Modelling mussel shell and flesh growth using a dynamic net production approach

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Abstract

Understanding and modelling bivalve growth dynamics under variable environmental conditions are crucial for the development of management and sustainability aquaculture plans. This work proposes a new dynamic bivalve growth model that combines net production Dynamic Energy Budget (DEB) theory and the species-specific growth dynamics of the Ecophysiological Model for Mussels (EMMY). In our approach, the assimilated energy is first used for metabolic requirements, and the surplus partitioned between shell formation, somatic growth, reserves and reproduction. We also incorporate site-specific estimates for feeding and spawning. We compare the performance of our model with a standard DEB model for the simulation of mussel growth in a low seston environment (Ría de Ares-Betanzos, NW Spain). Our model provides realistic estimations of shell and soft tissue growth, while the standard DEB model overestimates soft tissue growth. Indeed the Relative Mean Square Error (RMSE), which measures the discrepancy between field and simulated shell-soft tissue relationships, of our model is below 10% of that obtained with the standard DEB. Our model also captures the different effects of environmental variability on shell and flesh growth.

Keywords: energy fluxes, environmental variability, low seston, mussels, shell, soft tissue

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1. Introduction

Mussels play important ecological roles as habitat or prey for other organisms (Rilov et al., 2008), and as active participants in pelagic-benthic coupling (Dame, 1993; Zúñiga et al., 2014). Mussel aquaculture is a sustainable food production system with important commercial (Díaz et al., 2014; Labarta et al., 2004) and environmental value. Indeed mussel farming has been proposed as a tool to mitigate eutrophication in coastal areas (Lindahl et al., 2005). The growing importance of aquaculture in food production in the past decades, and the high dependence of extensive aquaculture on environmental conditions have increased the demand for diagnostic tools to check the effect of climate change on bivalve aquaculture (Filgueira et al., 2016; Montalto et al., 2016), as well as management and sustainability plans (Bergström et al., 2015; Byron et al., 2011; Costa-Pierce, 2008). Understanding bivalve growth dynamics and their response to environmental variability is crucial for the development of these plans, particularly in areas that support large aquaculture production, such as the Galician Rías (NW Spain) (Labarta et al., 2004).

Bivalve growth dynamics along their lifespan under variable environmental conditions have been modelled using net assimilation and net production dynamic models (Kooijman, 2010; Ledder, 2014; Lika and Nisbet, 2000). Net assimilation models assume that the acquired energy is stored in a reserve buffer prior to mobilization for maintenance, growth and reproduction. These models follow the formal Dynamic Energy Budget theory (Kooijman, 2010) and are referred as DEB models. Net production models (Lika and Nisbet, 2000) assume that the assimilated energy is first used for metabolic work and the surplus, if any, distributed between growth, reproduction and reserves. Although some net production approaches, such as Scope for Growth (SFG) models (Brigolin et al., 2009), or the species-specific ecophysiological model for mussels (EMMY, Scholten and Smaal (1998, 1999)), have also been proposed, the standard DEB model has been extensively used during the last decade to simulate mussel growth in natural environments (Béjaoui-Omri et al., 2014; Duarte et al., 2012; Picoche et al., 2014; Rosland et al., 2009; Sarà et al., 2012).

The application of DEB models to simulate bivalve growth has shown good agreement between observed and simulated shell lengths, but a poor performance in terms of soft tissue weight (Duarte et al., 2012; Picoche

et al., 2014; Saraiva et al., 2012; Troost et al., 2010). This disagreement may be attributed to the energy allocation rules (Picoche et al., 2014; Troost et al., 2010). Bivalve DEB models assume that these organisms have a single structure, the somatic soft tissue, which receives all the energy allocated for growth. The shell is considered a dissipation product, which formation costs are included in the metabolic expenditure (Pouvreau et al., 2006), and estimated through an allometric relationship with the structural tissue. However some works have pointed out that shell production is an energetically demanding process, mainly due to the formation of the organic matrix, that can consume a significant part (up to 50%) of the energy income (Arranz et al., 2016; Labarta et al., 1999; Palmer, 1992; Thomsen et al., 2013). In addition, the assumed link between shell and structural tissue may hinder a proper modelling of the mismatch between shell and soft tissue growth (Fuentes-Santos et al., 2017; Picoche et al., 2014). The species-specific ecophysiological model developed by Scholten and Smaal (1999), which allocates part of the net production to shell growth and assumes an age-dependent energy partitioning between reserves and growth, overcomes the potential limitations of DEB. However, since this approach estimates mussel growth through carbon and nitrogen fluxes, the shortage of organic carbon and nitrogen content data in both seston and mussels limits its application in nature.

The aim of this work is to develop a new dynamic growth model for bivalves that provides a realistic description of mussel growth in ecosystems with low seston concentration. Our proposal is based on a net production scheme and accounts for both shell and soft tissue growth costs. This new approach also incorporates site and species-specific information regarding the physiological and metabolic performance of mussels in low seston environments (Arranz et al., 2016; Fernández-Reiriz et al., 2007; Filgueira et al., 2008), to model energy uptake and maintenance costs, as well as about the phenology and extension of the reproductive cycle (Fuentes-Santos et al., 2016).

2. The species and its environment

The Mediterranean mussel *Mytilus galloprovincialis* was used as model species in this study. *M. gallprovicialis* is the dominant mussel species in the Galician Rías (NW Iberian coast). During the last decades CSIC-PROINSA Mussel lab has conducted a series of laboratory and field studies

dedicated to the culture of *M. galloprovincialis* in the Ría de Ares-Betanzos (Labarta and Fernández-Reiriz, 2019) (Figure 1). These studies have allowed us to understand the physiological performance and growth dynamics of mussels under the specific environmental conditions of this area, which shall be of great value in the formulation of our model.

The Galician Rias, at the northern limit of the eastern boundary upwelling system of the North Atlantic, are low seston environments with total particulate matter (TPM) and $Chl\,a$ usually below $3\,mg/l$ and $5\,\mu g/l$ respectively (Figueiras et al., 2002). Despite this low food availability, the synthesis of high quality seston during the upwelling season (from March-April to September-October), and the protection against strong winds and storms provided by the intricate topography of the rías, result in a favourable environment for suspended mussel culture (Álvarez Salgado et al., 2011).

Figure 2 shows the environmental conditions observed in the Ría de Ares-Betanzos during 2014-2015, which were used as input variables to validate our model. Daily values of global solar irradiance ($MJ/(m^2 day)$) at the neighbour meteorological station CIS-Ferrol (Figure 1) were provided by the Galician Meteorological Agency (Meteogalicia, http://www2.meteogalicia.es). Sea surface temperature, particulate organic matter (POM) and seston quality ($f = POM/TPM$) were provided by the weekly monitoring conducted by CSIC-PROINSA Mussel Lab at the cultivation area of Lorbé (Figure 1). Sea surface temperature was measured with a multiparameter probe YSI 556. Total (TPM) and organic (POM) particulate matter were determined gravimetricaly (see details in Aguiar et al. (2015)). Solar irradiance, sea surface temperature and food quality follow a clear seasonal pattern with high values in summer and low values in winter, while POM, which was below $1\,mg/l$ during the whole period, has a more irregular pattern (Figure 2).

3. Model formulation

The dynamic growth model developed in this work is based on a net production approach (Lika and Nisbet, 2000), which assumes that the assimilated energy is first used for maintenance and the surplus, if any, partitioned between growth and reserves, being part of these reserves allocated for reproduction. Our proposal also incorporates the species-specific energy allocation rules introduced in the EMMY (Scholten and Smaal, 1998, 1999),
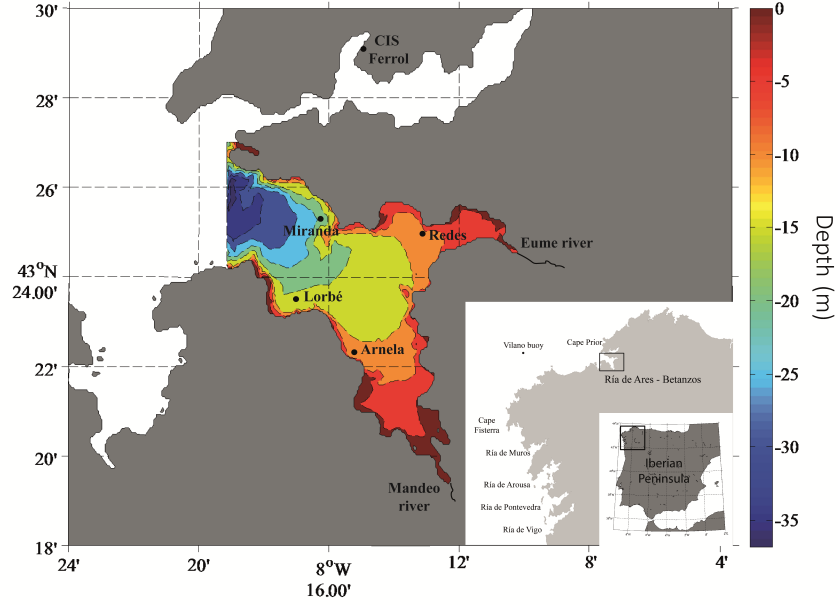
Figure 1: Ría de Ares Betanzos (NW Iberian coast), mussel growth was simulated under the environmental condition of the cultivation area of Lorbé. Solar irradiance data were taken from the meteorological station located in CIS-Ferrol. These maps were prepared with Matlab. version: MATLAB R2009b. URL: www.mathworks.com

which includes a state variable for shell formation. Following these assumptions our model describes the energy fluxes through four state variables.

- Shell (W_S), which comprises both the organic and inorganic shell compounds.

- Somatic organic tissue (OW_{som}).

- Reserves (E), corporeal material stored for future allocation to other components.

- Reproduction buffer (R), fraction of the reserves available for maturation processes in juveniles, which involves the development of the reproductive organs, and reproduction in adults, which involves gamete formation and energy stored for future spawning.

Shell (W_S) and somatic organic tissue (OW_{som}) are expresssed in grams (g), whereas reserves (R) and the reproduction buffer (R) are expressed in Joules

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(J). Therefore, following Kooijman (2010), we have a net production DEB model with two structures, shell (W_S) and somatic tissue (OW_{som}). DEB models assume isomorphy and express the structure in volume units, which is an abstract state variable related to shell length through a shape coefficient δ, which is obtained by fitting the relationship between shell length and soft tissue weight, $L = \delta V^{1/3}$, in starved mussels (Rosland et al., 2009). In this work structure is quantified in terms of dry weight, which can be directly measured. We estimate the total biomass of each component rather than the carbon and nitrogen fluxes of the EMMY (Scholten and Smaal, 1998, 1999). The dynamics and parameters of our model are outlined in Figure 4 and Table 1. Below we detail the assimilation and allocation rules used to formulate the model.

3.1. Feeding

Mussels obtain food by filtering water and retaining particles in their gills. The clearance rate, CR (l/h), depends on body size and may be depressed by high suspended matter concentration. Given the low seston concentration in our study area (see Section 2), we can assume that the clearance rate does not depend on food availability and estimate it by an allometric relationship with shell length (L) (Filgueira et al., 2008)

$$CR = min\left\{a_{CR}L^{b_{CR}}, maxCR\right\} \tag{1}$$

where $maxCR$ is the maximum clearance rate, a_{CR} and b_{CR} are species-specific allometric parameters (Table 1). The ingestion rate (IR) is obtained as the product of clearance rate by the particulate organic matter concentration ($IR = CR \times POM$). Food absorption and, consequently the energy assimilated by mussels, is determined by the ingestion rate and absorption efficiency (AE), which in our area is mainly driven by the organic content of seston (Fernández-Reiriz et al., 2007). Therefore the assimilation rate, A (J/h), is

$$A = \mu_{POM}IR \times AE = \mu_{POM}IR\left(a_{AE} - \frac{b_{AE}}{f}\right) \tag{2}$$

where μ_{POM} is the energy content of organic seston, and $f = POM/TPM$ is a measure of food quality. a_{AE} and b_{AE} are species-specific parameters (Table 1).

3.2. Maintenance

Part of the energy assimilated by mussels is expended on metabolic processes. In the same line as Scholten and Smaal (1998) we quantify metabolic expenditure (M) as the energy investment on respiration and excretion, therefore

$$M = \mu_{O_2} Resp + \mu_{NH_4-N} Exc \tag{3}$$

where μ_{O_2} and μ_{NH_4-N} are the conversion factors for oxygen consumption and ammonia excretion, respectively. Following Arranz et al. (2016) respiration, $Resp$ (mgO_2/h), and ammonia excretion, Exc $(\mu g_{NH_4-N}/h)$, can be estimated by allometric relationships with shell length (L)

$$Resp = a_{resp} L^{b_{resp}} \tag{4}$$

$$Exc = a_{exc} L^{b_{exc}} \tag{5}$$

where a_{resp}, b_{resp}, a_{exc} and b_{exc} are species-specific allometric parameters (Table 1).

3.3. Energy partitioning

Net production is defined as the difference between assimilated energy and metabolic expenditure $(A - M)$. In case of negative net production, i.e. when the assimilated energy cannot meet the metabolic costs $(A - M < 0)$, reserve energy (E) is used to cover the deficit. The individual dies when the reserve energy drops to 0. When the assimilated energy is larger than the metabolic requirements $(A - M > 0)$, the net production is partitioned between growth and reserves.

Partitioning of net production between growth and reserves depends on the total energy content of the individual $\Phi = \mu_{OT} OW_T$, where OW_T is the organic soft tissue dry weight, i.e. the sum of structure (OW_{som}), reserves (E/μ_{OT}) and reproductive buffer (R/μ_{OT}), and μ_{OT} the corresponding energy conversion factor (Table 1). Let t_1 denote a given day in the dynamic approach, if $\Phi(t_1) \leq \max_{0 < t < t_1} \Phi(t)$ all the energy is allocated to reserves, thus

$$dE/dt = A - M \tag{6a}$$

$$dW_S/dt = dOW_{som}/dt = 0 \tag{6b}$$

where, for any state variable X, $dX/dt = dX(t_1)/dt$ denotes its time derivative of X evaluated at time t_1, we omit t_1 in the model equations to simplify the notation. When $\Phi(t_1) > \max_{0<t<t_1} \Phi(s)$, the net production is partitioned between reserves and growth. Juveniles expend most energy in growth, while adults allocate a larger amount of resources to reproduction (Scholten and Smaal, 1999). Thus, as part of the reserve energy is used for maturation (in juveniles) or reproduction and gamete formation (in adults), the proportion of energy allocated to reserves increases with age. The energy allocated for growth is divided between shell formation and somatic tissue growth. The corresponding dynamic equations are

$$dE/dt = \kappa_E (A - M) - \kappa_R I (E_{frac} > E_{gamet}) \tag{7a}$$

$$dW_S/dt = \frac{(1 - \kappa_E) \kappa_S (A - M)}{E_{gS}} \tag{7b}$$

$$dOW_{som}/dt = \frac{(1 - \kappa_E) (1 - \kappa_S) (A - M)}{E_{gT}} \tag{7c}$$

In (7a) κ_E is the fraction of energy allocated for reserves and κ_R the fraction of reserves allocated for reproduction, $I(\cdot)$ is the indicator function, i.e. $I(E_{frac} > E_{gamet}) = 1$ if $E_{frac} > E_{gamet}$ and 0 otherwise, where $E_{frac} = E/\Phi$ is the reserve density, i.e. the fraction of the total energy content stored in the reserves, and E_{gamet} the minimum reserve density needed for gametogenesis. The fraction of energy allocated for reserves, κ_E increases with age as follows (Bayne and Newell, 1983; Scholten and Smaal, 1999)

$$\kappa_E = \left(1 + a_\kappa e^{-b_\kappa age)}\right)^{-1} \tag{8}$$

where a_κ and b_κ are species-specific parameters (Table 1). Returning to the partitioning dynamics (7), κ_S in expression (7b) is the fraction of energy allocated for growth that is invested in shell formation. $E_{gT} = \mu_{OT}$ (J/mg) is the unitary costs of organic soft tissue growth, which is assumed to be equal to the energy content of organic tissue. $E_{gS} = \mu_{OS}P_{OS} + \mu_{IS}(1 - P_{OS})$

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is the unitary cost of shell formation, where P_{OS} is the organic fraction of shell, and μ_{OS}, μ_{IS} the energy content of the organic and inorganic shell compounds.

When the reserve density, i.e. the fraction of the total energy content stored as reserves $E_{frac} = E/\Phi$, is higher than the gametogenesis threshold (E_{gamet}), $E_{frac} > E_{gamet}$, a fraction of the reserves, κ_R, is allocated in the reproductive buffer for gamete formation (Bayne, 1976)

$$dR/dt = \kappa_R E \tag{9}$$

Spawning occurs when the environmental conditions are favourable. in our study area spawning is triggered by an increase in solar radiation in late-winter (Fuentes-Santos et al., 2016). Spawning consists on the release of a fraction of gametes κ_{spawn} while the gonado-somatic index (gsi) is above a given threshold, $GSI > minGSI$ (Troost et al., 2010).

The allometric relationship between shell length and shell weight is used to estimate shell length in each step of the model $L = a_L W_S^{b_L}$, wher a_L and b_L are species-specific parameters (Table 1). Soft tissue dry weight (W_T) is obtained by adding the somatic, reserves and reproduction compounds as follows.

$$W_T = \frac{1}{P_{OT}} \left(OW_{som} + \frac{E}{\mu_{OT}} + \frac{R}{\mu_{OT}} \right) \tag{10}$$

where P_{OT} is the organic fraction of soft tissue (Table 1).

3.4. Effect of temperature

The effect of sea water temperature in the feeding and metabolic rates was included through the Arrhenius factor, T_{cief}, defined by the following equation

$$T_{cief} = exp \left(\frac{T_a}{T_1} - \frac{T_a}{T} \right) \tag{11}$$

where T_a is the arrhenius temperature, T_1 is the reference temperature, and $T = 273.15 + SST$ is the observed sea surface temperature in Kelvin. We

consider $T_a = 5800\,K$, as done by Béjaoui-Omri et al. (2014) to model the growth of *M. galloprovincialis* by a standard DEB, and the mean SST of our study area. $T_1 = 288.15\,K$ as reference temperature.

3.5. Determination of κ_s

To run the model we need to select a value for κ_s, the parameter that determines the partition of growth energy between shell and somatic organic tissue, that provides realistic simulations of mussel growth. To do that we use the allometric relationship between shell length and soft tissue observed in field data, $\log W_T = -12.38 + 3.07 \log L$, as criterion to select κ_s. Field data where provided by the culture monitoring of CSIC-PROINSA Mussel Lab, which follows mussel growth through sampling at seeding, thinning-out and harvesting.

We simulated the growth of mussels under constant environmental conditions for $\kappa_s \in [0, 0.9)$, where $\kappa_s = 0$ implies that mussels do not invest energy in shell formation, and $\kappa_s = 0.9$ allocates the 90% of the growth energy for shell formation. Simulations were performed with initial shell length $L_0 = 15\,mm$, soft tissue dry weight $W_{T0} = 0.02\,g$, and reserve density $E_{frac} = 1/3$ during $n = 350$ days under the following environmental conditions: $T = 15^oC$, $Rad = 11\,MJ/(m^2 day)$. $POM = 0.6\,mg/L$, $f = 0.6$. For each κ_s value we obtain the simulated shell length $\{L^\star_{\kappa_s,i}\}_{i=1}^{350}$ and dry soft tissue weight $\{W^\star_{T,\kappa_s,i}\}_{i=1}^{350}$ growth curves. Using the allometric relationship introduced above, we compute the predicted soft tissue dry weights, $\{W_{T,\kappa_s,i}\}_{i=1}^{350}$, for mussels with shell length $\{L^\star_{\kappa_s,i}\}_{i=1}^{350}$. Finally, we measure the discrepancy between simulated and allometric dry weight values through the relative mean square error (RMSE).

$$RMSE\left(\kappa_S\right) = \frac{1}{n} \sum_{i=1}^{n} \left(\frac{W^\star_{T,\kappa_s,i} - W_{T,\kappa_s,i}}{W_{T,\kappa_s,i}} \right)^2 \tag{12}$$

and select κ_s as the value that minimizes this measure. As we can see in Figure 3 (left) the minimum $RMSE$ is obtained with $\kappa_S = 0.7$, i.e. when 70% of the growth energy is allocated for shell formation. Figure 3 (centre) shows that small values of κ_S generates small with abnormally large tissue weight and slow shell growth, while large values of κ_s provides mussels with fast shell growth but low flesh weight. Figure 3 (right) shows that according to the energy partitioning determined by equation (8) and $\kappa_s = 0.7$ juvenile

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mussels allocate approximately 50% of the net production to shell formation (red line) and reduce the fraction of energy allocated for shell and soft tissue (blue line) growth in benefit of reserves (black line) during growth.
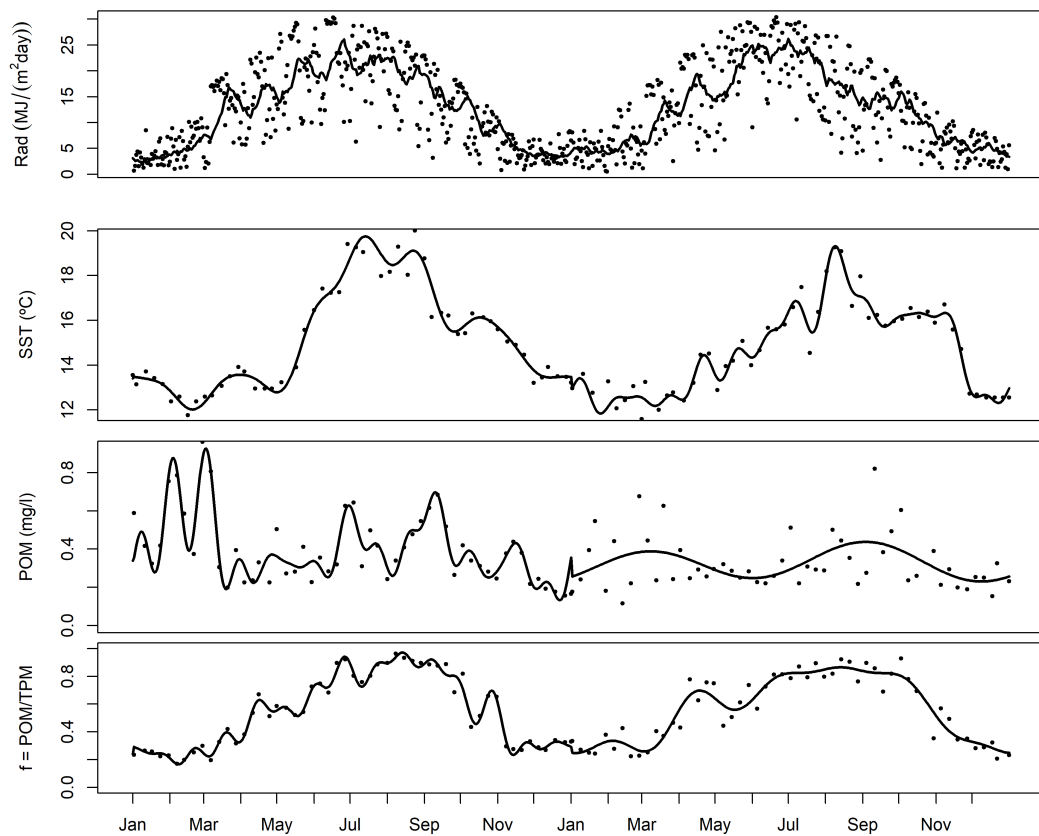
Figure 2: Environmental conditions in the Ría de Ares-Betanzos during 2014-2015. Daily vaules (dots) and fortnight mean (lines) of the global solar irradiance (Rad, $MJ/(m^2day)$). Weekly measures (dots) and curves obtained by functional smoothing with Fourier basis (line) of sea surface temperature (SST, ^aC), particulate organic matter (POM, mg/l) and seston quality ($f = POM/TPM$), where TPM is te total particulate matter
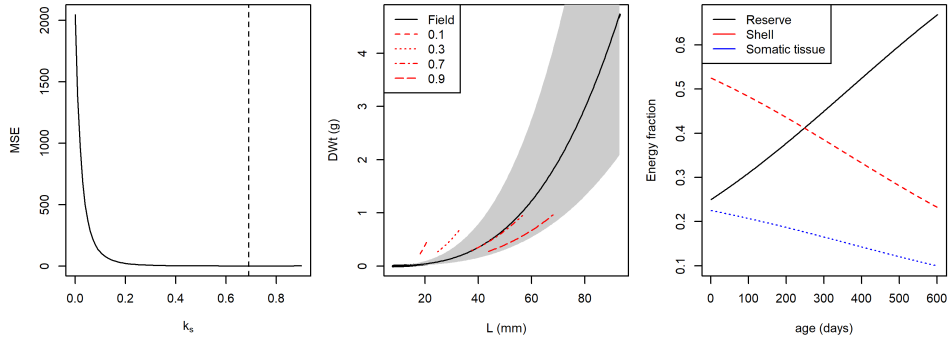
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Figure 3: Left: RMSE for each κ_S value, minimum identified by the vertical dotted line. Center: $L - W_T$ relationships with field data (black, 95% confidence band in grey) and simulations with different κ_S values. Rigth: fraction of energy allocated for reserves (black), shell growth (red) and somatic tissue (growth) over time, with $\kappa_s = 0.7$
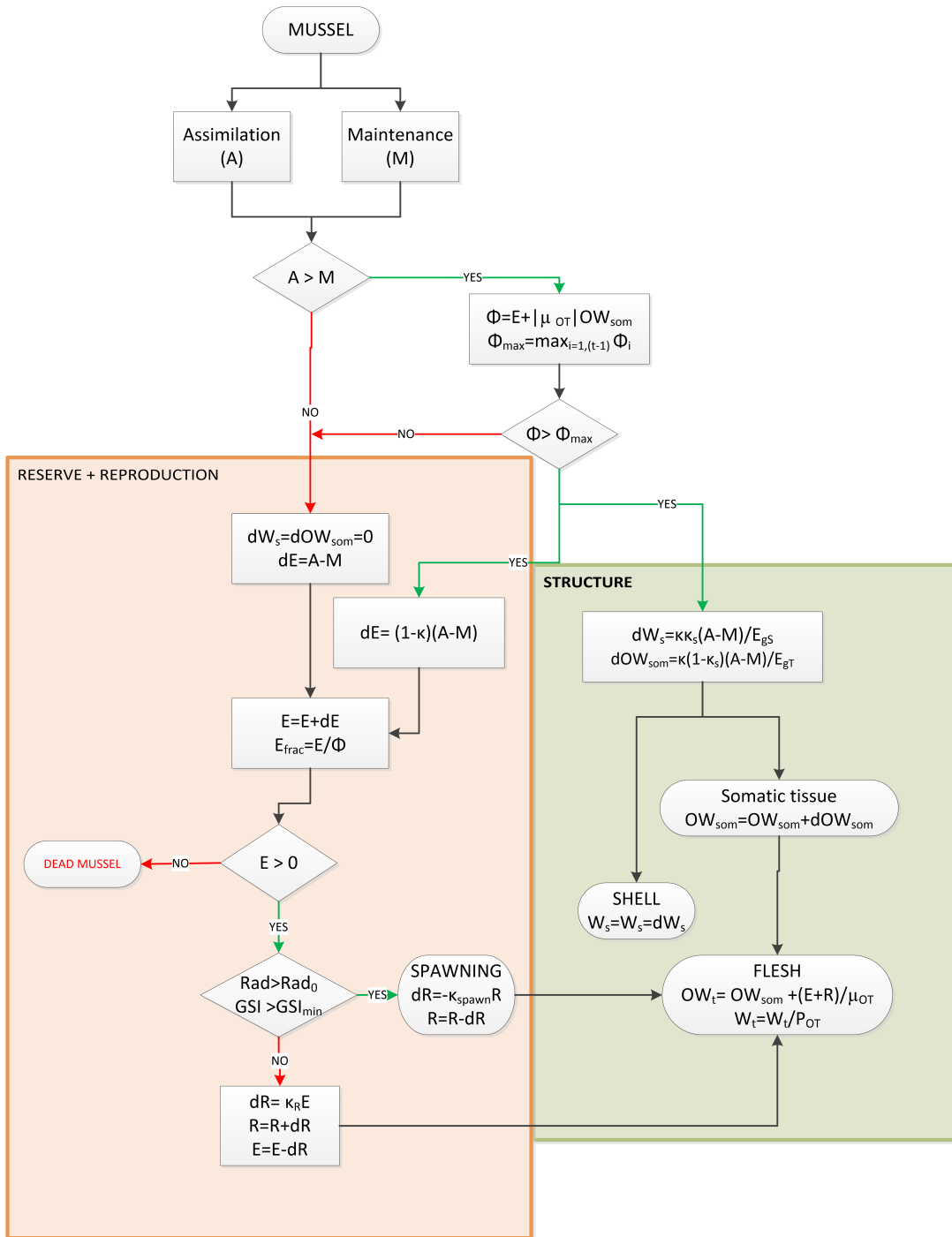
Figure 4: Diagram of our dynamic bivalve growth model. For any state variable X, dX/dt denotes its time derivative of X. See the definition and value sf parameters in Table 1

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Description	Name	Value	Value min	max	Units	Reference
Parameters in eq (1)	a_{CR}	0.00397				Filgueira et al. (2008)
	b_{CR}	1.71			1/h	
	$maxCR$	8				
Parameters in eq (2)	a_{AE}	0.95				Fernández-Reiriz et al. (2007)
	b_{AE}	0.18				
Parameters in eq (4)	a_{resp}	$5.6e^{-5}$				Arranz et al. (2016)
	b_{resp}	2.101				
Parameters in eq (5)	a_{exc}	0.004				Arranz et al. (2016)
	b_{exc}	2.066				
Parameters in eq (8)	a_κ	3	3	50		Scholten and Smaal (1999)
	b_κ	0.003	0.001	0.005		
Fraction of growth energy to shell	κ_S	0.7	0	0.9		calibrated (Figure 3)
Organic fraction of soft tissue	P_{OT}	0.85	0.65	0.90		Arranz et al. (2016)
Organic fraction of shell	P_{OS}	0.05	0.03	0.07		Arranz et al. (2016)
Gametogenesis threshold	E_{gamet}	0.2	0.15	0.5		Scholten and Smaal (1999)
Fraction of reserves to reproduction	κ_R	0.02	0.001	0.02		Scholten and Smaal (1999)
Radiance threshold for spawning	$minRad$	11.5			$MJ/(m^2 day)$	Fuentes-Santos et al. (2016)
Fraction of gametes released	E_{spawn}	0.05	0.01	0.1		calibrated from Troost et al. (2010)
Minimum GSI for spawning	$minGSI$	0.0005	0.0001	0.001		calibrated from Troost et al. (2010)
Conversion factors						
Energy content of POM	μ_{POM}	23.5			L/mg	Bayne et al. (1985)
Energy content of consumed O_2	μ_{o_2}	20.36			J/mg	Bayne et al. (1985)
Energy content of excreted $NH_4 - N$	μ_{NH_4-N}	0.0249			J/mg	Bayne et al. (1985)
Energy content of organic soft tissue	μ_{OT}	23.9			J/mg	Irisarri et al. (2015)
Energy content of organic shell	μ_{OS}	20.320			J/mg	Irisarri et al. (2015)
Energy content of inorganic shell	μ_{IS}	2			J/mg	Palmer (1992) Palmer (1992)
$L - W_s$ allometric parameters	a_L	31.5				Unpublished data
	b_L	0.3764				
Arrhenius temperature	T_a	5800			K	Béjaoui-Omri et al. (2014)
Reference temperature in the Arrhenius Law	T_1	288.15			K	Mean water temperature in our study area (see Figure 2).

Table 1: Parameters of the dynamic bivalve growth model.

4. Model performance

The performance of the dynamic growth model proposed in this work was checked by comparison with field data and with the standard DEB model (Duarte et al., 2012; Kooijman, 2010). We have applied both models to simulate the growth of Mediterranean mussels (*Mytilus galloprovincialis*) in suspended culture in the Ría de Ares-Betanzos (Section 2). Our model was implemented with the parameters outlined in Table 1. The standard DEB was implemented using the dynamics and parameters detailed in Duarte et al. (2012), but using the feeding rules of our model (Section 3.1).

We simulated the growth of mussels over $n = 420$ days starting in late winter (February), mid-spring (May) and late-summer (September), which are common seeding seasons for mussel culture in the Galician Rías. Simulations were conducted with initial shell length $L_0 = 15\,mm$, soft tissue dry weight $W_{T0} = 0.02\,g$, and reserve density $E_{frac} = 1/3$. The three culture cycles where simulated under the environmental conditions observed in the Ría de Ares-Betanzos during 2014-2015 (figure 2).

Figure 5 shows that the two dynamic models under comparison provide similar results in terms of shell length, although slightly larger values were obtained with the standard DEB model (Figure 5, top). However we observe important differences in terms of soft tissue weight (Figure 5, centre), as the standard DEB model simulate mussels with much larger flesh weight than those obtained with our model. In view of these results we have used the $L - W_T$ relationship observed in field data (see details in Section 2) as benchmark to check which model gives more accurate simulations of mussel growth. As indicated in Section 3.5. Figure 5 (bottom) shows that the DEB model tend to overestimate soft tissue growth, as the simulated curve falls above the prediction confidence band for the $L - W_T$ curve, while the $L - W_T$ relationship for mussels simulated with our model agrees with that observed in the field. Table 2, which shows the relative discrepancy between simulated and field curves (see eq 12), shows that the $RMSE$ obtained with our model is below 10% of that obtained with using DEB. It should also be noted that the accuracy of the dynamic model seems to depend on the seeding season, as we observe a drop in soft tissue weight in large mussels seeded in February and May. However this discrepancy between simulated and observed mussels may be attributed to a truncation on field data, as producers avoid harvesting when mussels have low flesh yield.

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	February	May	September
DEB	1.353	1.410	1.446
Our model	0.094	0.149	0.045

Table 2: Relative mean square error (RMSE) for $L - W_T$ of mussels during growth simulated with the standard DEB and the dynamic model proposed in this work

Comparison between the simulated shell and soft tissue growth curves show that our model is able to reproduce the different growth dynamics of shell, which has an increasing asymptotic behaviour, and soft tissue, which may suffer losses in response to environmental variability. The simulated growth patterns also varied across culture cycles, and we observe a faster growth in mussels seeded in late winter and spring than in those deployed in late summer (figure 5). Figure 6, which compares the simulated growth rates and the environmental conditions observed during the three culture cycles, shows that our model is able to reproduce the fast shell and soft tissue growth in periods with high food quality and warm sea water temperature, as well as the negative effect of low seston availability (grey band in Figure 6, bottom), which stagnates shell growth and can causes soft tissue losses. Finally, spawning events can be identified in the reduced soft tissue growth followed by periods of null shell growth, which indicate that mussels are recovering reserves, observed in spring for mussels seeded in May and September.

5. Discussion

The standard DEB model has been widely used during the last decade to model the growth of mussels under variable environmental conditions. Several studies have noticed that this model reproduces correctly shell growth but has a poor performance in the simulation of soft tissue growth (Béjaoui-Omri et al., 2014; Duarte et al., 2012; Picoche et al., 2014; Rosland et al., 2009; Sarà et al., 2012). This work aims to overcome this problem developing a new dynamic growth model for bivalves. Our proposal combines the generality of DEB theory, through the application of a net-production model (Lika and Nisbet, 2000), and the specificity of an ecophysiological species-specific model (Scholten and Smaal, 1998, 1999), which simulates
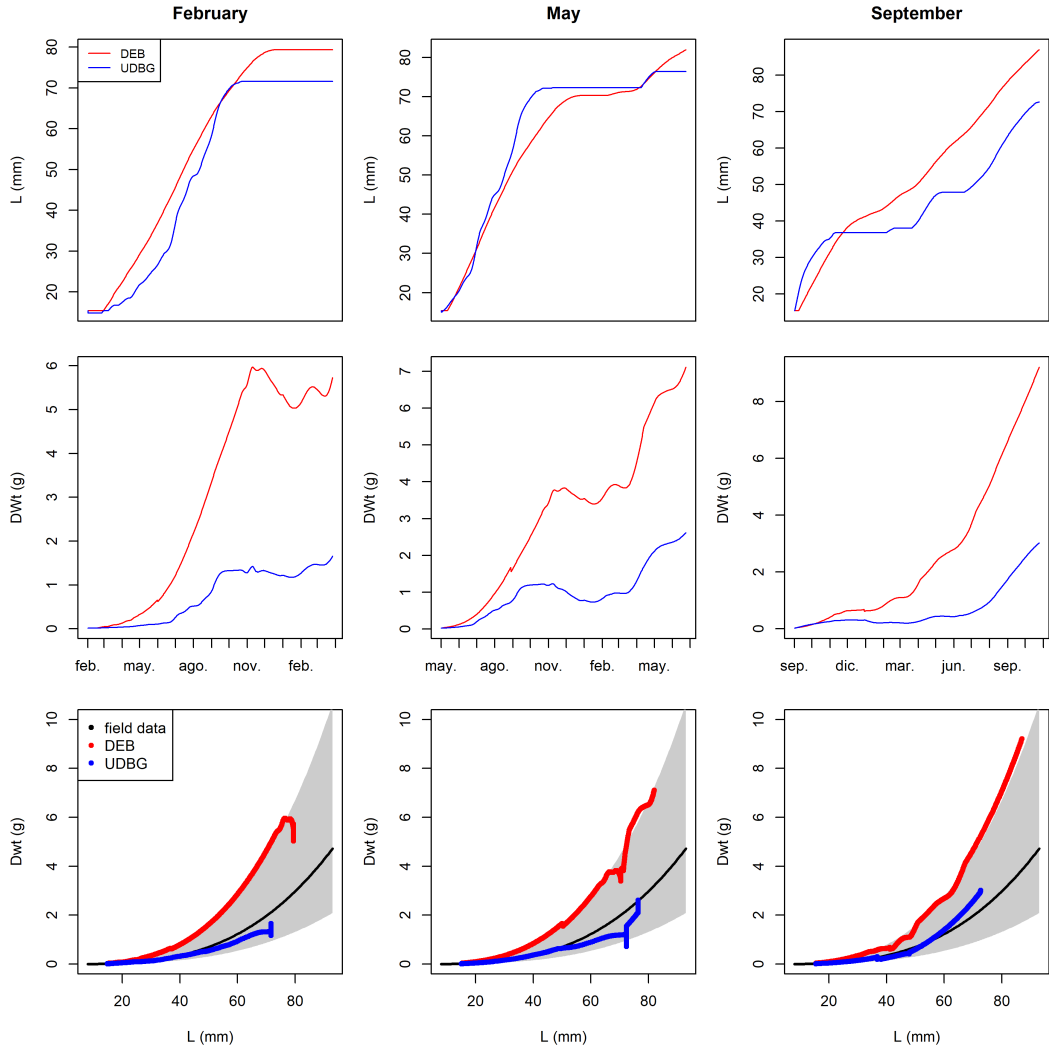
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Figure 5: Performance of our dynamic growth model (blue) and standard DEB model (red) models. Simulated growth patterns in terms of shell length (top) and tissue dry weight (centre). Shell length vs dry tissue weight relationships, comparison with the allometric relationship based on field data, $\log W_T = -12.38 + 3.07 \log L$ (bottom).
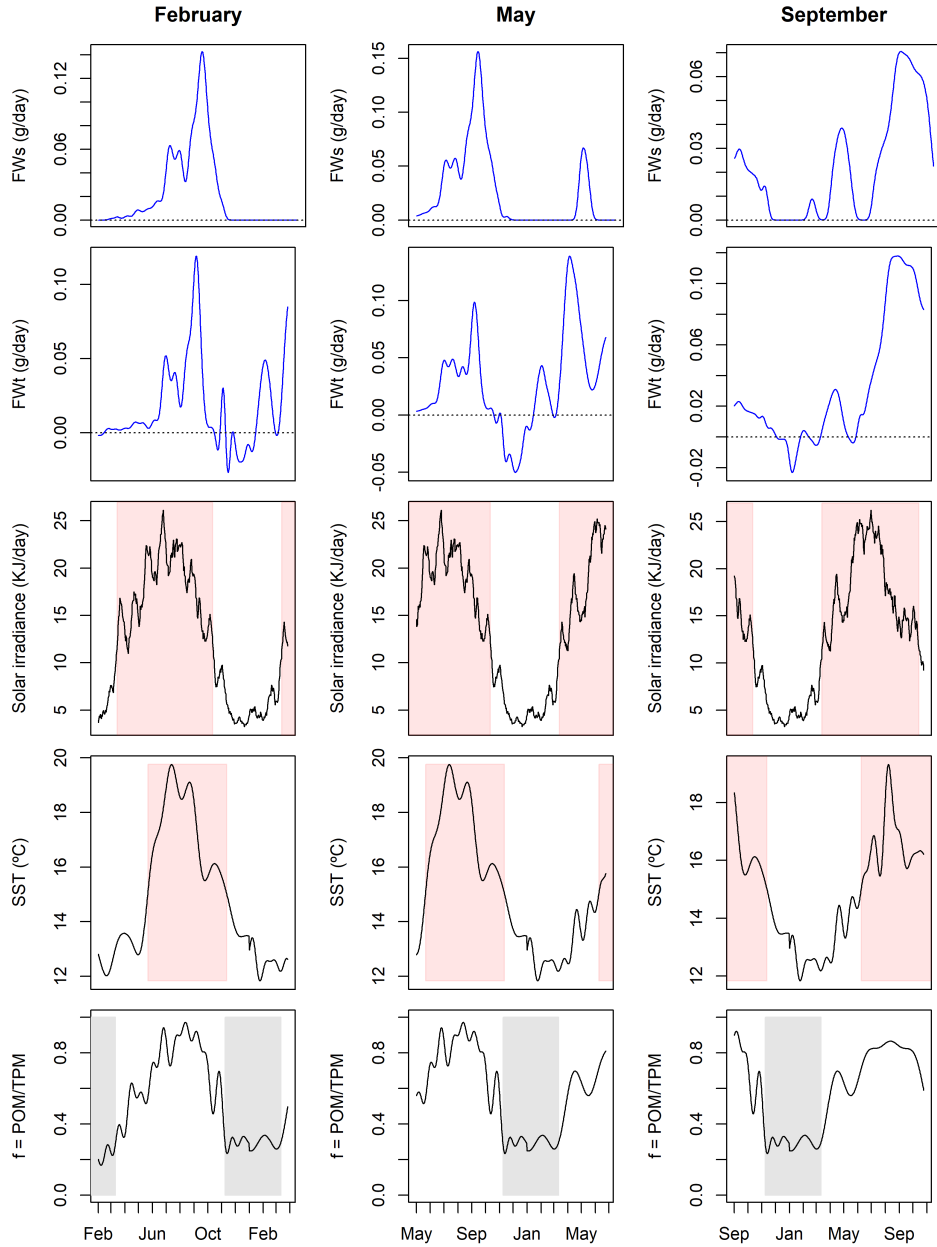
Figure 6: Performance of the dynamic growth model. Comparison between shell and soft tissue growth rates (fresh weight, g/day) and environmental conditions during the three culture cycles simulated. Red bands indicate periods with solar irradiance above the spawning threshold ($minRad = 11.5MJ/(m^2 day)$) and sea surface temperature above the reference value ($T_0 = 15^o C$). Grey bands indicate periods of low seston quality ($f < 0.3$),

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shell and soft tissue growth separately.

In order to define the energy partitioning scheme of our model we assume that the energy assimilated by the bivalve is first used to cover the maintenance costs, comprising both respiration and excretion rates, and the surplus is partitioned between shell formation, soft tissue growth and reserves, being part of these reserves allocated for maturation and reproduction. A proper estimation of environmental dependent processes such as energy acquisition, metabolic expenditure and reproduction is, as well as the partitioning scheme, crucial in the development of any dynamic growth model. This work focuses on modelling mussel growth in the Galician Rías, which are low seston environments. Taking into account the feeding strategies of mussels in low seston environments, energy acquisition was estimated through an allometric relationship between shell length and clearance rate (Filgueira et al., 2008), and using POM and the organic content of seston ($f = POM/TPM$) as proxies for food availability and quality to determine the assimilation rate (Fernández-Reiriz et al., 2007, 2017). Spawning, which in previous studies in the same areas was simulated as a single event in a fixed date, was simulated as a continuous process starting when solar irradiance is above a given threshold (Fuentes-Santos et al., 2016; Troost et al., 2010).

The shell and soft tissue growth curves provided by our model agree with growth patterns observed in the Galician Rías (Duarte et al., 2012; Fuentes-Santos et al., 2017). Comparison between our model and the widely used standard DEB model shows that our proposal outperforms the standard DEB model, which provides accurate estimations of shell length but tends to overestimate the soft tissue weight (see Figure 5 and Table 2). These results support the validity of our model and agree with prior works that have also pointed out the limitations of the standard DEB model in the simulation of soft tissue weight (Duarte et al., 2012; Picoche et al., 2014; Saraiva et al., 2012; Troost et al., 2010). Given the accuracy of the DEB model in terms of shell length, differences between observed and simulated tissue weights have been attributed to bias in the simulation of reserves and reproductive buffer (Troost et al., 2010), and to limitations derived from using shell length as reference measure for structural volume as we do not have access to the body length (Picoche et al., 2014). In contrast with the standard DEB model, which considers the shell as a dissipation prod-

uct, our model assumes that the shell is part of the structure accounting for the important cost of shell formation, which may require up to 50% of the energy budget (Arranz et al., 2016; Labarta et al., 1999; Palmer, 1992; Troost et al., 2010). This assumption defines new energy allocation rules that provide a more realistic modelling of the energy fluxes in mussels, and a better modelling for the mismatch between shell and soft tissue growth (Fuentes-Santos et al., 2017).

Comparison between environmental conditions and the simulated mussel growth patterns shows that our model is able to reproduce the response of mussels to changes in food availability and meteorological conditions. These results confirm the validity of the site-specific feeding and reproduction rules used in this model that, together with the independent simulation of shell and soft tissue growth, allow us to capture the different effects of food shortage on shell and soft tissue growth, as well as tissue weight losses during the spawning season.

In conclusion, the dynamic bivalve growth model developed in this work provides a realistic and accurate approach to the actual growth dynamics of mussels in variable environments. Although this work focusses on simulating the growth of mussels in a low seston environment, our model can be easily extended to other areas, and can also be used to simulate the growth of other bivalve species. Extension to other regions requires a previous knowledge of the life dynamics of mussels under the specific environmental conditions. Special attention should be paid to feeding processes in high seston environments where filter-feeders may reduce their clearance rates and conduct a pre-ingestive selection of high-quality particles that results in pseudofaeces production (Bricelj and Malouf, 1984; Prins et al., 1991). Calcification costs in areas with extreme conditions, such as low salinity (Sanders et al., 2018) or acidification (Gazeau et al., 2013; Thomsen et al., 2013), can be introduced modifying the unitary cost of inorganic shell and testing whether this increase affects κ_S, i.e. the energy partitioning between shell and somatic tissue growth. Extension to other bivalves requires species-specific information about energy acquisition and allocation processes. Finally, considering that DEB models have been lately used to analyze the potential effect of climate change on bivalve aquaculture (Filgueira et al., 2016; Montalto et al., 2016), and following the ideas of Saraiva et al. (2014), which integrated the standard bivalve DEB model into a population level approach, we can use

our model as the basis for a farm level approach. Although incorporating all the intra and inter-specific interactions present at the ecosystem level in a single model is a challenging task, an individual based dynamic population model would be a valuable tool for the development of aquaculture management and sustainability plans (Byron et al., 2011; Costa-Pierce, 2008).

Acknowledgements

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