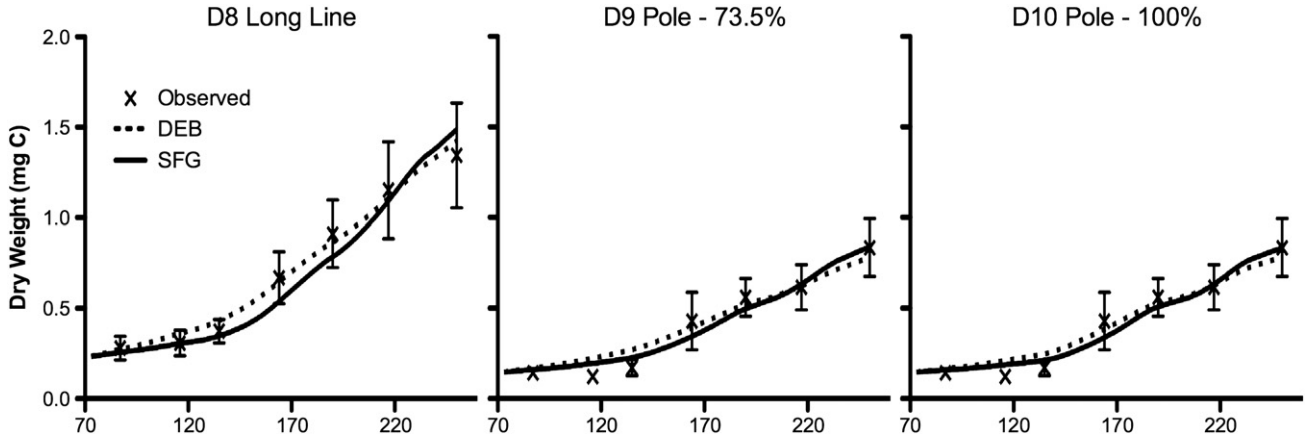

Fig. 2. Simulated (dashed and continuous lines for DEB and SFG, respectively) and observed (crosses with bars showing standard deviation) dry flesh mass (g) for the French datasets.

experiment, culture characteristics, sampling procedure and forcing time series can be found in Garen et al. (2004).

2.6. Sensititivity to changes in Xk

The models were tested for sensitivity to changes in the X_K values (+/− 10% of the calibrated X_K). The sensitivity was measured as the relative difference in mussel mass at the end of the model simulations:

$$S = \frac{M_{diff} - M_c}{M_c} * 100 \quad (4)$$

where M_{diff} and M_c are the final mussel mass for the simulation with calibrated and alternated X_K values respectively.

3. Results

3.1. Mussel growth simulation

Both models provide a prediction of mussel growth that is in good agreement with the observed values (Figs. 1 and 2, Table 2). For the Norwegian datasets (Fig. 1), the simulated weight is generally within the range of observed standard deviation. In Norwegian laboratory experiments, the growth is slightly overestimated by the SFG model in mid March (Julian day 438) in dataset D4 and by both approaches in late February (Julian day 415) in datasets D1 and D3. Despite this overestimation in dataset D1, at the end of the simulated period in mid April (Julian day 466) both models underestimate the mussel weight. The same underestimation pattern at the end of the simulation period (mid April, Julian day 466) is observed in the Toskasundet dataset (D5), reaching an average estimated weight 35% lower than the observed one. On the contrary, the Flødevigen dataset (D7) is slightly underestimated at the beginning of the simulation, between mid April and late June (Julian day 102 and 179, respectively). However this trend is corrected through time, yielding a good agreement at the end of the simulated period between observed and modeled values. Nevertheless, these discrepancies result in the highest deviation with the observed values of the study, a total of 36.10% and 23.93% (Table 2) for SFG and DEB respectively for the Flødevigen dataset (D7). The averaged deviation when all the datasets of the study are pooled together is 17.3% and 12.0% for SFG and DEB respectively, indicating an overall better fit for DEB compared to SFG.

For the French datasets (Fig. 2), the growth of the mussels cultivated on longlines (D8) is well simulated by both approaches, producing all the predicted values within the range of observations for both models, SFG and DEB. For mussels cultivated on poles, the two emersion simulations (26.5% and 0% for D9 and D10 respectively) are similar and in fairly good agreement with observed values (Fig. 2) with the exception of the period late April (Julian day 116) to mid May (Julian day 135) when both methods overestimate the weight of the mussels. The difference between emersion time in both datasets, 26.5% and 0%, is reflected in the X_K values, being 2.38 and 4.08 μg chla l^{-1} and 1.33 and 3.30 μg chla l^{-1} for SFG and DEB respectively. The deviations between

Table 2
Averaged chlorophyll content as well as optimized X_K values, deviation between modeled and observed values (calculated with Eq. 3) and, relative change in weight (calculated with Eq. 3) decreasing and increasing the optimized X_K by 10% in both SFG and DEB approaches for all datasets.

Dataset		SFG				DEB			
	Chlorophyll	X_K	Deviation	Relative weight change (%)		X_K	Deviation	Relative weight change (%)	
	μg chla l^{-1}	μg chla l^{-1}	%	X_K − 10%	X_K + 10%	μg chla l^{-1}	%	X_K − 10%	X_K + 10%
D1 exp. treat 1	0.66	2.78	22.80	3.98	−3.33	1.93	9.58	5.75	−4.95
D2 exp. treat 2	0.39	4.84	17.15	1.97	−0.99	2.71	10.02	5.69	−4.82
D3 exp. treat 3	0.14	6.76	14.76	0.75	−0.62	0.88	6.77	6.27	−5.32
D4 exp. treat 4	0.01	54.90	12.14	0.12	−0.10	0.04	4.81	6.23	−5.28
D5 Toskasundet	0.91	2.49	15.35	4.77	−4.00	2.26	11.19	8.17	−6.88
D6 Austevoll	1.17	2.93	9.98	7.20	−5.97	2.62	10.53	5.21	−4.78
D7 Flødevigen	1.65	0.43	36.10	6.06	−5.49	0.41	23.93	6.42	−5.53
D8 Pertuis Breton — longline	3.07	1.61	14.77	6.48	−5.75	1.06	4.79	4.73	−4.33
D9 Pertuis Breton — pole 26.5%	4.65	2.38	15.29	7.39	−6.48	1.33	17.27	7.53	−6.11
D10 Pertuis Breton — pole 0%	4.65	4.08	14.69	8.56	−7.33	3.30	20.67	4.18	−3.86
Pooled data	1.7 ± 1.77	8.3 ± 16.46	17.3 ± 7.39	4.7 ± 2.94	−4.0 ± 2.64	1.6 ± 1.08	12.0 ± 6.57	6.0 ± 1.20	−5.2 ± 0.86

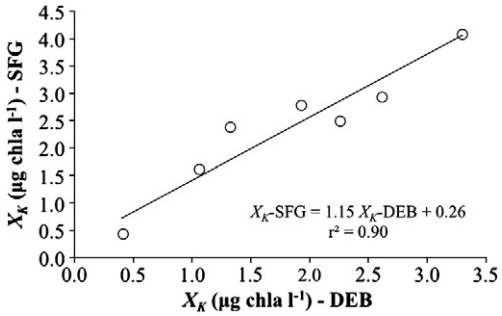

Fig. 3. Optimized X_K values for DEB and SFG for datasets D1, D5–D10 and the corresponding Type II linear regression (continuous line).

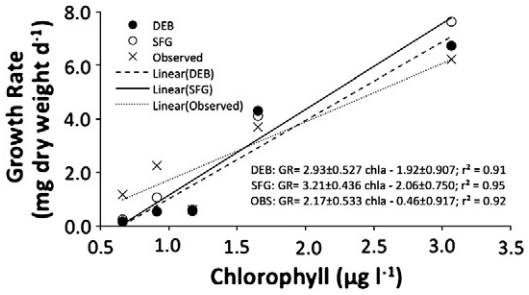

Fig. 5. Growth Rate for DEB, SFG and observations versus the chlorophyll content for datasets D1 to D8 as well as the corresponding linear regressions (DEB: dashed line, SFG: continuous line, OBServations: pointed line).

estimated and observed weight indicate that the simulations for mussels cultivated in long lines, 14.77% and 4.79% for SFG and DEB respectively, are better than those for poles, with averaged values of 15.0% and 19.0% for SFG and DEB respectively.

3.2. Comparing X_K values in both modeling approaches

A sensitivity test was carried out to quantify the effect of X_K values on growth at the end of the simulated period. Two new scenarios were run in each dataset varying the optimal X_K value by ±10%. The final mussel weight observed in these simulations was compared to that observed in the optimal scenario, with differences expressed as a relative change in weight (Table 2). The results indicate that mussel weight is not sensitive to changes in X_K values in low chlorophyll content datasets in the SFG approach, which reflects the extremely high estimated X_K values. Given this lower sensitivity of the weight to X_K changes at low chlorophyll content (lower than 2%, Table 2), datasets D2, D3 and D4 were not considered in the comparison of X_K from both approaches. In addition, the reproductive buffer in the DEB model turns negative in datasets D2, D3 and D4. Given that a state variable with a negative value is neither consistent with mass conservation rule nor with DEB theory, these simulations have been removed from further analysis.

The relationship between the X_K values DEB and SFG can be expressed in a statistically significant Type II linear relationship that explains 90% of the variance (Fig. 3). The slope of the regression, 1.15 ± 0.164, is not statistically different than unity ($t = 0.933$, $p = 0.394$, Zar, 1984), indicating that both approaches follow the same pattern in the different datasets. In addition, the intercept, 0.26 ± 0.337, includes the origin, indicating that the values of X_K –(SFG) are not statistically different than those of X_K –(DEB).

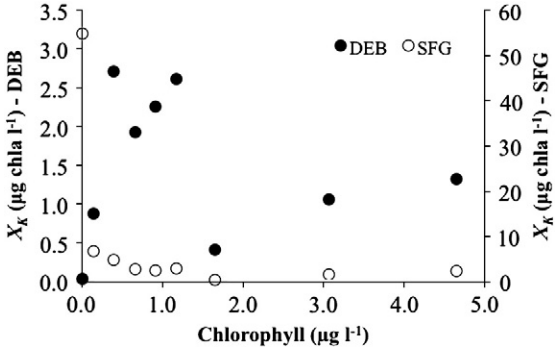

Fig. 4. Optimized X_K values for DEB and SFG versus the chlorophyll content for datasets D1 to D8.

3.3. X_K values and chlorophyll content

The optimized value of X_K was analyzed according to the observed average chlorophyll content of each dataset (Fig. 4). Datasets D9 and D10 were not included in this analysis because they represent situations in which the mussels were not always submerged, in which case they can exert a bias when compared with the other datasets. In the case of the DEB model, we were not able to determine an obvious relationship between X_K and the chlorophyll content. In the SFG approach, the relationship could be expressed as a negative power function; however, the significance of the regression would depend mainly on of the low sensitivity of X_K values for the three datasets, D2, D3 and D4, with lower chlorophyll and extremely high estimated X_K values. Therefore, in order to avoid this bias, those three points were not considered. In this new scenario and similar to the DEB model, no significant relationships were observed between X_K and chlorophyll content.

3.4. Growth rate and chlorophyll content

The mussel growth rate for the entire study period was calculated for each dataset based on the initial and final weights as well as the period length and compared to the corresponding average chlorophyll content. As in the previous section, datasets D9 and D10 were not included in this section because they are not comparable to the others. Three statistically significant linear regressions were obtained for DEB, SFG and observed values (Fig. 5). Their comparison using ANCOVA yields a common slope (ANCOVA: $F = 0.759$, $p = 0.587$, Zar, 1984), emphasizing the good agreement of both modeling approaches with the observations.

4. Discussion

A use of both DEB and SFG approaches has often been in modeling bivalve growth (see Introduction for references). Given that growth integrates all the processes involved in model development, the agreement between observations and predictions is crucial for groundtruthing the validity of these simulations. In addition to the obvious importance of predicting production of commercial species, the implications of bivalves as “ecosystem engineers” (Jones et al., 1994) position bivalve growth modeling as a cornerstone for more complex ecological models used for ecosystem-based management (e.g. Filgueira and Grant, 2009). SFG and DEB approaches share the same goal, that is, to describe the energetic processes of an organism. However, the conceptual foundation is different in each case. Assuming that the specific hypotheses of both approaches are valid, SFG and DEB models should be able to successfully represent the real world, and consequently provide similar results in agreement with the observations. Therefore, from a practical point of view, both modeling approaches require the translation of the hypotheses into

mathematical equations and the parameterization of those equations according to the environmental conditions.

Model parameterization is one of the most challenging steps in the development. Recently, a number of mathematical tools have been applied to estimate parameters. Duarte et al. (2010) designed an objective protocol for model calibration based on a multi-scenario analysis using different sets of parameters. An alternative approach is the use of non-linear optimization processes that estimate the value of a set of parameters, minimizing the discrepancies between the model results and observed values. For example, Bacher and Gangnery (2006) used the Nelder–Mead method implemented in Matlab® to calibrate two parameters of DEB to simulate the growth of *Crassostrea gigas*. In the same way, Rosland et al. (2009) calibrated three parameters of DEB for different *M. edulis* populations in Norwegian waters.

In this study, growth of *M. edulis* was modeled using SFG and DEB approaches. Given the several ways observed in different studies and ecosystems to trigger the spawning (see Introduction for references), reproduction processes have been not modeled. In addition, reproduction might exert a minimum effect in this study because a distinct spawning signal in terms of a distinct flesh mass reduction is not evident in these datasets. Both models were parameterized using available data taken from the literature with the exception of X_K, which was calculated for each dataset by auto-calibration. This parameter was previously used as the sole basis for calibrating a DEB model of growth in *C. gigas* (Pouvreau et al., 2006; Ren and Schiel, 2008; Bourlès et al., 2009). Both modeling approaches were able to reproduce the general growth pattern in all datasets, although some deviations were observed. Datasets with the lowest chlorophyll content, D2, D3 and D4, provided a good estimation of mussel growth in both SFG and DEB models. However, estimated X_K were unrealistic, extremely high and not sensitive in the case of SFG and generated negative reproductive buffer in the DEB model, which is neither consistent with mass conservation rules nor with DEB theory. For these reasons, D2, D3 and D4 were not considered for further analysis. In addition, neither model is able to simulate the steep growth rate observed at the end of D1 and D5 datasets, as well as at the beginning of D7, following the nomenclature used by Rosland et al. (2009) for the different datasets. These discrepancies could be caused by errors associated with these time series, the model itself or both. For example, Strohmeier et al. (2009) found that there were no correlation between clearance rate of mussels and temperature in datasets D1–D5. The temperature regulation of feeding rate, which in the DEB model is based on the Arrhenius function, may put too high constraints on the feeding rate compared to the real system. Thus, the lack of feeding response in the high Chl *a* and low temperature periods in D1 and D5 could be due to erroneous temperature regulation of the feeding process. Nevertheless, both SFG and DEB growth models performed well by tuning only this single parameter, X_K, providing agreement with the observed growth datasets, as well as consistency of X_K values between both approaches. Therefore, these sets of parameters and an optimization procedure to calibrate X_K seem an adequate way to successfully apply both modeling approaches to these datasets. Minimizing the number of parameters that must be estimated constitutes an important advance for future studies, reducing complexity and uncertainties caused by overtuning the model. In addition, the use of an optimization tool is an objective way to calibrate the model, and avoids the need for "eyeball" estimations.

Both approaches required specific calibration to local conditions, restricting their general application to different ecosystems. The calibration is performed only for the half-saturation constant of the Michaelis-Menten term that regulates the ingestion of food. This feeding parameter requires that for higher X_K values, more food is required to reach maximum ingestion rates. This can be observed by comparing D9 and D10, which use the same forcing time series, but with immersion time 26.5% higher in D10, allowing the mussels to feed longer. Consequently, a higher X_K value is necessary at D10 to compensate for the longer feeding time in order to achieve the observed growth results. Therefore, with the exception of D9 and D10 datasets, in which the emersion variable is involved, a relationship between food supply and X_K would be expected, if the quantifier of food was appropriate. The observed pattern between average growth rate and chlorophyll content suggests the use of chlorophyll content as a quantifier to describe mussel performance. In addition, this relationship was carried out with pooled datasets from two different environments, Norwegian fjords and Atlantic French waters, suggesting that higher chlorophyll values result in higher mussel growth independent of the studied ecosystem. However, this response should be tested across other different ecosystems to establish further conclusions about its general application. In addition, other characteristics of the ecosystem, e.g. hydrodynamics, and mussel population, e.g. cultured density, can affect the available food, e.g. local chlorophyll depletion, and therefore they have to be considered in further experimental designs.

The relationship between X_K and the food quantifier should permit the construction of a general model that does not need calibration in order to perform in different ecosystems. Given that such a relationship was not obtained in this study, the calibration of the model using X_K is limited to use as an empirical adjustment to a specific environments. Although chlorophyll has been commonly used as a variable to represent food availability and is correlated with observed growth rate, other environmental variables can exert an important effect on bivalve feeding and growth. Similar results were observed in *C. gigas* by Pouvreau et al. (2006), who suggested that site-specific responses are due to phenotypic adaptation in clearance rate and selection capacities of oysters or to variation in phytoplankton chlorophyll to carbon ratio. Kooijman (2006) demonstrated that silt and other particles bivalves shunt to pseudo-feces production may affect the X_K value. Similarly, Ren (2009) confirmed the importance of particulate inorganic matter in the functional response of energy uptake by *Perna canaliculus*, suggesting that its inclusion in X_K could improve the estimation of ingestion rate. The effect of changes in the chlorophyll to carbon ratio was also discussed by Ren and Schiel (2008) and demonstrated by Grangeré et al. (2009), who used carbon as a food level variable in simulating the growth of *C. gigas*. Other quantities such as particulate organic matter, particulate organic carbon and phytoplankton enumeration expressed both in cell concentration and biovolume have been studied by Bourlès et al. (2009), demonstrating that phytoplankton enumeration yields better growth model performance than chlorophyll concentration. In addition, the potential contribution of other food sources such as heterotrophic plankton (Davenport et al., 2000; Trottet et al., 2008) or detritus (e.g., Bacher and Gangnery, 2006) may be important in bivalve nutrition.

These different approaches of quantifying food availability and the need for site-specific calibration to simulate growth reflect the complexity of bivalve feeding behavior. In fact, although bivalve feeding ecology has been widely studied under controlled laboratory conditions and in situ experiments (see review of Bayne et al., 1993), the effect of different trophic variables as well as their interaction with ingestion rate is yet inconclusive. The improvement of food level quantifiers and/or the sophistication of the functional response to food availability directed to successfully determine ingestion constitutes the future of bivalve research. This is crucial in low food environments where the models have greater difficulties to reproduce the bioenergetics of the mussels. Recent model studies (Bourlès et al., 2009) on Pacific oyster (*C. gigas*) showed that phytoplankton enumeration was a better food proxy than particulate organic matter and carbon, chlorophyll a concentration. Recent studies on mussels (Alunno-Bruscia et al., in prep) have not revealed any clear differences between chlorophyll *a*, phytoplankton enumeration or particulate carbon as food proxies.

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