From classical to nonparametric growth models: towards comprehensive modelling of mussel growth patterns

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Abstract

Understanding biological processes, such as growth, is crucial to development management and sustainability plans for bivalve populations. von Bertalanffy and Gompertz models have been commonly used to fit bivalve growth. These models assume that individual growth is only determined by size, overlooking the effects of environmental and intrinsic conditions on growth patterns. The comparison between classical models and nonparametric GAM (generalized additive models) fits conducted in this work shows that the latter provide a more realistic approach of mussel growth measured in terms of shell length, and dry weight of hard and soft tissues. GAM fits detected a reduction in growth during the cold season, under unfavourable nutritional conditions. These fits also captured the decoupling between hard and soft tissue growth, widely addressed in the literature but not incorporated in growth models. In addition a GAM fit of condition index allowed us to explain annual changes in resources allocation, identifying the asymptotic growth of shell and the effects of the reproductive cycle on soft tissue fluctuations.

Keywords: condition index, GAM, Gompertz, shell, soft tissue, von Bertalanffy

Introduction

Mussels are dominant organisms on many rocky shores worldwide, where they play an important ecological role as habitat or prey for a multitude of organisms (Rilov et al., 2008), and in the pelagic-benthic coupling (Alonso-Pérez et al., 2010; Dame, 1993; Zúñiga et al., 2014). In addition, mussel aquaculture is a sustainable food production system with important commercial (Díaz et al., 2014; Labarta et al., 2004) and environmental value, since mussel farming has been proposed as a tool to mitigation of eutrophic coastal areas (Lindahl et al., 2005). The growing importance of aquaculture in food production along the past decades has resulted on an increasing demand for management and sustainability plans (Bergström et al., 2015). Understanding how biological processes, such as reproduction or growth, respond to environmental changes is crucial to improve management strategies.

The most commonly applied growth models are those proposed by Gompertz (1825) and von Bertalanffy (1938). The latter is thought to be a better describer of growth in fish and bivalves (Gosling, 2003). These models focus on characterizing the mean growth pattern of a given species along its lifespan. For this purpose both von Bertalanffy and Gompertz models assume that individual growth is asymptotic and that the growth rate is only determined by size. However development of management and sustainability plans requires understanding the growth dynamics and seeks for models able to detect seasonal or short-term changes in bivalve growth.

It is well known that bivalve growth is driven by intrinsic physiological processes and influenced by environmental conditions. During the past decades several works have highlighted the effect of factors such as physiological dynamics, ecological memory, and environmental conditions on bivalve growth (Babarro et al., 2000; Blicher et al., 2010; Borrero and Hilbish, 1988; Hilbish, 1986; Kautsky, 1982; Lewis and Cerrato, 1997; Mallet et al., 1987; Okumuş and Stirling, 1994; Pérez-Camacho et al., 2014, 1995). Two different strategies have been adopted to account for these effects. Some works have fitted von Bertalanffy (Bagur et al., 2013; Connor and Robles, 2015; Nedoncelle et al., 2013; Ozernyuk and Zotin, 2006) and Gompertz (Cubillo et al., 2012; Irisarri et al., 2015; Peteiro et al., 2008, 2006) models to populations growing under different conditions and compared the fitted parameters to test whether the factors under study affected bivalve growth. Other works have developed extended von Bertalanffy models incorporating the effects of food availability (Marambio et al., 2012) or maturity status (Ohnishi et al., 2012) on bivalve growth.

An important feature of bivalve growth, which deserves special attention to schedule aquaculture production, is the decoupling between hard and soft tissue (Blicher et al., 2010; Borrero and Hilbish, 1988; Hilbish, 1986; Lewis and Cerrato, 1997; Witbaard et al., 2015). This decoupling can be attributed to a mismatch between the favourable conditions to shell growth and those leading to increases of soft tissue (Borrero and Hilbish, 1988), and to seasonal changes in the allocation of resources between growth and reproduction (Peterson and Fegley, 1986). Despite these evidences, changes in shell length and soft tissue have been wrongly used as equivalent measures of growth and consequently classical and new parametric growth models have overlooked this uncoupling. For instance the extended von Bertalanffy model introduced by Ohnishi and Akamine (2006) to incorporate hard and soft tissue growth patterns assumes an allometric relationship between hard and soft tissue growth rates, in contrast with the observed uncoupling.

The common practice in fish and bivalve growth modelling is to select a model, usually von Bertalanffy or Gompertz, and fit this model to the data. This procedure can lead to biased estimators, and consequently wrong decisions, when the observed data are inconsistent with the selected model. Recent studies (Katsanevakis and Maravelias, 2008; Rabaoui et al., 2007; Rogers-Bennett, 2003) have pointed out this problem and proposed the Akaike Information Criterion (AIC) as goodness-of-fit measure to select the best growth model among a set of candidates. Once again this procedure relies on the subjective selection of some candidate models leading to unrealistic estimates if none of them is consistent with the real data.

Recent works have applied semiparametric approaches, such as generalized additive models (GAM, Hastie and Tibshirani, 1990) to include environmental and endogenous variables in fish growth curves (Ligas et al., 2015; Olsen et al., 2006; Smith et al., 2005). For bivalves, some authors have computed instantaneous growth rates as the ratio between shell length increase and time between sequential samplings and applied GAM to fit the corresponding temporal pattern (Katsanevakis, 2007; Witbaard et al., 2015). To our knowledge any comparison between the performance of classical and semiparametric approaches, which would check the goodness-of-fit of the former, has not been conducted up to date.

To address the management of both wild and cultured bivalve populations at ecosystem level we need procedures able to detect short-term or seasonal changes in the growth pattern of bivalves. This

work is a first attempt to test whether the commonly used von Bertalanffy and Gompertz provide accurate fits for the growth patterns of hard and soft tissues in the mussel *Mytilus galloprovincialis* (Lamarck, 1819) or more flexible procedures are required. For this purpose, we have considered our dataset used previously in Babarro et al. (2003), which analyzed mussel growth in suspended culture using the classical models. We tested the goodness-of-fit of the von Bertalanffy and Gompertz models through comparison with GAM fits. Instantaneous growth rates were also estimated as the first derivatives of the fitted models, in contrast with previous works that estimated instantaneous growth rates as the average change in size between samplings. Finally we tested whether GAM models can detect differences between the growth patterns of hard and soft tissues.

Materials and methods

Experimental design

Seed of *Mytilus galloprovincialis* with a mean shell length of 21.2 mm (sd =8.5) was gathered from collector ropes on a raft located in the mid-to-outer area of the Ría de Arousa (Galicia, NW Iberian Coast, see Figure A.1 in appendix A), and were socked on culture ropes deployed in an adjacent commercial raft in January 1998. Culture ropes were kept in the water up to July 1999 (526 days) covering both pre-fattening, up to November 1998, and fattening, from November 1998 to harvest in July 1999, phases of mussel culture (see details in Babarro et al. (2003)).

Sampling procedure

Sequential samplings were conducted on 28 January (seeding), 11 March, 6 May, 3 June, 1 July, 24 September and 11 November during 1998; and on 24 February, 28 April, 26 May and 7 July (harvest) during 1999. Duplicated samples of 200-300 individuals were taken from adjacent ropes in each sampling date. Individual mussel length (L, mm) was measured to the nearest 1 mm using callipers to obtain the mean shell length of each sample. Subsamples of 5-15 mussels each from 5-6 length classes covering the whole size range were used to determine total (TDW, g), shell (DWs, g) and tissue dry weight (DWt, g) by dissection and after drying at 100º C until constant weight. Condition index was calculated as the ratio between tissue and shell dry weights, CI=DWt/DWs (Lucas and Beninger, 1985).

Data analysis

110 *Classical growth models*

111 Specific von Bertalanffy (vB) and Gompertz (G) models were used to fit growth curves in terms
112 of shell length (mm), total, shell and tissue weight (g). The von Bertalanffy and Gompertz models for
113 shell length are defined as follows:

114 $$vB: \quad L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \tag{1}$$

115 $$G: \quad L_t = L_\infty \exp\left(-e^{-k\left(t-t^*\right)}\right) \tag{2}$$

116 where L_∞ (mm) represents the asymptotic length, L_t (mm) is the shell length at time t (months), k is the
117 growth parameter indicating the speed at which asymptotic growth is attained, t_0 (1) represents the
118 theoretical time at which length is 0, and t^* (2) denotes the time of growth inflexion. The same models
119 were used to fit growth curves in terms of weight.

120 The first derivatives of the models under comparison were computed to estimate growth rates
121 along the culture period. For the von Bertalanffy and Gompertz model we used the expressions:

122 $$vB: \quad \frac{\partial L}{\partial t} = kL_\infty e^{-k(t-t_0)} \tag{3}$$

123 $$G: \quad \frac{\partial L}{\partial t} = ke^{-k(t-t_0)} L_\infty \exp\left(-e^{-k(t-t_0)}\right) = kL_t e^{-k(t-t_0)} \tag{4}$$

124 *GAM fit of growth curves*

125 Despite von Bertalanffy (eq. 1) and Gompertz (eq. 3) models have been widely used to estimate
126 mussel growth in terms of shell length (mm) and dry weight (g), they can be very restrictive and lead to
127 biased estimations and consequently incorrect conclusion when the data do not support the relationships
128 imposed by these models. Nonparametric regression techniques provide an approach to growth curves
129 without specifying in advance any function for the effect of time on size. Therefore mussel growth can be
130 expressed as follows

131 $$Y = E\left[Y \middle| t\right] + e = m(t) + e \tag{5}$$

132

where Y is the size measure, m is an unknown smooth function and e is the error term. In this work, m was fitted using regression splines, i.e. we applied a generalized additive model (GAM, Hastie & Tibshirani, 1990; Wood, 2006), which can be defined as follows:

$$E\left[Y\middle|t\right] = H\left(\alpha + f\left(t\right)\right) \tag{6}$$

where α is the intercept, f_j is an unknown smooth function, which in this case was fitted by thin plate regression splines, and H is a fixed, known, monotone link function, selected according to the distribution of the response variable, Y. In this work we fitted GAM with Gaussian family and "identity" link function for shell length and dry weight, which were normally distributed (Shapiro test, p-value > 0.05). A GAM (1) with Gamma family and logarithmic link was applied to fit the temporal pattern of condition index. We also computed the first derivative of the GAM fits to obtain instantaneous growth rates.

Testing the goodness-of-fit of the classical growth models

Graphical comparison of the growth curves provided by the classical and GAM fits can be used to check the accuracy of von Bertalanffy and Gompertz models. Classical models are correct when the corresponding growth curves lay within the 95% confidence interval of the GAM growth curves. Nevertheless we also conducted a formal goodness-of-fit test for this purpose.

We applied a Generalized likelihood ratio (GLR) test (Fan and Jiang, 2007) to check the goodness-of-fit of the classical von Bertalanffy and Gompertz models, that is, to test whether any of these models provides a correct specification of the growth curves. Thus, considering the general model in equation (3), we test the null hypothesis H_0: *m(time)* = m_0*(time)*, where m_0 is given by expression (1) for von Bertalanffy and expression (2) for Gompertz, respectively, versus the general alternative hypothesis H_1 where m is an unknown smooth function estimated by GAM. Let $\left\{t_i, Y_i\right\}_{i=1}^{n}$ be the observed data, the likelihood ratio test is

$$T = \frac{n}{2}\log\frac{RSS0}{RSS1} = \frac{n}{2}\log\frac{\sum_{i=1}^{n}\left(Y_i - m_0\left(t_i\right)\right)^2}{n^{-1}\sum_{i=1}^{n}\left(Y_i - m\left(t_i\right)\right)^2} \tag{7}$$

where *RSS0* and *RSS1* are the maximum likelihood estimators for the error variance under H_0 and H_1, respectively. For a fixed significance level α, we reject the null hypothesis when $T > T^{1-\alpha}$, where $T^{1-\alpha}$ is the 100(1-α)-percentile of *T* under H_0. As asymptotic theory for nonparametric tests is not closed yet, we can apply resampling methods such as bootstrap (Efron and Tibshirani, 1994) to calibrate the test. Wild bootstrap (Hardle and Mammen, 1993) was used in this case to generate the resamples. Thus the empirical p-value of the test is the proportion of simulated T values larger than that obtained for the observed data. The algorithm performed to conduct this goodness-of-fit test is detailed in Appendix A.2.

Comparison of shell and soft tissues growth patterns

In order to test whether hard and soft tissue growths are coupled, we used a GAM fit with interaction factor (type of tissue) by curve (time) defined as follows:

$$E\left[Y\middle|t,Z\right] = H\left(\alpha_j I(Z=Z_j) + \sum_{j=1}^{2} f_j\left(t\right) I(Z=Z_j)\right) \tag{8}$$

where, *j*=1,2 identifies the group defined by hard (shell) and soft tissue, α_j, is the intercept for the *j*th type of tissue. And f_j is the smooth function that describes the effect of time on the response for the *j*th type of tissue. As well as in model (5) we used Gaussian family with "identity" link function (*H*).

We used the shrinkage variable selection procedure proposed by Marra and Wood (2011) to test whether the effect of time on each response variable depends on type of tissue, i.e. to select between model (8) and the model without interactions:

$$E\left[Y\middle|time,Z\right] = H\left(\alpha_j I(Z=Z_j) + f\left(time\right)\right) \tag{9}$$

Once model selection was conducted, normality and independence of residuals were tested by the Shapiro-Wilk and Ljung–Box tests, respectively. In addition to the growth curves, we fitted their first derivatives in order to estimate growth rates along the culture period.

Software

Data analysis was performed with the statistical software R.3.1.3 (R Development Core Team, 2015). In particular, the nls function in the stats package was used to fit Gompertz and von Bertalanffy

models by nonlinear least squares (Bates and Watts, 1988), and the *mgcv* package (Wood, 2006) was used to fit the GAM models.

Results

Figure 1 shows that the GAM (eq. 5) and classical growth models -von Bertalanffy (eq. 1) and Gompertz (eq. 2) provide similar growth curves up to September 1998. Although the GLR tests accept the goodness-of-fit of both classical models (p-value > 0.1, Table B1 in Appendix B), we observe differences between models from autumn onwards when the GAM detects stagnation in shell length growth, which was not identified by the classical models. In Appendix B (Figure B1, Table B1) we report the result for growth curves in terms of weight. The GLR tests (Table B1) point out the lack of fit of the classical growth models, mainly for tissue dry weight. In view of these results GAM fits shall be used to estimate the different growth curves considered along this work.

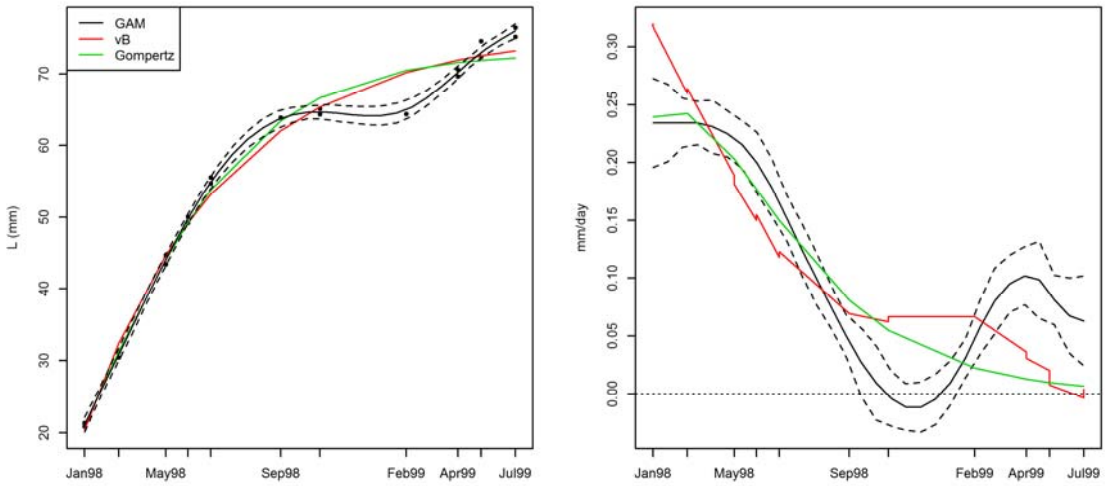

Figure 1: Comparison of growth models. Observed shell lengths (points), GAM (black), von Bertalanffy (vB, red), Gompertz (G, green) fits of growth curves (left) and their first derivative (right). Fitted values (solid line) and 95% confidence intervals (dashed lines) for GAM fit.

The model selection conducted to test for differences between the growth patterns of shell and soft tissue detected a significant effect of type of tissues on the intercept (p-value ≈ 0) and smooth terms of the growth curves in terms of dry weight (p-value ≈ 0), indicating a mismatch between the growth of hard and soft tissues. Indeed the AIC for model (8), which assumed different growth patterns for hard and soft tissue (AIC = 16.33) was smaller than that obtained overlooking the differences between tissues

200 (model (9), AIC=152.29). Therefore, model (8) was used to estimate the growth patterns of shell (DWs)
201 and tissue (DWt) dry weight.

202 A summary of the fitted models, goodness-of-fit measures and tests conducted for model
203 checking is shown in Table 1. Shell length increased up to October; stagnated during autumn-winter, and
204 increased again from February onwards, but at a lower rate than during the first spring (Figure 1). As
205 observed for shell length (Figure 1), total (Figure 2, top) and shell dry weight (Figure 2, bottom, black
206 lines) stopped growing from October to March. Nevertheless, soft tissue (Figure 2, bottom, grey lines)
207 increased up to September, decreased from November to February and increased again from March
208 onwards.

209 **Table 1:** GAM fits of mussel growth in terms of shell length (L, mm) total dry weight (TDW, g), shell dry weight
210 (DWs, g), tissue dry weight (DWt, g), and condition index (CI = DWt/DWs). Normality of residuals was tested
211 through the Shapiro–Wilk (SW) while independence of residuals was checked through the Ljung–Box (LB) tests.

		Parametric coefficients					Goodness of fit		Residuals	
		Estimate	Std. Error	t value	Pr(>|t|)		Adj R^2	%Dev Exp	SW	LB
L (mm)	Intercept	54.903	0.169	325.5	<2e-16	***	0.998	99.90%	0.0969	0.4327
		Smoth terms								
		edf	Ref.df	F	p-value					
	s(time)	6.673	9	1194	<2e-16	***				
		Parametric coefficients					Goodness of fit		Residuals	
		Estimate	Std. Error	t value	Pr(>|t|)		Adj R^2	%Dev Exp	SW	LB
TDW (g)	Intercept	6.027	0.103	58.62	8.7e-16	***	0.997	99.20%	0.1462	0.1760
		Smoth terms								
		edf	Ref.df	F	p-value					
	s(time)	7.327	9	162.2	<2e-16	***				
		Parametric coefficients					Goodness of fit		Residuals	
		Estimate	Std. Error	t value	Pr(>|t|)		Adj R^2	%Dev Exp	SW	LB
DWs vs DWt (g)	(Intercept)	4.981	0.054	91.77	<2e-16	***	0.994	99.60%	0.0495	0.0179
	Tissue	-3.936	0.077	-51.27	<2e-16	***				
		Smoth terms								
		edf	Ref.df	F	p-value					
	s(time):Shell	8.594	9	417.4	<2e-16	***				
	s(time):Tissue	4.872	9	13.98	2.5e-14	***				
		Parametric coefficients					Goodness of fit		Residuals	
		Estimate	Std. Error	t value	Pr(>|t|)		Adj R^2	%Dev Exp	SW	LB
CI	Intercept	-1.525	0.026	-59.53	3.2e-15	***	0.803	91.90%	0.5895	0.2529
		Smoth terms								
		edf	Ref.df	F	p-value					
	s(time)	7.936	8.684	14.02	1.6e-06	***				

212 (***) p-value < 0.001, (**) p-value < 0.01, (*) p-value < 0.05, (.) p-value < 0.1.

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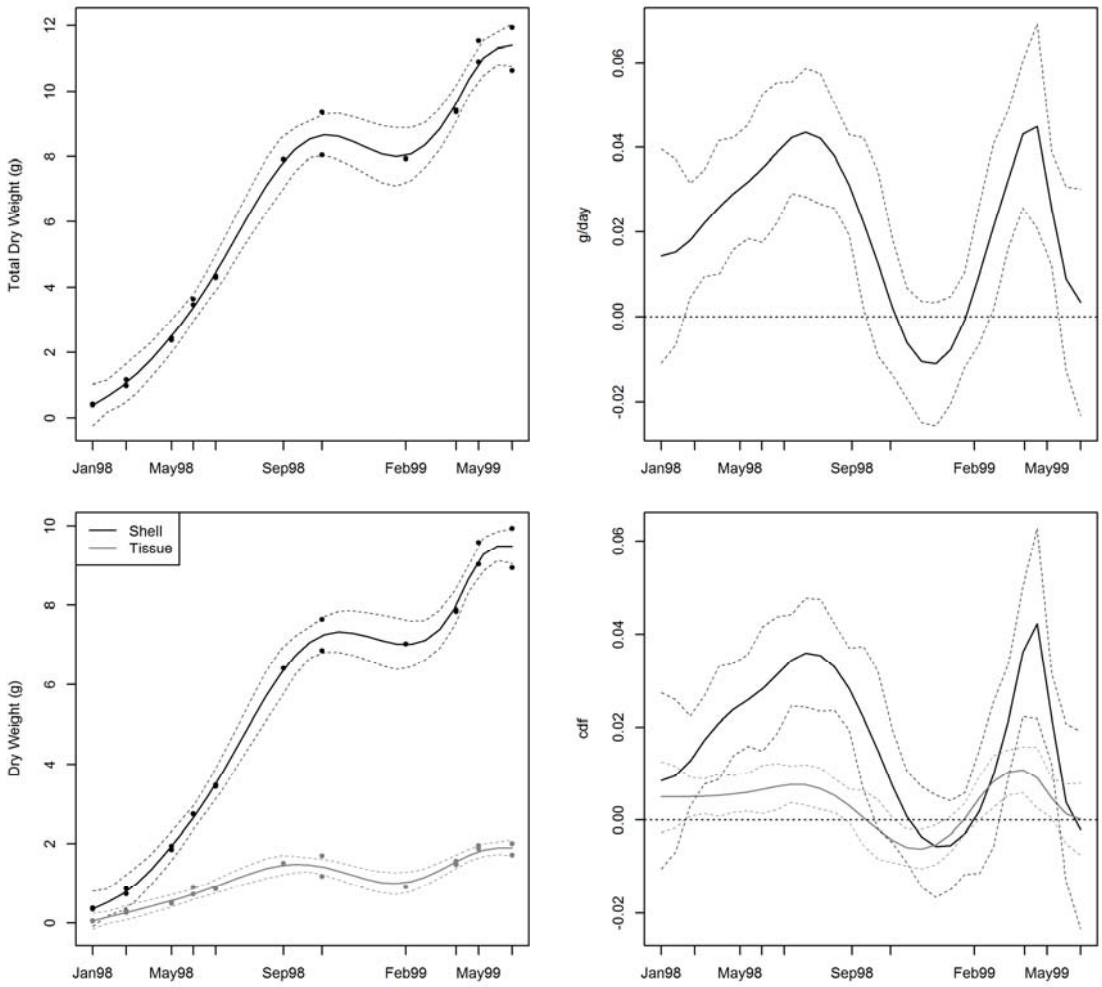

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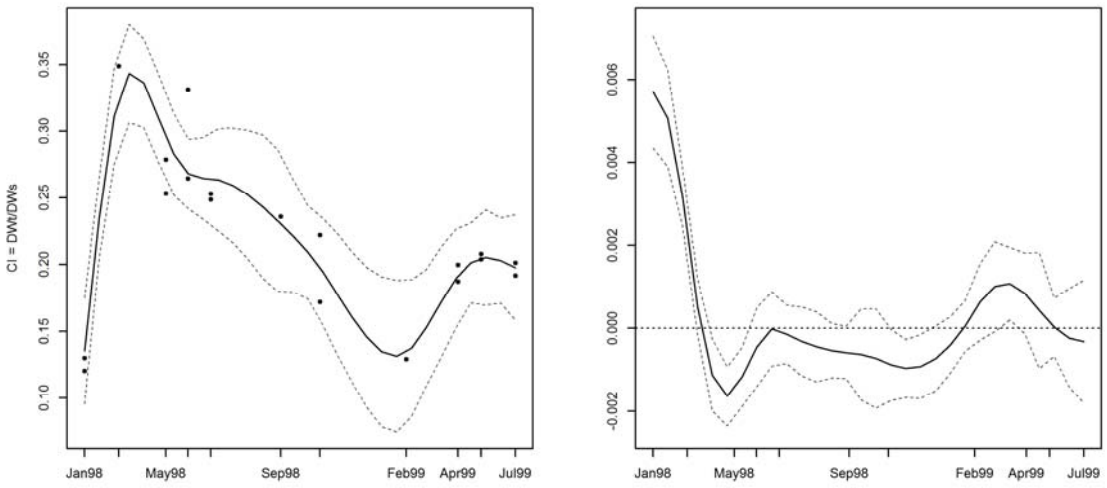
215 **Figure 2:** Mussel growth. Top: total dry weight (TDW, top). Bottom: shell (black) and tissue dry weight (grey).
216 Observed values (points), and GAM fits of growth curves (left) and their first derivative (right). Fitted values (solid
217 line) and 95% confidence intervals (dashed lines).

218 The differences between hard and soft tissue growth curves and the significant effect of time on
219 the condition index (Table 1) indicate a temporal mismatch between the investment of mussels on shell
220 and soft tissue. The decrease in CI during the first spring and winter (Figure 3) reflects two different
221 situations: during spring both tissue and shell grew, but the latter grew at a higher rate; while the decrease
222 in winter is caused by soft tissue losses (Figure 2, bottom). We also observe opposite behaviours between
223 the first and second spring, as the latter reported an increase in the condition index (Figure 3), i.e. higher
224 growth rates in soft tissue than in shell.

225 

226 **Figure 3:** Condition index (CI=DWt/DWs). Observed values (points), and GAM fit of the temporal pattern of mussel
227 CI (left) and its first derivative (right). Fitted values (solid line) and 95% confidence intervals (dashed lines).

228 **Discussion**

229 The important ecological and commercial role of bivalve aquaculture have motivated an
230 increasing demand for management and sustainability plans (Bergström et al., 2015). Modelling
231 individual growth is a key factor to understand the dynamics of these species and, consequently in the
232 development of management and sustainability plans for aquaculture. Up to date, the majority of works
233 have focused on spatial planning through the comparison of bivalve growth patterns at different locations
234 (Bergström et al., 2015; Brigolin et al., 2009; Pérez-Camacho et al., 2014, 1995). Short term variability
235 on bivalve growth in response to changes on the environmental conditions, which is crucial for site
236 specific management plans, have received less attention.

237 Bivalve growth has been modelled by the classical von Bertalanffy and Gompertz models,
238 which aim to estimate the mean growth along the individual lifespan and assume that growth is only
239 determined by size. However a proper understanding of the growth dynamics requires detecting changes
240 in the growth patterns along the culture period, as well as differences between hard and soft tissue growth.
241 For this reason this work tests whether the classical growth models provide realistic fits of bivalve growth
242 or more flexible techniques, such as GAM, are required

243 Although the small sample size (n = 20) can limit the power of the goodness-of-fit test, we have
244 confirmed that von Bertalanffy and Gompertz models miss-specify mussel growth in terms of dry weight.

245 The GAM fit detected temporal variability in mussel growth, extensively described (Borrero and Hilbish,
246 1988; Gangnery et al., 2004; Hilbish, 1986; Kautsky, 1982; Lewis and Cerrato, 1997; Pernet et al., 2012;
247 Urrutia et al., 1999; Witbaard et al., 2015). The large amount of endogenous and exogenous variables
248 involved in a complex process such as bivalve growth, which hampers the development of accurate
249 parametric models for age-size relationships, and the goodness-of-fit of GAMs, which do not need to
250 assume any restrictive relationship between the response and the explanatory variables, support the use of
251 the latter to fit bivalve growth. The first order derivatives of the fitted growth curves provide accurate
252 estimates of the instantaneous growth rates, which up to date have been obtained as the ratio between size
253 increases and time between samplings (Katsanevakis, 2007; Witbaard et al., 2015), GAM fits also
254 detected a decoupling between hard and soft tissues, widely addressed in the literature (Blicher et al.,
255 2010; Borrero and Hilbish, 1988; Hilbish, 1986; Lewis and Cerrato, 1997; Witbaard et al., 2015) but not
256 incorporated to growth models.

257 The temporal variability on mussel growth detected by the GAM fits is in agreement with
258 important features such as the effect of the environmental conditions and the reproductive cycle on
259 bivalve growth, which have been described along several decades. The fitted growth curves and rates in
260 terms of shell length and shell weight reflect the common pattern at temperate latitudes, where shell
261 growth from spring to early autumn is favoured by optimal nutritional conditions and increasing
262 temperatures, in contrast with the low food availability in colder months (Kautsky, 1982; Loo and
263 Rosenberg, 1983; Mallet et al., 1987). Soft tissue losses during winter can be attributed to an early
264 spawning event. *Mytilus* species are thought to synchronize their reproductive cycle with favourable
265 environmental conditions (Edwards and Richardson, 2004; Newell et al., 1982; Philippart et al., 2012). In
266 coastal upwelling systems spawning of many invertebrate and fish species occurs during the upwelling
267 season (Otero et al., 2009; Snodden and Roberts, 1997; Suárez et al., 2005), which in the Galician Rías
268 extends between spring and autumn (Torres et al., 2003; Wooster et al., 1976).

269 The temporal pattern of the condition index suggest a higher investment in shell up to summer
270 followed by a period of isometric growth up to mid-autumn, i.e. the end of the upwelling season. In
271 agreement with these findings, Hilbish (1986) argued that in *Mytilus edulis* shell growth preceded soft
272 tissue growth. The decrease in CI during winter reflects soft tissue losses, which may be attributed to
273 energy investment on gametogenesis coupled with unfavourable nutritional and environmental conditions

(Witbaard et al., 2015) and the subsequent spawning event in late winter. The increase in CI during the second spring indicates a higher investment on tissue than on shell, in contrast with the first spring. This interannual shift may be attributed to the progressive reduction in shell growth as asymptotic size is approached, and the post-spawning recovery of soft tissue. Accordingly, Peterson and Fegley (1986) found that shell growth in juvenile clams was much higher than in adult clams. These results are in agreement with the different hard and soft tissue growth patterns of bivalves. While shell growth is asymptotic (Sebens, 1987), soft tissue of adult mussels undergo substantial annual changes mainly driven by their reproductive cycle (Peterson and Fegley, 1986).

The decoupling between shell and soft tissues points out the need for testing whether mussels fulfil the allometric length-weight relationship, widely used to describe relative bivalve growth (Cubillo et al., 2012; Irisarri et al., 2015; Peteiro et al., 2008, 2006, Rabaoui et al., 2011, 2007). In this line Sestelo and Roca-Pardinas (2011) and Martínez-Silva et al. (2014) show that nonparametric regression provides a better fit for the relative growth of barnacles and sea urchins, which condition index also exhibit seasonal variation, than allometric models.

The productivity of mussel farming, depend on individual size and meat yield, defined as the ratio between meat and total fresh weight, since market prices are based on these parameters (Fuentes-Santos et al., 2015; Pérez-Camacho et al., 2013). More exhaustive sampling procedures than those required by the classical models, and the flexibility of nonparametric approaches, such as GAM, shall capture short term variability of bivalve growth and meat yield. These approaches shall contribute to the development of site specific management strategies through a proper schedule of seeding and harvesting.

Appendix A: Supporting information for Materials and Methods

A.1 Experimental design

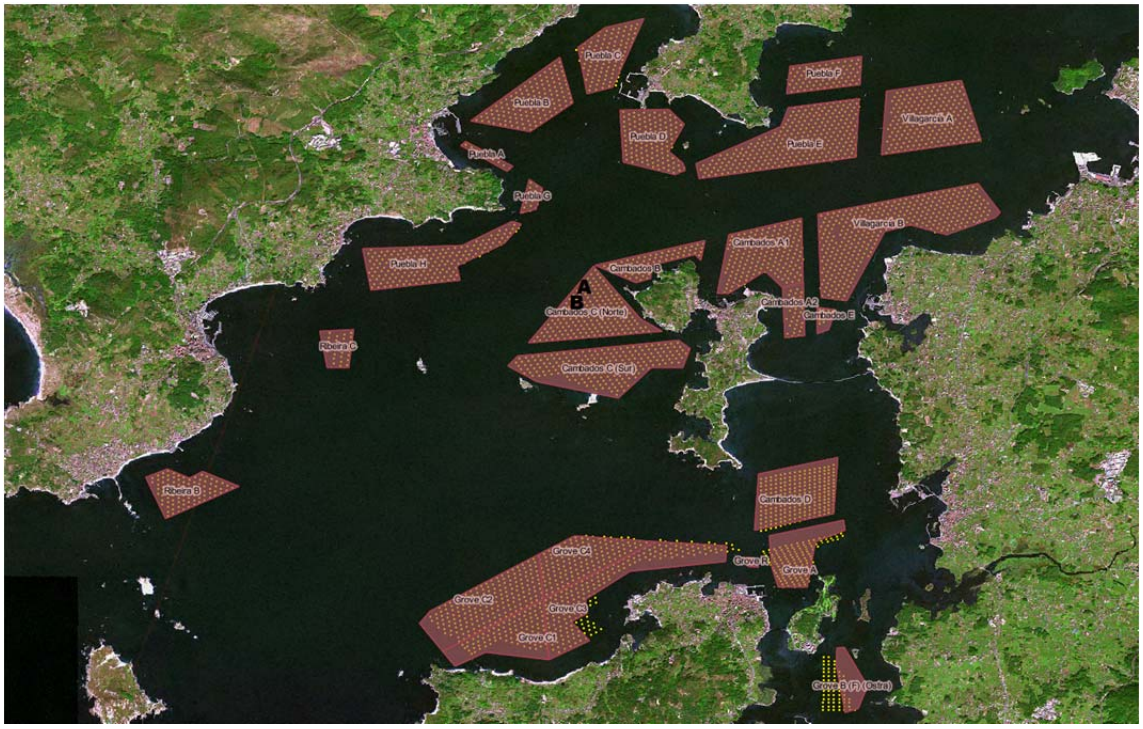


Figure A 1: Mussel culture polygons in the Ría de Arousa (Galicia, NW Spain). A: raft where the experimental culture was conducted. B: raft where mussel seed was collected.

A.2 Details of the goodness-of- fit test.

We applied a Generalized likelihood ratio test (Fan and Jiang, 2007) to check the goodness-of-fit of the classical von Bertalanffy and Gompertz models, that is, to test whether any of these models provides a correct specification of the growth curves. Thus, considering the general model in equation (3), we test the null hypothesis H_0: $m(t) = m_0(t)$, where m_0 is given by expression (1) for von Bertalanffy and expression (1) for Gompertz, respectively, versus the general alternative hypothesis H_1 where m is an unknown smooth function estimated by GAM. Let $\{t_i, Y_i\}_{i=1}^{n}$ the observed data, the likelihood ratio test is

$$T = \frac{n}{2}\log\frac{RSS0}{RSS1} = \frac{n}{2}\log\frac{\sum_{i=1}^{n}\left(Y_i - m_0\left(t_i\right)\right)^2}{n^{-1}\sum_{i=1}^{n}\left(Y_i - m\left(t_i\right)\right)^2} \qquad (10)$$

where *RSS0* and *RSS1* are the maximum likelihood estimators for the error variance under H_0 and H_1, respectively. For a fixed significance level α, we reject the null hypothesis when $T > T^{1-\alpha}$, where $T^{1-\alpha}$ is the 100(1-α)-percentile of the *T* under H_0. As asymptotic theory for nonparametric tests is not closed yet, we can apply resampling methods such as bootstrap (Efron and Tibshirani, 1994) to calibrate the test. Wild bootstrap (Hardle and Mammen, 1993) was used in this case to generate the resamples. Thus, we applied the following algorithm to test the goodness-of-fit of the classical growth model.

1. Obtain the null, $m_0(t)$,, and alternative, $m(t)$, regression functions for the sample data $\{t_i, Y_i\}_{i=1}^n$ and compute the test statistic T_{obs} as defined in expression (7).
2. For b = 1,..,B (B = 10000 in this work)

   2.1. generate bootstrap resamples $\{t_i, Y_i^*\}_{i=1}^n$, with $Y_i^* = m_0(t_i) + e_i^*$ being

$$e_i^* = \begin{cases} \dfrac{(1-\sqrt{5})e_i}{2} & \text{with probability } p = \dfrac{5+\sqrt{5}}{10} \\ \dfrac{(1+\sqrt{5})e_i}{2}_i & \text{with probability } p = \dfrac{5-\sqrt{5}}{10} \end{cases}$$

   where $e_i = Y_i - m_0(t_i)$ are the errors of the parametric model in H_0.

   2.2. Given $\{t_i, Y_i^*\}_{i=1}^n$, compute T^{*b} as in step 1.

3. The empirical p-value of the test is the proportion of simulated T-statistcs larger than that obtained for the observed data.

Appendix B: Supplementary data for the Results Section

This Appendix provides the parameters and the p-values of the likelihood ratio tests for the fitted von Bertalanffy and Gompertz models (Table B1). Figure B1 provides graphical comparison between classical and GAM fits of mussel growth in terms of total, shell and soft tissue weight .

Table B1: Parameters of the von Bertalanffy and Gompertz fits for shell length (L), total (TDW), shell (DWs), and tissue (DWt) dry weight. GoF test: p-value of the Generalized likelihood ratio goodness-of fit test calibrated by wild bootstrap (B = 10000).

		von Bertalanffy						**Gompertz**					
		Estimate	Std.Error	t-value	Pr(>|t|)		GoF test	Estimate	Std.Error	t-value	Pr(>|t|)		GoF test
L (mm)	L_∞	75.83	1.423	53.28	<2.e-16	***	0.314	72.96	1.043	69.94	<2.e-16	***	0.313
	K	0.175	0.014	12.30	7e-10	***		0.274	0.012	22.18	5e-14	***	
	t_0	-1.760	0.230	-7.661	7e-07	***		0.831	0.077	10.730	5e-09	***	
TDW (g)	w_∞	16.44	3.334	4.93	0.0001	***	0.013	11.19	0.469	23.89	2e-14	***	0.065
	K	0.065	0.023	2.87	0.0106	*		0.246	0.012	21.13	1e-13	***	
	$t0$	0.163	0.437	0.372	0.7142			4.907	0.242	20.290	2e-13	***	
DWs (g)	w_∞	14.57	3.146	4.63	0.0002	***	0.012	9.74	0.423	23.01	3e-14	***	0.056
	K	0.060	0.021	2.83	0.0116	*		0.226	0.011	21.26	1e-13	***	
	t_0	0.232	0.413	0.562	0.5814			5.362	0.266	20.200	2e-13	***	
DWt (g)	w_∞	2.118	0.375	5.64	3e-05	***	0.007	1.584	0.122	13.02	3e-10	***	0.01
	K	0.103	0.041	2.48	0.0237	*		0.383	0.038	9.97	2e-08	***	
	t_0	-0.048	0.657	-0.073	0.9426			3.269	0.332	9.858	2e-08	***	

(***) p-value < 0.001, (**) p-value < 0.01, (*) p-value < 0.05, (.) p-value < 0.1.

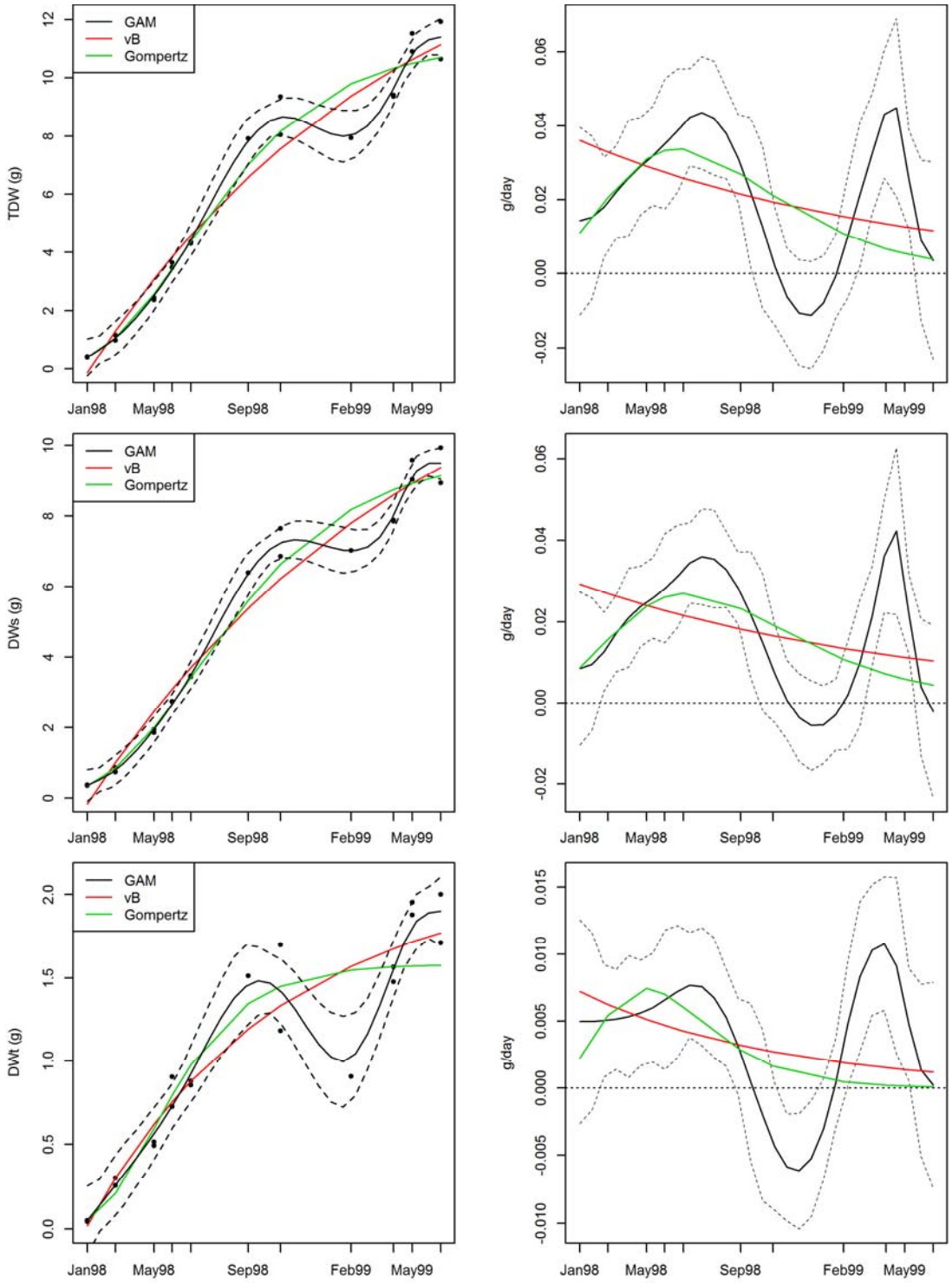


Figure B2: Observed dry weights (points), GAM (black), von Bertalanffy (vB, red) and Gompertz (green) fits of growth curves (left) and their first derivative (right) for mussels gathered from collector ropes (subtidal mussels) . Fitted values (solid line) and 95% confident intervals (dashed lines) for GAM fit. Top: total dry weight (TDW), centre: shell dry weight (DWs) , bottom: tissue dry weight (DWt).

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