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1 **A TWO-STAGE GROWTH MODEL FOR GILTHEAD SEA BREAM (*Sparus***
2 ***aurata*) BASED ON THE THERMAL GROWTH COEFFICIENT**

3 **Mayer, P.¹; Estruch, V.D.² and Jover, M.¹**

4 ¹ Biodiversity and Aquaculture Group. Institute of Animal Science and Technology. Universitat
5 Politècnica de Valencia. Camino de Vera, s/n. 46071 Valencia (Spain), E-mail:
6 pabmagon@gmail.com, mjover@dca.upv.es

7 ² Research Institute for Integrated Management of Coastal Area. Universitat Politècnica de
8 Valencia. C/Paranimf, 1. 46730 Grao de Gandia. Valencia (Spain), E-mail:
9 vdestruc@mat.upv.es

10
11 **Corresponding author:** Vicente D. Estruch, , Email: vdestruc@mat.upv.es, Research Institute
12 for Integrated Management of Coastal Area. Universitat Politècnica de Valencia. C/Paranimf, 1.
13 46730 Grao de Gandia. Valencia (Spain), telephone number: +34 9602849321, Fax number:
14 +34 9602849309

15 **Abstract**

16 Several authors have proposed models to describe fish growth taking the influence of temperature into
17 account, and one of most interesting is the “Thermal unit Growth Coefficient” (*TGC*). Recent research
18 has demonstrated that *TGC* varies throughout the growth cycle of fish, making it necessary to establish
19 different stanzas. In this work, the original *TGC* model using 1/3 as exponent was compared with a new
20 model considering 2/3. Likewise, two stages for the growth of gilthead sea bream under commercial
21 conditions in marine farms were detected by means of *TGC* seasonal models using the continuous
22 temperature curve. A critical value for weight around 117g was obtained, which could mark the
23 transition between two growth dynamics. To describe the weight evolution during a complete production
24 cycle, the two growth stages were described by two separate seasonal *TGC* models (1/3-*TGC* model and
25 2/3-*TGC* model), and with an integrated model named Mixed-*TGC* model, which presents interesting
26 properties of continuity and differentiability and could be an important tool for fish farm management.

27 **Keywords:** Seasonal growth, temperature curve, marine cages production

28 **1.- Introduction**

29 The importance of growth models in aquaculture has been demonstrated by the
30 publication of a large number of papers in recent years (Baer *et al.*, 2011; Dumas *et al.*,
31 2007, 2010; Dumas and France, 2008; Libralato and Solidoro, 2008; Mayer *et al.* 2008,
32 2009; Moses *et al.*, 2008; Seginer and Halachmi, 2008), most of which are based on the
33 metabolic growth model developed early last century (Pütter, 1920; Bertalanffy, 1938,
34 1957; Parker and Larking, 1959; Ursin, 1967) to describe fish growth. Most of the
35 classic models were based on the assumption that growth depends on live weight

36 affected by the exponent $2/3$ (surface rule), and later models (Cho, 1992; Cho and
37 Bureau, 1998) have also used this value. Nevertheless, some authors have questioned
38 the general use of this exponent because Ursin (1968) estimated lower values than $2/3$
39 in some fish, and Moses *et al.* (2008) cited values around $3/4$ in some vertebrates.

40 An alternative is to use the “thermal unit growth coefficient (*TGC*)” model reported by
41 Iwama and Tautz (1981) in hatcheries, and developed by Cho (1992), Cho and Bureau
42 (1998) and Dumas *et al.* (2007) in growing trout, and Mayer *et al.* (2008, 2009) in
43 gilthead sea bream. This model is a particular version of the von Bertalanffy equation
44 that incorporates a cumulative water temperature, which allows an estimation of fish
45 growth in several temperature conditions, constituting an interesting tool for aquaculture
46 management. In the case of gilthead sea bream, growth patterns were considered as a
47 function of cumulative effective temperature $\Sigma (T_i - 12)$, because growth is zero, or
48 negative, for water temperature below 12 °C (Mayer *et al.* 2008, 2009). Other models
49 have also considered the average temperature (Petridis and Rogdakis, 1996; Lupatsch
50 and Kissil, 1998; Lupatsch *et al.*, 2003) but their practical application was difficult.

51 Ursin (1963), Akamine (1993), Moreau (1987) and Fontoura and Agostinho (1996)
52 studied the inclusion of sinusoidal temperature curve in the Bertalanffy growth model,
53 and recently Leon *et al.* (2006) used a temperature function applied to growth model
54 from Hernandez *et al.* (2003). Alternatively, Dumas and France (2008) proposed a
55 model to illustrate the seasonal *TGC* growth of ectotherms using a one year temperature
56 periodic function. Seginer and Halachmi (2008) also applied the sinusoidal temperature
57 curve to the exponential growth model from Lupatsch and Kissil (1998) to study
58 management aspects in intensive gilthead sea bream aquaculture.

59 Another advantage of the *TGC* model was the simplicity of application in aquaculture,
60 as it was possible to estimate the weight throughout the production cycle using a single
61 value of *TGC* (obtained in the same production conditions). However, Dumas *et al.*
62 (2007) suggested the need to use different *TGC* values for different trout stages during
63 the growth period (< 20 g, 20-500 g, > 500 g). This would indicate that new studies
64 revising the *TGC* model in other species are necessary.

65 In a previous paper Mayer *et al.* (2008) studied various growth models for the gilthead
66 sea bream considering the variability of water temperature. The evolution of a set of

67 average weights calculated from different samples obtained in 20 batches where
68 analysed. One of the key findings of the paper was that the best models (including *TGC*
69 model) were those that considered the accumulated effective temperature as an
70 independent variable, instead the time. In a second work, Mayer *et al.* (2009) explored
71 full samples considering all the individual weights of sea bream from the batches
72 studied in Mayer *et al.* (2008) using a discriminant analysis and quantile regression
73 techniques, with reference to the classic *TGC* model. It was suggested that it was
74 possible to differentiate two groups of gilthead sea bream with homogeneous and
75 heterogeneous growth characterized by a different evolution of the weight dispersion.
76 The factors that influenced the dynamics and the diversity of growth were the seasonal
77 change of water temperature and the weight distribution of the fishes provided by the
78 hatchery.

79 The aim of this paper was to develop a new approach to the growth of gilthead sea
80 bream under commercial production conditions with great fluctuations in water
81 temperature, including the sinusoidal temperature curve in the *TGC* model, and
82 considering the different stages throughout the growth period, in order to improve the
83 estimation of growth on aquaculture farms. Our initial goal was to detect the existence
84 of significant changes in the dynamics of the evolution of the average weight of fish
85 over a complete cycle of production considering two-step *TGC* model that established
86 the existence of a “critical or transition” live weight, which indicates indicated a change
87 point in the dynamics of growth of the gilthead sea bream.

88

89 **2.-Material and Methods**

90 **2.1. Mathematical Models**

91 Considering a general model of growth given by the initial value problem,

$$92 \quad \begin{cases} \frac{dW}{dt} = g(W, t), \\ W(t_0) = W_0, \end{cases} \quad (1)$$

93 where W is the weight and t is the time, a model can be achieved that takes into account
94 seasonal fluctuations in temperatures by replacing in (1) the time variable t , by a

95 function $ST(t_0, t)$ (ST was used for simplicity) which represents the accumulated
 96 temperature in the time interval $[t_0, t]$ (Akamine, 1993). Indeed, assuming that at the
 97 initial time t_0 , the accumulated temperature is zero, $ST(t_0, t_0)=0$ we have

$$98 \quad \begin{cases} \frac{dW}{dST} = g(W, ST), \\ W(0) = W_0, \end{cases} \quad (2)$$

99 Models (1) and (2) describe different temporal dynamics. The model (2) takes the sum
 100 of temperature as an independent variable to describe the evolution of time and the
 101 growth is described from the instantaneous rate of weight gain per unit of accumulated
 102 temperature.

103 Taking into account the chain rule

$$104 \quad \frac{dW}{dt} = \frac{dW}{dST} \cdot \frac{dST}{dt} \quad (3)$$

105 and that

$$106 \quad \frac{dST}{dt} = T(t) \quad \text{i.e.} \quad ST(t_0, t) = \int_{t_0}^t T(x) dx \quad (4)$$

107 where $T(t)$ is the continuous function that provides the temperature at any moment t ,
 108 from the model (2) we obtain immediately a seasonal time-dependent model

$$109 \quad \begin{cases} \frac{dW}{dt} = g(W, ST)T(t), \\ W(t_0) = W_0, \end{cases} \quad (5)$$

110 In the case of indeterminate allometric growth the basic model (Parker and Larkin,
 111 1959, Gamito, 1998) is quite common,

$$112 \quad \frac{dW}{dt} = kW^{1-b} \quad (6)$$

113 where k is a constant related with the metabolic loss of an individual unit weight and the
 114 achievement of assimilated food for growth and b is a constant ($0 < b < 1$). The model
 115 given by (6) assumes that the allometric growth rate decreases with time due to the

116 decrease that occurs in metabolic rate with increasing fish size and that W increases
117 without limit (Gamito, 1998).

118 From (3), (4) and (6), we obtain the associated seasonal model

$$119 \quad \frac{dW}{dST} = k \cdot W^{1-b}, \quad (7)$$

120 i.e.

$$121 \quad \frac{dW}{dt} = k \cdot T(t) \cdot W^{1-b} \quad (8)$$

122 In what follows, we assume that the time, t , is given in days (d), the units of the constant
123 rate k (>0) are $g^b \cdot (^\circ\text{C} \cdot \text{d})^{-1}$, $T(t)$ is the function that provides the water temperature at
124 each time ($^\circ\text{C}$), and the allometric exponent b ($0 < b < 1$) is dimensionless.

125 If we suppose initially that $t=t_0$, $ST(t_0, t_0)=0$ and $W=W_0$, the solution of (7) is

$$126 \quad W^b(t) = W_0^b + k \cdot b \cdot ST(t_0, t). \quad (9)$$

127 An immediate discrete version of (9) can be obtained by considering for each day, i ,
128 $i=1,2,\dots,n$, the mean of the daily temperature, T_i . so we have the model

$$129 \quad W_n^b = W_0^b + k \cdot b \cdot \sum_{i=1}^n T_i, \quad n = 1,2,\dots \quad (10)$$

130 If $b=1/3$ in (10), and denote $k=TGC/b$, we obtain the classic *TGC*-model (Cho, 1992)

$$131 \quad W_n^{\frac{1}{3}} = W_0^{\frac{1}{3}} + TGC \cdot \sum_{i=1}^n T_i \quad (11)$$

132 which was developed from empirical results without any mathematical or dynamical
133 previous consideration (Dumas *et al.*, 2007).

134 Equations (7) or (8) allow modelling the indeterminate seasonal growth. The function
135 $T(t)$ can take different expressions depending on environmental conditions (Akamine,
136 1993).

137 The integral solution of equation (8) is given by the expression

138
$$W^b(t) = W_0^b + k \cdot b \cdot \int_{t_0}^t T(t) \cdot dt \quad (12)$$

139 i.e.

140
$$W(t) = \left(W_0^b + k \cdot b \cdot \int_0^t T(t) dt \right)^{\frac{1}{b}} \quad (13)$$

141 As mentioned above, the temperature function $T(t)$ depends on the context. In the case
 142 of marine farms in fixed locations, fish live in an environmental where the water
 143 temperature evolves according to regular annual cycles. A simple one-year periodic
 144 expression, which allows us to include the seasonal influence of temperature on growth
 145 in the model, is based on the sinusoidal function (14) used in different studies

146
$$T(t) = T_m + T_D \cdot \sin\left(\frac{2\pi}{365} \cdot (t - \alpha)\right) \quad (14)$$

147 where $t \geq 0$, and T_m is the average annual temperature, T_D is the amplitude and α is a
 148 tuning parameter. From (14), we obtain a compact expression for the cumulative
 149 temperature function in the time interval $[t_0, t]$,

150
$$ST(t_0, t) = \int_{t_0}^t T(t) dt = T_m (t - t_0) - T_D \frac{365}{2\pi} \left(\cos\left(\frac{2\pi(t - \alpha)}{365}\right) - \cos\left(\frac{2\pi(t_0 - \alpha)}{365}\right) \right) \quad (15)$$

151 In the case of gilthead sea bream, it is more appropriate to use the effective temperature,
 152 $T(t)-12$, instead of $T(t)$ (Mayer *et al.* 2008), which only involves replacing T_m by $T_m - 12$
 153 in (15).

154
$$ST(t_0, t) = \int_{t_0}^t (T(t) - 12) dt = (T_m - 12)(t - t_0) - T_D \frac{365}{2\pi} \left(\cos\left(\frac{2\pi(t - \alpha)}{365}\right) - \cos\left(\frac{2\pi(t_0 - \alpha)}{365}\right) \right) \quad (16)$$

155 By substituting (16) in (13), and solving the integral, we obtain an expression for the
 156 weight in the instant t (Dumas and France, 2008)

157
$$W(t) = \left(W_0^b + k \cdot b \cdot \left((T_m - 12) \cdot (t - t_0) - T_D \frac{365}{2\pi} \left(\cos\left(\frac{2\pi(t - \alpha)}{365}\right) - \cos\left(\frac{2\pi(t_0 - \alpha)}{365}\right) \right) \right) \right)^{\frac{1}{b}} \quad (17)$$

158 i.e.

159
$$W(t) = \left(W_0^b + TGC_b \cdot \left((T_m - 12) \cdot (t - t_0) - T_D \frac{365}{2\pi} \left(\cos\left(\frac{2\pi(t - \alpha)}{365}\right) - \cos\left(\frac{2\pi(t_0 - \alpha)}{365}\right) \right) \right) \right) \frac{1}{b} \quad (18)$$

160 where $TGC_b = k \cdot b$.

161 Dumas and France, (2008) obtained good results for describing the growth of different
 162 species of ectotherms, using models analogous to that given by equation (18), assuming
 163 different values of b for different species and contexts, but fixing different values for
 164 different time periods under study.

165 From equation (18), three models were developed in order to simulate the seasonal
 166 indeterminate growth of gilthead sea bream. Two of them were obtained by fitting the
 167 data to equation (11), assuming the values $b = 1/3$ and $b = 2/3$, based on actual values of
 168 accumulated temperature. The third model is built by aggregation of the two models
 169 mentioned above, establishing two stages of growth.

170 **2.2. Data description**

171 Models have been developed considering data on weight and accumulated temperature
 172 from 20 batches of farmed gilthead sea bream in real conditions of growth (Mayer *et al.*
 173 2008).

174 To validate the models the weight data from 6 batches of gilthead sea bream (Table 1)
 175 were used. The production conditions of these 6 batches were similar to those described
 176 in Mayer *et al.* (2008) and corresponded to an initial production period between April
 177 and October (Table 1).

178 **TABLE 1**

179 **2.3 Statistical analysis and design of the models**

180 A preliminary exploratory analysis of the data from the 20 batches was performed,
 181 considering the discrete model

182
$$W_f = \left(W_0^b + TGC_b \cdot ST \right) \frac{1}{b} \quad (19)$$

183 where parameters b and TGC_b were estimated from available actual data of accumulated
 184 effective temperatures, by the Levenberg-Marquard iterative method available in

185 Statgraphics[®] plus version 5.1. The exploratory analysis studying the model (19) with
186 both $b=1/3$ and $b=2/3$ was continued using a least squares fit after linearisation,
187 obtaining the values for the *TGC*, named $TGC_{1/3}$ and $TGC_{2/3}$, respectively.

188 For integrating two models it was necessary to establish the transition point of change in
189 the dynamics of growth we consider the expression (7) with $b=1/3$ and $b=2/3$, and solve
190 the equation

$$191 \quad k_{1/3} \cdot W^{2/3} = k_{2/3} \cdot W^{1/3} \quad (20)$$

192 Note that in (7) we must distinguish two values of k which are different for the two
193 values of b , so $k_b = TGC_b/b$ for $b=1/3$, $b=2/3$, respectively. The non-zero solution for W
194 in (20), $W_c = 1/8 (TGC_{2/3} / TGC_{1/3})^3$ is a theoretical critical value of the weight for which
195 the instantaneous rate of change in terms of weight depending on accumulated
196 temperature is the same for both models (see Figure 1). We assumed the hypothesis
197 that the critical weight obtained indicates a smooth transition from the dynamics
198 described by the model given by equation (19) with $b=1/3$ to the dynamics described by
199 the model with $b=2/3$.

200 To estimate the final weight of gilthead sea bream, two simulation models were
201 developed from equation (18) with $b=1/3$ ($TGC_b = TGC_{1/3}$) and $b=2/3$ ($TGC_b = TGC_{2/3}$),
202 respectively, and from the temperature function, $T(t)$, given in (14). These models were
203 designated the seasonal 1/3-*TGC* model and seasonal 2/3-*TGC* model, respectively. The
204 parameters T_m , T_d and α , of the temperature function $T(t)$, (14) were adjusted for the
205 environmental conditions where the studied batches were located. This was done using
206 a large sample of daily temperatures of sea water for a period of three years (March
207 1998-March 2001) and the Levenberg-Marquardt algorithm available in MATLAB[®] v.
208 5.3 was used.

209 From the seasonal models 1/3-*TGC* and 2/3-*TGC*, taking into account the transition
210 value of the weight obtained previously ($W_c \approx 117$ g), a new simulation model was
211 designed which is a combination of both of the previous versions, named seasonal
212 Mixed-*TGC* model. To analyse and validate the seasonal models, 1/3-*TGC*, 2/3-*TGC*
213 and Mixed-*TGC*, various techniques were applied, using the statistical package
214 Statgraphics[®] plus 5.1.

215 The three models were tested using the 6 batches described in Table 1, which were not
216 used in model development. We have considered jointly, the actual average weight data,
217 from different samples taken in the 6 batches obtaining a single large sample. Samples
218 in each batch were taken at different times of the production cycle. The estimated
219 weights for the three models, from the initial weight and for each batch, for the same
220 times in which samples were taken, were computed. Finally the actual and estimated
221 values were compared. On the one hand, we contrasted the equality of the means of the
222 absolute errors (absolute value of the difference between real values and estimated
223 values of weight) for the three models by means of an ANOVA, using the t -test. On the
224 other hand, the differences between actual weights and estimated weights were also
225 studied considering contrasts for paired values (using the t -test). It was thus verified
226 whether each model estimated suitably, overestimated or underestimated the final actual
227 weight.

228 Finally, by contrasting hypotheses about the equality of standard deviations of the
229 absolute errors, it was determined which model estimates more accurately the actual
230 weight.

231 **3.-Results**

232 Considering the data from the 20 batches and equation (19), the parameters b and TGC_b
233 were estimated from real data of actual accumulated temperatures. A value for
234 $b=0.6478$ very close to $2/3$ was obtained, with the 95%-asymptotic confidence interval
235 being for b , (0.5576, 0.7180), and a value for $TGC_b=0.014437$, with the 95%-asymptotic
236 confidence interval being for TGC_b (0.007744, 0.021129) and $R^2=97.8\%$. Asymptotic
237 confidence intervals showed that the parameters were significant and the coefficient of
238 determination indicated a strong model fit to the data. These results led us to propose
239 the viability of the TGC model with $b = 2/3$.

240 The results for the value TGC_b obtained by least squares, after linearisation, for models
241 with $b=1/3$ and $b=2/3$, respectively, are shown in Table 2. Obviously, TGC values are
242 different in the two models, $TGC_{1/3} = 0.00164$ and $TGC_{2/3} = 0.01609$, but remain highly
243 significant.

244 **TABLE 2**

245 Figure 1 shows graphs corresponding to the instantaneous rates of growth, dW/dST ,
 246 depending on the weight, W , given in (6), for the cases $b=1/3$ (1/3-model) and $b=2/3$
 247 (2/3-model), considering the values $k=k_{1/3}$ and $k=k_{2/3}$, showed in Table 2, respectively.
 248 Both curves allow us to compare the dynamics of the evolution of weight for both
 249 models. Instantaneous growth rates based on the cumulative effective temperature
 250 (dW/dST , $g\ ^\circ C^{-1}$) are equal for the non-zero intercept point corresponding to the value of
 251 weight $W \approx 117$ g (transition value of weight). From $W=0$ to $W=117$ g, instantaneous
 252 growth rate of weight with respect to the cumulative effective temperature is higher and
 253 grows faster for the 2/3-model. After $W=117$ g, the instantaneous growth rate is higher
 254 for 1/3-model. These results clearly suggest a pattern of gilthead sea bream growth in
 255 two stages.

256

FIGURE 1

257

258 The fitted values for the parameters of the temperature function $T(t)$, described in (14),
 259 are $T_m=18.8525$, $T_D=-6.6997$ and $\alpha=-312.4609$. Figure 2 shows the temperature
 260 function $T(t)$ and actual temperature data over a period of time established by the
 261 available actual data (available time interval started at day 69, March 10). Note that by
 262 periodicity, the first day of January would be day $1+365 \cdot j$, where j is any integer value.

262

FIGURE 2

263

264 So, two seasonal models were established based on equation (18), in order to describe
 265 the growth of gilthead sea bream; the seasonal 1/3-TGC model ($b=1/3$,
 266 $TGC_{1/3}=0.001646$) and the seasonal 2/3-TGC model ($b=2/3$, $TGC_{2/3}=0.016095$). From
 267 the former models, 1/3-TGC and 2/3-TGC, we constructed the seasonal Mixed-TGC
 model, which is defined in (21) and (22).

268

$$W_f(t) = \left(W_0^{\frac{1}{3}} + TGC_{1/3} \cdot ST(t_0, t) \right)^3, \text{ if } W_f(t) < 117 \quad (21)$$

269

$$W_f(t) = \left(W_0^{\frac{2}{3}} + TGC_{2/3} \cdot ST(t_0, t) \right)^{\frac{3}{2}}, \text{ if } W_0(t) \geq 117 \quad (22)$$

270 To estimate final weights greater than 117 g from initial weight less than 117 g, first we
 271 calculated the value t_1 for reaching 117 g using the 1/3-TGC model and the expression

272 (23), and then we estimated the final weight using the 2/3-*TGC* model and expression
273 (24).

$$274 \quad W_f(t_1) = \left(W_0^{\frac{1}{3}} + TGC_{1/3} \cdot ST(t_0, t_1) \right)^3 = 117 \quad (23)$$

$$275 \quad W_f(t) = \left(117^{\frac{1}{3}} + TGC_{2/3} \cdot ST(t_1, t) \right)^{\frac{3}{2}} \quad (24)$$

276 Therefore, until a final weight less than 117, the Mixed-*TGC* model coincides with the
277 1/3-*TGC* model. In the case of an initial weight greater than or equal to 117g, the
278 Mixed-*TGC* model coincides with the 2/3-*TGC* model. The Mixed-*TGC* model leads to
279 a continuous curve for representing the final weight of the gilthead sea bream.
280 Moreover, the curve is also differentiable at all time because the Mixed-*TGC* model is
281 constructed so that when the weight is exactly 117 g, the derivatives of the functions
282 that define the models 1/3-*TGC* and 2/3-*TGC* coincide. Thus, the transition from the
283 1/3-*TGC* model to the 2/3-*TGC* model occurs smoothly, without sharp points.

284 Figure 3 shows actual weight points together with estimated weight curves obtained
285 from the three models, 1/3-*TGC*, 2/3-*TGC*3 and Mixed-*TGC*, for the six new batches
286 reserved for validating the theoretical models.

287 **FIGURE 3**

288 Table 3 shows the results for the averages of absolute errors of estimation for the
289 complete cycle (long-term using data from all monthly samples), for the periods before
290 the critical weight ($W_f < 117$) and after the critical weight ($W_0 > 117$) and for final weight
291 at the end of the cycle. The estimated absolute error (absolute value of the difference
292 between real and estimated value), is a measure of the adjustment of the values
293 estimated by models to the real data. The results show a lower value of the average of
294 the absolute errors for the 1/3-*TGC* model than 2/3-*TGC* when $W < 117$ g, and for the
295 2/3-*TGC* model than 1/3-*TGC* when $W \geq 117$ g, but if the complete production cycle is
296 considered and the Mixed *TGC* model is compared with the 1/3-*TGC* model and the
297 2/3-*TGC* model, differences were not statistically significant. When final weight was
298 estimated from initial weight with three models, differences were not significant.

TABLE 3

300 Finally, Table 4 shows the outcomes of the hypothesis tests considering the resulting
301 variable by subtracting the actual weight minus the estimated weight, $D=W_{real}-W_{est}$.
302 When considering the sign of the difference between real and estimated weight, we can
303 determine if a model overestimates or underestimates real weight. Analysis
304 distinguishes the case in which the real final weight is less than 117 g (first stage) from
305 that where the real initial weight is greater than or equal to 117 g (second stage). The
306 Mixed-*TGC* model does not appear in the analysis because for final weights less than
307 117g the Mixed-*TGC* model coincides with 1/3-*TGC* model, and if initial weight is
308 greater than or equal to 117, then Mixed-*TGC* model coincides with 2/3-*TGC* model.

TABLE 4

310 For a significance level $\alpha = 0.05$, on the one hand the results indicate that there are no
311 statistically significant differences between the real weight and the weight estimated by
312 the 1/3-*TGC* model for the first stage, and that the 1/3-*TGC* model tends to overestimate
313 the final weight in the second stage of growth. On the other hand, the 2/3-*TGC* model
314 overestimated the final weight in the first stage of growth while there were no
315 statistically significant differences between the real weight and weight estimated by the
316 2/3-*TGC* model in the second stage of growth.

4.-Discussion

318 Final weight of gilthead sea bream in real conditions of production, seems to be better
319 explained using the *TGC* model with $b=2/3$ than with $b=1/3$, because estimated value of
320 exponent was $b=0.648$, very close to 2/3. Lupatsch and Kissil (1998) developed a
321 growth model for gilthead sea bream and obtained a coefficient for weight similar to 2/3
322 ($b= 0.613$), although in a new model (Lupatsch *et al.*, 2003) the coefficient was lower
323 ($b=0.514$).

324 When the two models, 1/3-*TGC* and 2/3-*TGC* were assayed, a change in the pattern of
325 growth for gilthead sea bream under commercial production conditions was noted, as
326 the presence of a transition weight value from around 117 grams was detected, which
327 indicates a turning point for the dynamics of growth in weight of fish. If we start with
328 an initial weight of 10 grams, this value can be matched with a value of the sum of

329 effective temperatures $ST = 1670$ °C. We cannot explain the hypothetical physiological
330 process of change that occurs at 117 grams. The results indicate the need to address a
331 more detailed study of allometric growth of gilthead sea bream under production
332 conditions. Nevertheless, the reasons for the change in the pattern of growth should be
333 related with aspects such as the compensatory growth, genetic potential, allometric
334 growth, nutrients or physiology of reproduction. Dumas *et al.* (2007) showed that to
335 describe the growth of rainbow trout over a full cycle of production, there are three
336 stanzas with different values for b . Growth changes associated with these stages are
337 explained by morphological changes due to muscle growth dynamics, nutrient
338 utilisation and reproduction investment. It seems clear that parameter b should not be
339 considered a priori as a constant for a *TGC* model intended to explain the growth of
340 gilthead sea bream in a full production cycle. Specifically, in the case of gilthead sea
341 bream, when considering a complete production cycle, the *TGC-1/3* model tends to
342 overestimate the final weight (Mayer *et al.* 2008).

343 The *1/3-TGC* model gives statistically significant better results for the estimated weight
344 of fish in early stages, to lower final weights of 117 g, while *2/3-TGC* model gives
345 better results in estimating the final weight of fish with initial weights higher than 117
346 g. The result is consistent with the fact that the *1/3-TGC* model is based on the model
347 proposed by Iwama and Tautz (1981) for fingerling growth in hatcheries. If we assume
348 that the temperature varies continuously over time, therefore the model assumes that the
349 growth rate is allometrically related to the weight, W , and the allometric constant of
350 proportionality is directly related to temperature that varies during the rearing period.

351 When we compare the real weight with the estimated weights along the complete
352 growth cycle, we cannot establish statistically significant differences, because the large
353 dispersion of the absolute errors corresponding to the *1/3-TGC* model and *2/3-TGC*
354 model (Figure 4). The three models seems to provide acceptable results for estimating
355 the long term weight, as evidenced by the analysis of absolute errors of estimation
356 (Table 3). If we consider only the weights at the end of the cycle, the absolute error
357 analysis does not allow statistically significant differences between the three models,
358 but the final error clearly seems to be lower with Mixed or *2/3-TGC* models than *1/3-*
359 *TGC*-model. In view of the graphs in Figure 3, it seems clear that both *2/3-TGC* model
360 and further the *1/3-TGC* model, tend to overestimate the weights at the final of the cycle

361 of production. Notably, the absolute errors for models *1/3-TGC* and *2/3-TGC* show a
362 wide dispersion, which prevents us establishing significant discrepancies in absolute
363 errors considering the complete cycle in the three models. In Figures 4 and 5, the value
364 for the standard error reflects the variation within each sample, and we can observe that
365 the mean of absolute errors for the *Mixed-TGC* model is the lowest.

366 FIGURE 4 – FIGURE 5

367 It appears that the errors for the *Mixed-TGC* model have statistically significant lower
368 dispersion when estimating the average absolute errors. Indeed, to test if the differences
369 between standard deviations of the errors are statistically significant when considering
370 the whole cycle, hypothesis tests were performed comparing the standard deviations of
371 the long-term absolute errors of estimation for *1/3-TGC*, *2/3-TGC* and *Mixed-TGC*
372 models. First, we tested the null hypothesis that the standard deviation from the
373 absolute error for *1/3-TGC* model is equal to that corresponding to the *Mixed-TGC*
374 model ($H_0: \sigma_{1/3} = \sigma_{Mix}$), against the alternative hypothesis that the standard deviation of
375 the absolute error for the *1/3-TGC* model is greater ($H_1: \sigma_{1/3} > \sigma_{Mix}$), obtaining the p -
376 value=0.0073 which leads to rejection of H_0 . When the null hypothesis that the standard
377 deviations of the absolute errors for *2/3-TGC* model and *Mixed-TGC* model are equal
378 ($H_0: \sigma_{2/3} = \sigma_{Mix}$) was tested against the alternative hypothesis that the standard deviation
379 is greater for the model *2/3-TGC* ($H_1: \sigma_{2/3} > \sigma_{Mix}$), it yielded a p -value=0.0009, which
380 also led to rejection of H_0 . Statistically significant differences between the standard
381 deviations of the absolute errors cannot be set for the *1/3-TGC* and *2/3-TGC* models.
382 The results of these contrasts showed lower uncertainty in estimates from the *Mixed-*
383 *TGC* model and confirmed what Figure 4 seemed to show. Moreover, the *1/3-TGC*
384 model and the *2/3-TGC* model tended to overestimate the weight in the second stage of
385 growth and in the first stage of growth, respectively.

386 From the above considerations, the *Mixed-TGC* model clearly seems to be the most
387 appropriate for describing the growth over the complete production cycle.

388 5.-Conclusions

389 The family of *TGC* seasonal models obtained by considering different values for the b
390 parameter in the metabolic equation provides a framework for studying and explaining

391 indeterminate growth patterns. In the case of gilthead sea bream, the use of 1/3-*TGC*
392 model is useful for estimating the weight in the initial period of growth (in this case the
393 1/3-*TGC* model matches with the Mixed-*TGC* model). In the case where the initial
394 weight exceeds 117 grams, it is advisable to use the 2/3-*TGC* model to estimate the
395 weight (which in this case also coincides with the Mixed-*TGC* model). The study of
396 *TGC* models has revealed a change in the growth pattern that occurs when the fish
397 reaches a weight around 117g.

398 A continuous growth curve including temperature function and integrating the two
399 models was developed to establish a practical tool for fish farmers.

400 The results indicate that the Mixed-*TGC* model is the most appropriate for long-term
401 and final weight estimations along the complete cycle of growth.

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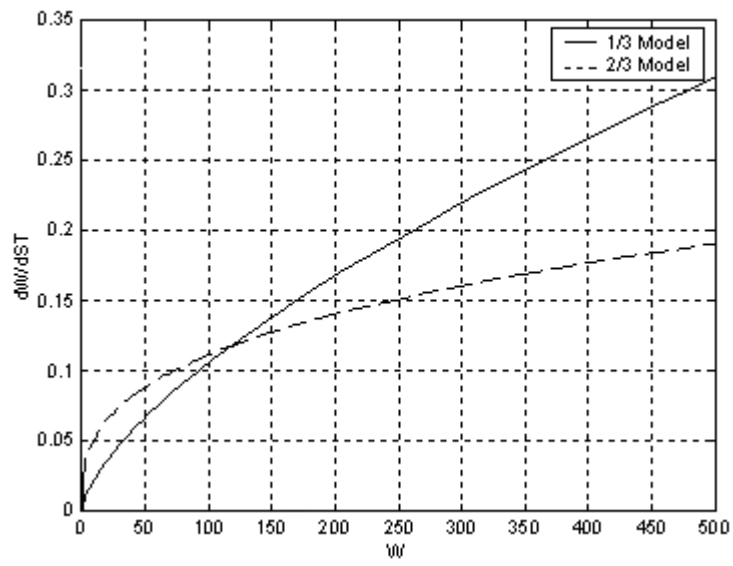
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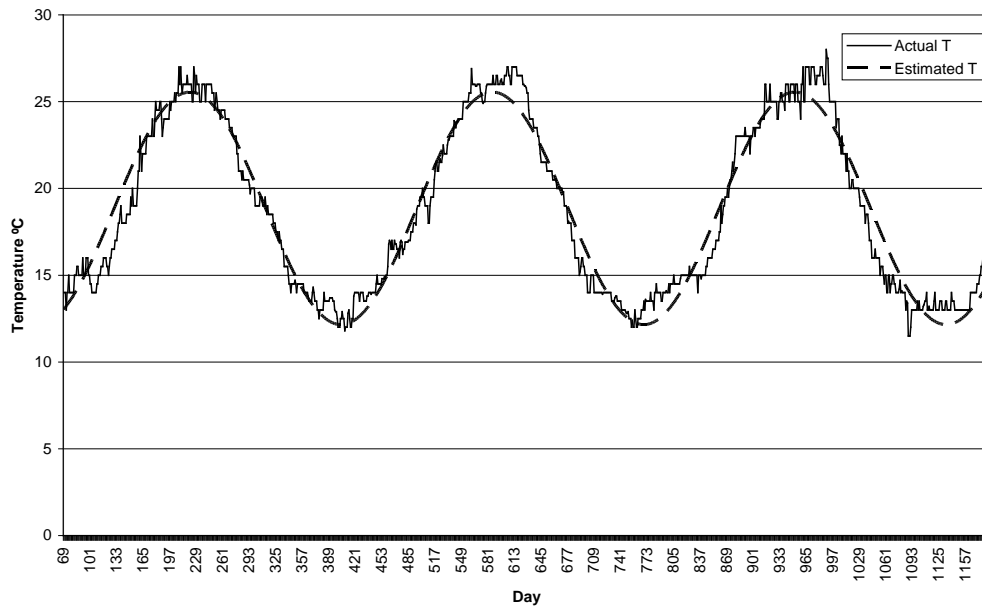
Figure 1. Curves representing instantaneous growth rate dW/dST for two models (1/3-TGC and 2/3-TGC)

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487 **Figure 2. Temperature curve obtained and available actual data from**
488 **Mediterranean Sea in Spanish southwest coast**

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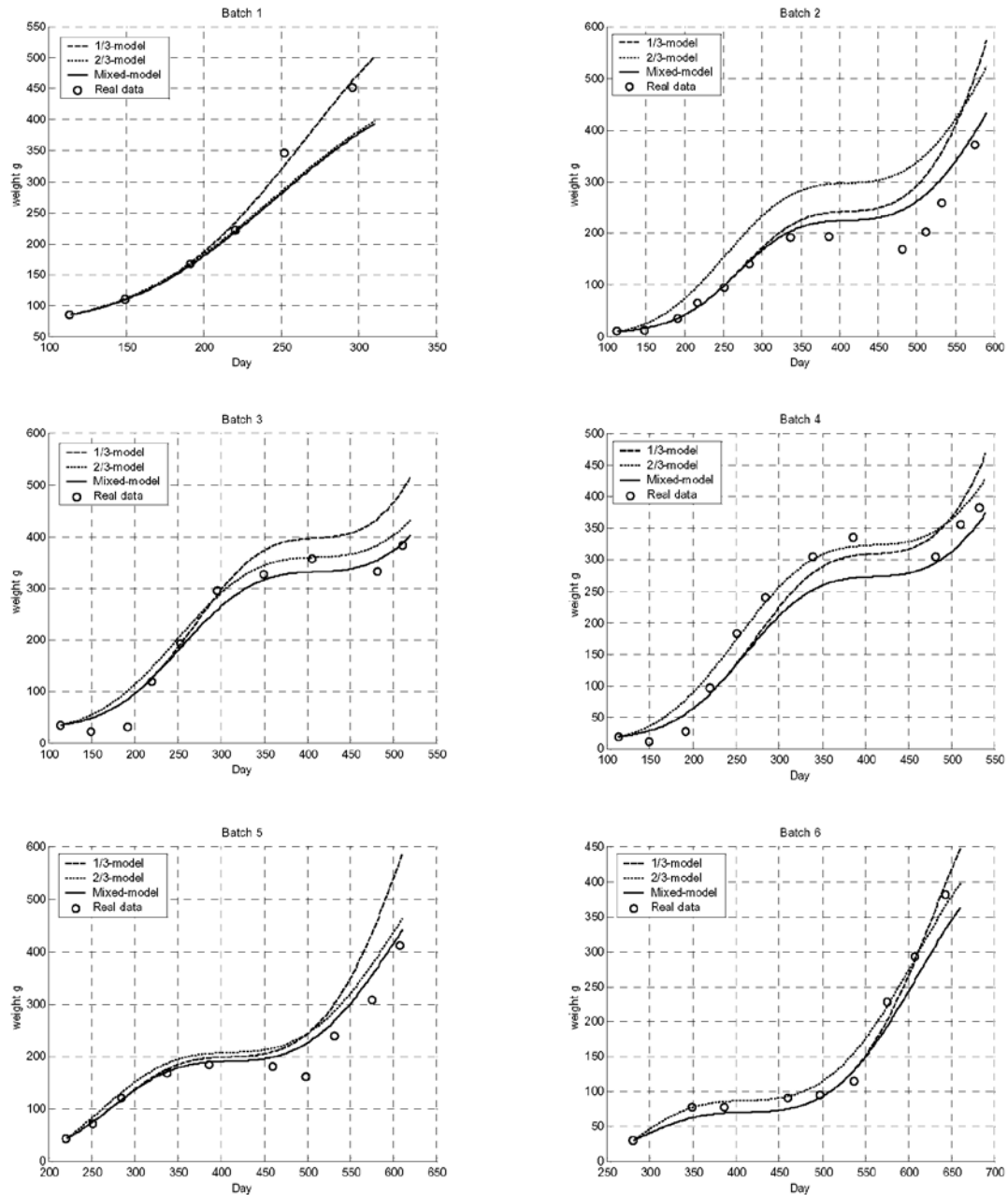


Figure 3. Growth curves generated with three models (*1/3-TGC* and *2/3-TGC* and *Mixed*) and real data from six new batches. (The abscissa axis shows the value of the time variable t day within a year. So, $t=1$ corresponds to the first day of the year, January 1 and a time value $t > 365$ indicates a transition from a year to the next)

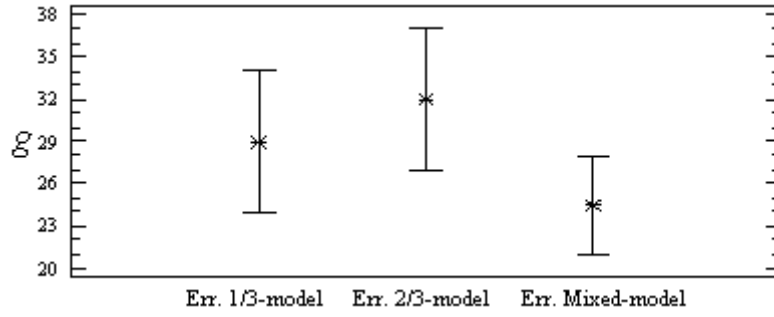


Figure 4. Mean and standard errors for absolute error of long term estimation using three models and real values of new six batches.

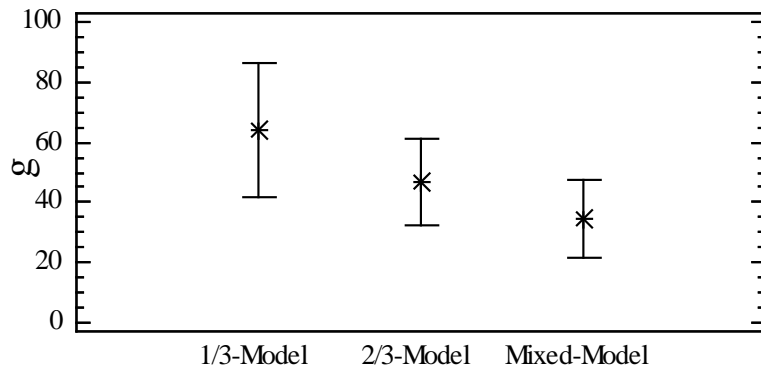


Figure 5. Mean and standard errors for absolute error of final weight estimation using three models and real values of new six batches.

Table 1. Description data from six new batches used for validation of models

Batch	Samples along the period	Initial weight, W_0 (g)	Final weight, W_f (g)	Days	T ($^{\circ}\text{C}$)	ST ($^{\circ}\text{C}$)	TGC ($\text{g}^{1/3} \text{ }^{\circ}\text{C}^{-1}$)	SGR ($\% \text{ d}^{-1}$)
1	5	85.1	452.1	183	23.7	2141.1	0.001530	0.91
2	10	10.0	371.4	463	19.8	3611.4	0.001394	0.78
3	7	35.0	384.4	399	19.0	2793	0.001432	0.60
4	9	19.3	382.8	420	19.2	3024	0.001514	0.71
5	8	43.8	411.6	388	19.7	2987.6	0.001310	0.57
6	8	30.0	381.4	364	20.6	3130.4	0.001324	0.69

T : average temperature of the period, ST : cumulative effective temperature (effective temperature is temperature in degrees Celsius minus 12), TGC : Thermal Growth Coefficient $\left(\frac{W_f^{1/3} - W_0^{1/3}}{ST}\right)$, SGR : Specific

$$\text{Growth Rate} \left(\frac{\ln(W_f) - \ln(W_0)}{\text{Days}} \right)$$

Table 2. Thermal Growth Coefficients obtained using the two models ($b=1/3$ and $b=2/3$) considering growth data from 20 batches

Model	TGC_b	95% TGC_b Confidence interval	K_b	R^2
$\left(b = \frac{1}{3}\right)$	$TGC_{1/3}=0.00164561$	0.00156 - 0.00174	0.0049368	97.3%
$\left(b = \frac{2}{3}\right)$	$TGC_{2/3}=0.0160949$	0.0153 - 0.0169	0,02414235	98.1%.

Table 3. ANOVA results for the averages of absolute errors of estimation (g), and the three models, for the complete cycle (long-term using data from all monthly samples), for the periods before the critical weight ($W_f < 117$) and after the critical weight ($W_0 > 117$) and for final weight at the end of the cycle, considering data from six new batches.

	1/3-TGC Model	2/3-TGC Model	Mixed-TGC model
Long-term	28.9	31.9	24.4
$W_f < 117^{(1)}$	9.5 ^a	28.8 ^b	-
$W_0 \geq 117^{(2)}$	48.7 ^a	29.0 ^b	-
<i>Final Weight</i>	64.1	46.6	34.6

The results must be interpreted by row. (1) P -Value = 0.0328 (2) P -Value= 0.0349

Table 4. Hypothesis tests for paired variables distinguishing two stages of growth: first $W_f < 117$ g and second $W_0 \geq 117$ g

Model	$W_f < 117$ g	$W_0 \geq 117$ g
1/3-TGC	$H_0: D=0$ $H_1: D \neq 0$ $P\text{-value}=0.890$ Not Reject H_0	$H_0: D=0$ $H_1: D < 0$ $P\text{-value}=0.0005$ Reject H_0
2/3-TGC	$H_0: D=0$ $H_1: D < 0$ $P\text{-value}=0.0021$ Reject H_0	$H_0: D=0$ $H_1: D \neq 0$ $P\text{-value}=0.60$ Not Reject H_0