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## Typology of individual growth in sea bass (*Dicentrarchus labrax*)

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**Abstract** – The individual growth variability of passive integrated transponder tagged sea bass was studied using data sets from two different experiments. In experiment 1 ( $n = 485$ ), fish submitted to different photoperiod regimes were held in fourteen groups of individual weight of  $88 \pm 13$  g (mean  $\pm$  SD). In experiment 2 ( $n = 748$ , initial weight  $243 \pm 30$  g) fish were held in fifteen groups and had either free or restricted access to diets with three lipid levels. After adjustment for treatment and tank effects, individual growth curves were analysed using multivariate analysis (principal component analysis and clustering) and were modelled using the summary statistics technique. Different growth profiles were characterized. All of them appeared to be curvilinear. They differed in their level (initial and final weight), slope (slope, specific growth weight, gain) and especially the ratio of males, which showed sexual growth dimorphism. The fish with similar initial weight proved to have very different growth performances, regardless of the treatment effect. Within the same sex, part of the variability between the growth profiles could be explained by differences in the social interactions and in the genetic potential of growth among individuals. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

growth curves / modelling / sea bass / typology / variability

**Résumé** – Typologie des courbes individuelles de croissance chez le bar. La variabilité individuelle de croissance chez le bar est étudiée à partir de données provenant de deux expérimentations où les poissons ont été marqués individuellement avec des transpondeurs passifs. Dans l'expérimentation 1 ( $n = 485$ ), les poissons, dont le poids initial était de  $88 \pm 13$  g (moyenne  $\pm$  écart type), sont soumis à différents régimes photopériodiques. Dans l'expérimentation 2 ( $n = 748$ , poids initial moyen =  $243 \pm 30$  g), les poissons élevés dans quinze bacs reçoivent une alimentation soit en accès limité, soit en accès libre, combinés à trois taux de lipides alimentaires. Après ajustement des données de l'effet traitement et de l'effet bac, une typologie des courbes individuelles de croissance est réalisée par analyse de données multidimensionnelle (analyse en composantes principales et classification ascendante hiérarchique). Les courbes-types de croissance sont modélisées par la technique des variables résumées. Différents profils de croissance sont caractérisés. Ils sont tous curvilinéaires et diffèrent par leur niveau (poids initial et final), leur pente (pente, taux de croissance spécifique, gain de poids) et leur proportion de mâles, montrant ainsi un dimorphisme sexuel de croissance. Des groupes de poissons ayant un poids initial de même ordre de grandeur peuvent avoir des performances de croissance très différentes. Intra sexe, une partie de la variabilité entre profils types de croissance peut être expliquée par des phénomènes de dominance et par des différences de potentiel génétique de croissance entre individus. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

courbes de croissance / modélisation / bar / typologie / variabilité

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### 1. INTRODUCTION

In fish, the individual variability in weight is often high within a specific group and differs frequently

from group to group although maintained in the same environmental conditions (coefficient of variation in weight ranging between 20% and 50% or more). Thus, a group of fish of the same age, the same genetic

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origin, and homogeneous in their initial weight will not always show homogeneous growth (Gardeur et al., 2001). This important difference in weight gain among replicates, is leading to low statistical significance of experiments when the number of replicates is small. This variability, can lead to failure to detect differences between treatments (Schimmerling et al., 1998).

It is obvious that growth performance can differ among individuals originating from the same parents and reared under the same environmental conditions. Different authors have shown an effect of the feeding protocol on the growth heterogeneity (Gélineau et al., 1998), and on the defensibility of the food resource (Carter et al., 1993). The apparition of a more or less significant hierarchical structure among dominant fish eating a large part of the distributed feed (McCarthy et al., 1992, 1993) may partly explain the growth variability among fish. The reason why a fish turns out to become dominant or dominated is still unclear. Among the reasons most frequently put forward is the initial size of the fish, but sexual dimorphism may also lead to differences in growth: Toguyeni et al. (1997) demonstrated that the growth of males was higher than that of females in the case of Nile tilapia. In contrast, in the case of sea bass, females were larger than males when commercial size was reached, and the onset of sexual growth dimorphism was prior to the age of 10 months. For *Perca* (Malison et al., 1993; Fontaine et al., 1997) and turbot (Imsland et al., 1997), sexual growth dimorphism also led to larger females.

The aim of this work was to study the individual variability in the growth of sea bass siblings reared under the same environmental conditions, at different stages of development. To do so, a typology of individual growth curves was performed, using two data sets derived from growth experiments. The

growth profiles were modelled in order to identify the discriminating parameters. The influence of sex and initial individual weight on the growth profiles were also studied.

## 2. MATERIALS AND METHODS

### 2.1. Data sets

Two data sets with individual records of weight were used. The first data set (485 individuals) came from an experimental study on the effects of seven different photoperiod length (treatments duplicated) on the growth of sea bass (*Dicentrarchus labrax*) with initial individual weights of  $88 \pm 13$  g (mean  $\pm$  SD). After the elimination of 15% of the smallest and 15% of the biggest fish, the remainder was allotted by randomization from five classes of weight into fourteen tanks (*table I*). Each group was kept for an experimental period of 105 days in 1000 L tanks supplied with a continual flow of sea water at a renewed rate of  $1 \text{ m}^3 \cdot \text{h}^{-1}$ , at  $21.5 \pm 0.2^\circ\text{C}$ . The oxygen level was constantly maintained above  $6.3 \text{ g} \cdot \text{m}^{-3}$  and salinity was  $38.0 \pm 1.6\text{‰}$ . The fish were fed on demand using computerized self-feeder devices (Boujard et al., 1992). Each activation of the trigger delivered a reward of 2.2–2.5 g.

The second data set (748 individuals, *table I*) came from a study on the effects of dietary lipid level and feeding rate on growth of sea bass with initial individual weights of  $243 \pm 30$  g. This experiment lasted 90 days, during which three dietary lipid levels were tested in groups of fish fed on demand (each lipid level in triplicate) and in groups of fish fed a fixed amount of food (each lipid level in duplicate). The photoperiod

**Table I.** Fish characteristics per tank.

Tanks	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	All
Data set 1																
Number of fish	100	100	100	100	100	100	100	100	100	100	100	100	100	100	–	
Number of P.I.T. tagged fish	35	35	35	35	35	35	35	35	35	35	35	35	35	35	–	
Number of dead fish	4	1	0	0	0	0	0	0	0	0	0	0	0	0	–	5
Final number of fish	31	34	35	35	35	35	35	35	35	35	35	35	35	35	–	485
Mean initial weight (g)	86	85	90	90	83	84	88	94	87	90	81	87	94	92	–	88
CV mean initial weight	15	14	17	15	17	15	15	13	17	15	15	15	13	14	–	15
Mean final weight (g)	143	139	215	215	209	220	218	211	231	244	243	248	175	210	–	209
CV mean final weight	26	20	22	22	22	21	19	20	19	15	13	15	15	16	–	19
Data set 2																
Number of fish	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	
Number of P.I.T. tagged fish	50	50	50	50	50	50	50	50	50	50	50	50	50	50	50	
Number of dead fish	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2
Final number of fish	50	50	50	49	50	50	50	50	50	49	50	50	50	50	50	748
Mean initial weight (g)	241	231	226	232	243	244	247	256	248	238	249	248	250	250	240	243
CV mean initial weight	11.0	12.0	15.0	12.0	14.0	11.0	12.0	12.0	14.0	14.0	13.0	14.0	13.0	11.0	12.0	13
Mean final weight (g)	436	441	449	419	262	178	490	491	464	403	402	431	438	459	437	413
CV mean final weight	15	14	18	15	18	15	15	13	18	18	19	18	17	16	17	16

CV: coefficient of variation (%); P.I.T.: passive integrated tagged sea bass.

length was set at 16L:8D. The fish were siblings and were fed using the same computerized self-feeder devices as in experiment 1, but the feed reward level was set to 1.7–1.9 g per trigger activation.

In both experiments, the fish were individually tagged by injecting a P.I.T. Tag (Passive Integrated Transponder, FISH EAGLE) into the left dorsal muscle behind the supra-occipital region with a syringe, five weeks before the start of the experiment 1 for 35 fish per tank, and four weeks before the start of the experiment 2 for all individuals. The fish were individually weighed at different day ( $D_d$ ):  $D_0$ , beginning of the experiment,  $D_{21}$ ,  $D_{42}$ ,  $D_{64}$ ,  $D_{84}$ , and  $D_{105}$  in experiment 1 and at  $D_0$ ,  $D_{21}$ ,  $D_{42}$ ,  $D_{63}$ , and  $D_{90}$  in experiment 2. Necropsy was performed on each fish for visual sex determination at the end of both experiments. At the end of the experiment 2, the sexual maturity was determined according to the Barnabé scale (Barnabé, 1986).

The following parameters were used during this study:

- $W_i, L_i$ : initial individual fish weight (in grams) and fork length (in centimetres) at  $D_0$ ,
- $W_d, L_d$ : individual fish weight and fork length at  $D_d$ ,
- $W_f, L_f$ : final individual fish weight and fork length at  $D_f$  (i.e.  $D_{105}$  and  $D_{90}$  respectively in experiments 1 and 2),
- $G$ : individual weight gain,  $G = W_f - W_i$ ,
- $G_d$ : individual weight gain between two different measurements,  $G_d = W_d - W_{d-1}$ ,
- $CV_G$ : individual coefficient of variation of  $G$ ,  $CV_G = 100 \times \text{standard deviation on } G_d \times \text{mean } G^{-1}$ ,
- $SGR$ : individual specific growth rate,  $SGR = 100 \times [\ln(W_f) - \ln(W_i)] \times (D_f - D_0)^{-1}$ ,
- $SGR_d$ : individual specific growth rate between two consecutive measurements,  $SGR_d = 100 \times [\ln(W_d) - \ln(W_{d-1})] \times (D_d - D_{d-1})^{-1}$ ,
- $CV_{SGR}$ : coefficient of variation of  $SGR$  within individual (%),  $CV_{SGR} = 100 \times \text{standard deviation on } SGR_d \times \text{mean } SGR^{-1}$ ,
- $S$ : individual condition factor,  $S = W \times L^{-3}$

## 2.2. Statistical analysis

In order to eliminate the influence of the treatment and the tank effect, and to analyse the part of the variability due to the individual effect, the original data was adjusted for the treatment effect and the tank effect. The data analysed corresponded to the residual (about constant) of the mixed hierarchical model of analysis of variance used to analyse the treatment effect (general linear models procedure, SAS, 1989; Univariate procedure, SAS, 1990).

$$Y'_{ijk} = Y_{ijk} - \alpha_i - A_{j(i)} = \mu + \varepsilon_{ijk}$$

where:

- $Y'_{ijk}$ : adjusted data,
- $Y_{ijk}$ : recorded data,

- $\alpha_i$ : treatment effect, with  $i = 1, \dots, 7$  in data set 1;  $i = 1, \dots, 6$  in data set 2,
- $\mu$ : general mean,
- $A_{j(i)}$ : hierarchical tank random effect in treatment, with  $j = 1, 2$  in data set 1;  $j = 1, 2$  or  $1, \dots, 3$  in data set 2,
- $\varepsilon_{ijk}$  = residual, with  $k = 1, \dots, 35$  in data set 1,  $k = 1, \dots, 50$  in data set 2.

The multivariate analysis (principal components analysis: PCA) and the hierarchical clustering with the aggregation criteria of Ward (Ward, 1963) of the corrected data were performed to build a typology of growth curves with the SPAD4.0 software (Lebart et al., 1996).

The values of variables  $W$ ,  $L$  and  $S$  at different stages of growth measurements were used as active variables in a preliminary PCA, in order to determine which of these three variables was the best one to use for data analysis. The projection plot of  $W$ ,  $L$  and  $S$  of each growth measurement on the plane 1 of the PCA did not differ much. The weight was thus chosen as a variable characteristic of growth. The active variables used were weights at different growth measurements. Five of the individuals were missing in one or more weighing in the data set 1 and two in the data set 2. Therefore they were not taken into account in the overall analysis. The characteristics of the principal components and the growth profiles were tested with the test value (Morineau, 1984; Lebart et al., 1996). The growth profiles were modelled and statistically analysed, using the summary statistics technique (Grizzle, 1969; Kenward, 1987) with the SAS software (GLM procedure, SAS 1990). The means by growth profiles were compared using a Scheffe test. As for the adjusted variables, the Lsmmeans (adjusted means) were compared to the adjusted Scheffe test. The size of the growth profiles per tank were analysed with the  $\chi^2$  test per box with the Statbox software.

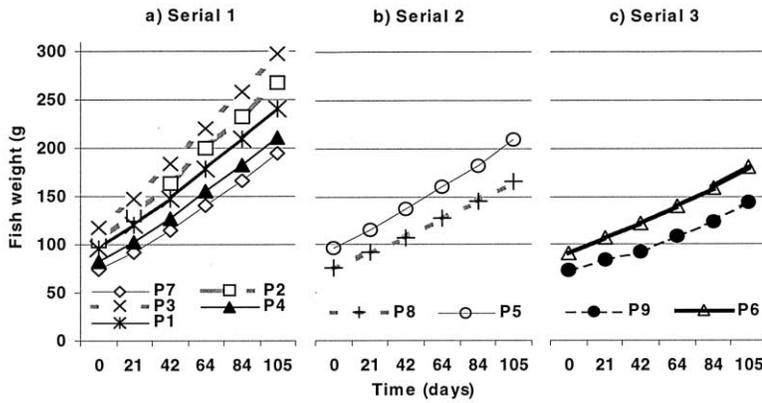
All statistics tests were analysed using a risk level  $\alpha$  of 5% (noted  $P < 0.05$  for a significant effect, and NS for a non significant effect).

## 3. RESULTS

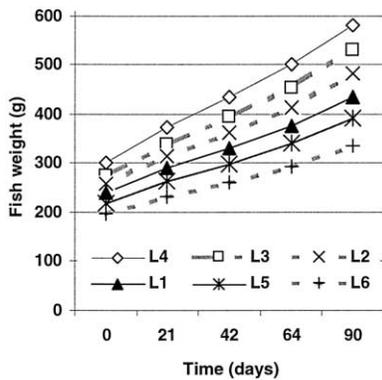
### 3.1. Comparison of growth profiles

The optimal partitioning of the dendrogram resulting from the hierarchical clustering showed nine growth profiles in the case of data set 1 (P1 to P9, figure 1) and 6 growth profiles in data set 2 (L1 to L6, figure 2).

The polynomial modelling of growth profiles shows that they are different from each other in the two experiments (MANOVA test,  $P < 0.05$ ). They differ significantly in their level (initial weight, final weight) and slope (slope,  $SGR$ , gain) but not in their form (quadratic component: growth profile effect NS, table II). However, the general form of the curves is curvilinear (quadratic component significantly different from zero).



**Figure 1.** Fish growth profiles, data set 1, P1 to P9: 9 growth profiles; total:  $n = 485$ , P1:  $n = 68$ , P2:  $n = 50$ , P3:  $n = 16$ , P4:  $n = 94$ , P5:  $n = 59$ , P6:  $n = 42$ , P7:  $n = 63$ , P8:  $n = 65$ , P9:  $n = 28$ .



**Figure 2.** Fish growth profiles, data set 2, L1 to L6: 6 growth profiles; total:  $n = 748$ , L1:  $n = 168$ , L2:  $n = 155$ , L3:  $n = 104$ , L4:  $n = 53$ , L5:  $n = 187$ , L6:  $n = 81$ .

### 3.2. Characteristics of growth profiles

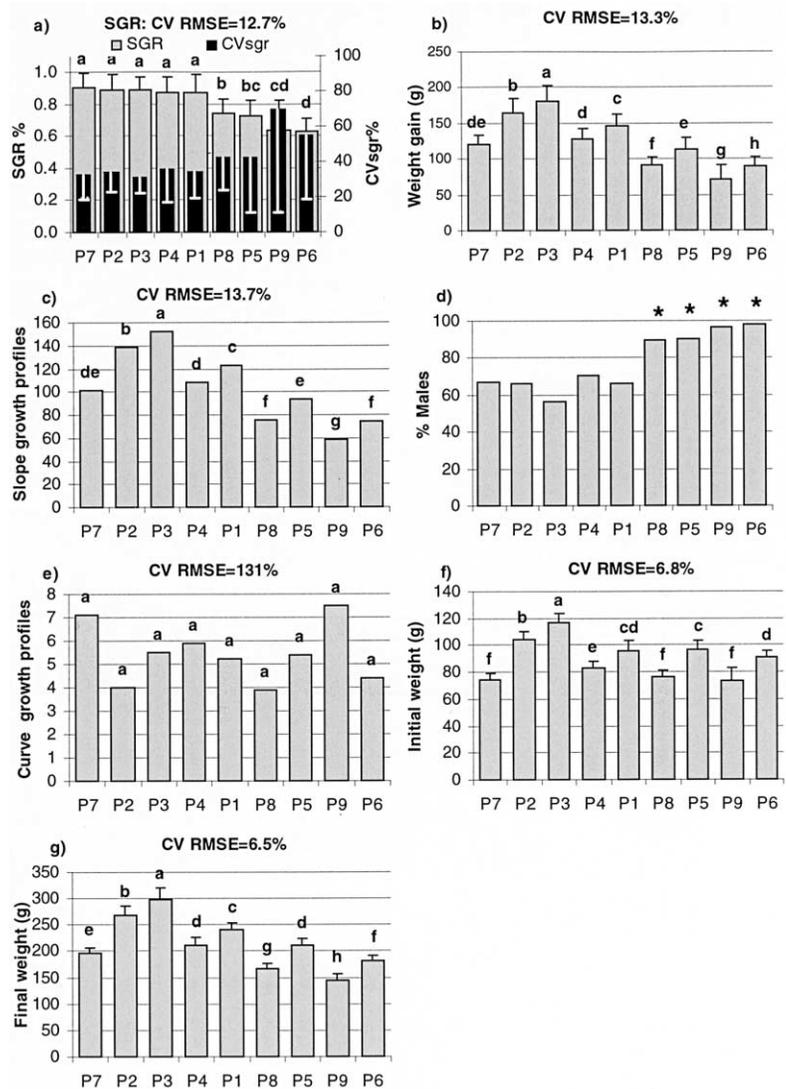
From data set 1, three types of curves can be distinguished on the basis of *SGR*:

- First type: growth profiles P7, P2, P3, P4 and P1 (figure 1a) with *SGR* between 0.87 and 0.90 (NS, figure 3a). These curves are heterogeneous in gain (figure 3b) and slope (figure 3c), and their initial and final weights are significantly different (figure 3f, g). The ratio of males is not different from the mean value (test value  $< 2.0$ , figure 3d).
- Second type: growth profiles P8 and P5 (figure 1b) with a *SGR* range between 0.73 and 0.74 (NS, figure 3a). They have lower gains and slopes than the curves of the first type (excepted in P5 and P7, figure 3b, c)

**Table II.** Analysis of the growth curves: type effect.

Dependent Variable	<i>F</i>	Num. <i>df.</i>	Den. <i>df.</i>	<i>Pr &gt; F</i>	CV RMSE (%)
Data set 1, $n = 485$					
$W_i$	228,9	8	476	0,0001	6,8
$W_f$	437,6	8	476	0,0001	6,5
$W_f$ -adjusted $W_i$	414,4	8	475	0,0001	6,3
<i>SGR</i>	53,5	8	476	0,0001	12,7
<i>SGR</i> -adjusted $W_i$	192,9	8	475	0,0001	8,1
Gain	178,0	8	476	0,0001	13,3
Gain-adjusted $W_i$	232,7	8	475	0,0001	10,9
Linear component (slope)	175,9	8	476	0,0001	13,7
Linear component-adjusted $W_i$	236,2	8	475	0,0001	11,2
Quadratic component (curve)	1,6	8	476	0,1390	131,0
Data set 2, $n = 748$					
$W_i$	857,2	5	742	0,0001	4,8
$W_f$	934,1	5	742	0,0001	6,1
$W_f$ -adjusted $W_i$	861,8	5	741	0,0001	5,8
<i>SGR</i>	26,8	5	742	0,0001	14,7
<i>SGR</i> -adjusted $W_i$	198,0	5	741	0,0001	9,9
Gain	222,9	5	742	0,0001	15,9
Gain-adjusted $W_i$	249,1	5	741	0,0001	12,7
Linear component (slope)	218,5	5	742	0,0001	16,2
Linear component-adjusted $W_i$	253,6	5	741	0,0001	12,8
Quadratic component (curve)	0,4	5	742	0,8830	159,1

Statistics techniques: GLM, SAS. Num. or Den. *df.*: numerator or denominator degrees of freedom; *F*: test F of Fisher; *Pr > F*: realization probability of *F*; CV RMSE: coefficient of variation of root mean square error;  $W_i$ : initial weight;  $W_f$ : final weight; *SGR*: specific growth rate.



**Figure 3.** Growth profiles characteristics, data set 1 (means + SD): P1 to P9, 9 growth profiles. Summary statistics techniques: procedure GLM, SAS. *SGR*: specific growth rate; *CV<sub>SGR</sub>*: coefficient of variation of *SGR*; *CV RMSE*: coefficient of variation of root mean square error. Values with different letters are significantly different ( $P < 0.05$ ). Values with \* are significantly higher than the mean of the population (test value  $> 2$ ).

and their ratio of males is significantly higher than the mean value (89 and 90%, test value  $> 2.0$ , figure 3d). – Third type: the growth profiles P9 and P6 (figure 1c) with low *SGR* (between 0.64 and 0.63, NS, figure 3a), show low gains and slopes (figure 3b, c). These growth profiles are almost exclusively composed of males (96 and 98%, figure 3d).

Furthermore, within each of the three types of growth profiles, the *SGR*, the gain, the slope and the  $W_f$  are significantly different when the data are adjusted to the initial weight (figure 4).

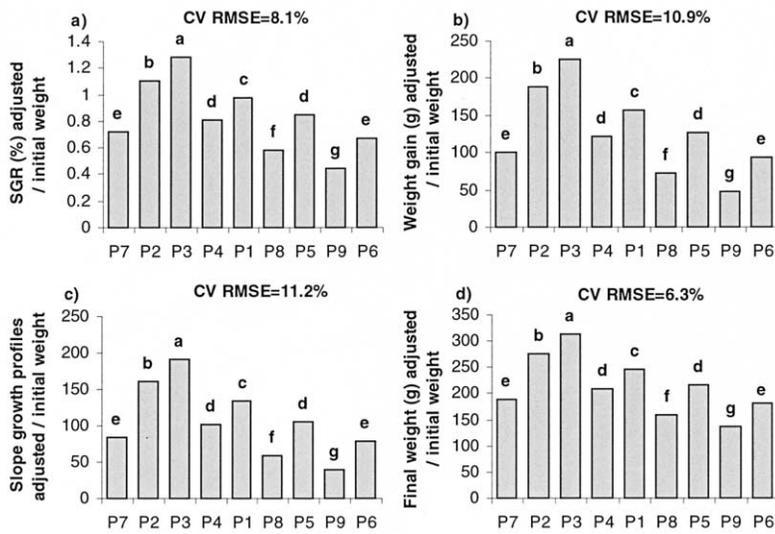
The mean *CV<sub>SGR</sub>* varies from 31 to 69% (figure 3a) and the correlation between *CV<sub>SGR</sub>* and *SGR* is highly significant ( $r = -0.91$ ,  $n = 9$ ). The highest *SGR* is observed when growth is regular over time.

In the case of experiment 2, the growth profiles are more or less parallel (figure 2). The *SGR* varies from 0.59 to 0.73 and the *CV<sub>SGR</sub>* are homogeneous (33 to 36%, figure 5a), so the correlation between *SGR* and

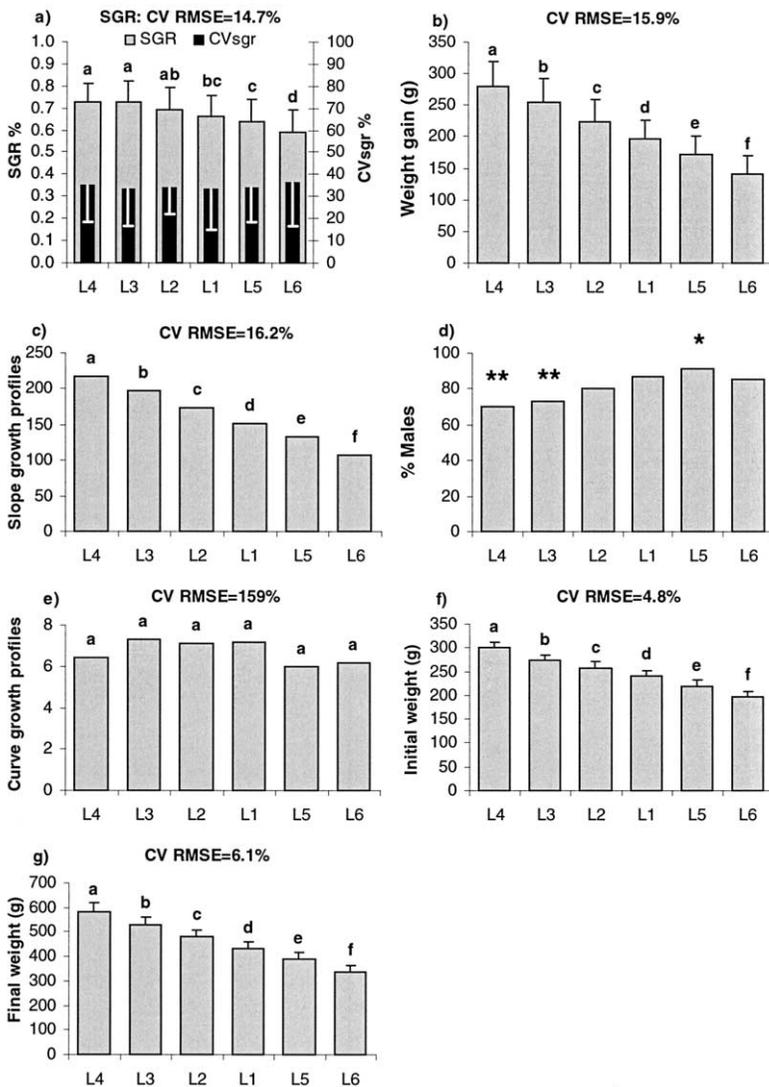
*CV<sub>SGR</sub>* is smaller than in experiment 1 ( $r = -0.43$ ,  $P < 0.05$ ,  $n = 6$ ). Nevertheless, the curves differ in the gain, the slope, the initial and the final weights (figure 5). As in experiment 1, the best growth performances are obtained when the ratio of males is low (figure 5d). The *SGR* becomes different among all the curves and the differences in the gain, the slope, and the  $W_f$  becomes higher when the data are adjusted to the initial weight (figure 6).

### 3.3. Origin of individuals of growth profiles

Individuals in almost every tank made up each growth profiles (table III). However, twelve sizes per type and per tank in the first experiment, and two in the second experiment, are under- or over-represented, compared to the random theoretical size ( $P < 0.05$ ).

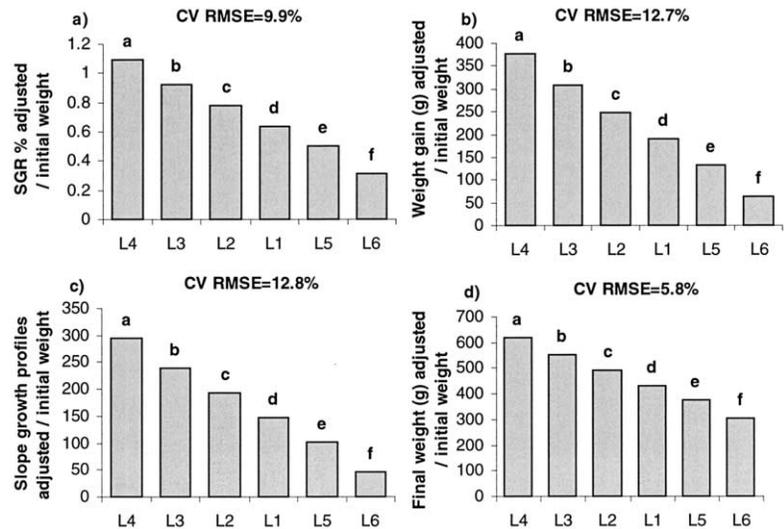


**Figure 4.** Growth profiles characteristics, data set 1, P1 to P9: 9 growth profiles. Adjusted variables: Lsmeans: adjusted means. Summary statistics techniques: procedure GLM, SAS. SGR: specific growth rate; CV RMSE: coefficient of variation of root mean square error. Values with different letters are significantly different ( $P < 0.05$ ).



**Figure 5.** Growth profiles characteristics, data set 2 (mean + SD), L1 to L6: 6 growth profiles. Summary statistics techniques: procedure GLM, SAS. SGR: specific growth rate;  $CV_{SGR}$ : coefficient of variation of SGR; CV RMSE: coefficient of variation of root mean square error. Values with different letters are significantly different ( $P < 0.05$ ). Values with \* or \*\* are significantly higher or lower than the mean of the population (test value > 2).

**Figure 6.** Growth profiles characteristics, data set 2, L1 to L6: 6 growth profiles. Adjusted variables: Lsmeans: adjusted means. Summary statistics techniques: procedure GLM, SAS. *SGR*: specific growth rate; *CV RMSE*: coefficient of variation of root mean square error. Values with different letters are significantly different ( $P < 0.05$ ).



**Table III.** Percent of individuals by type and by tank.

Size (%)	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	All
'Photoperiod' experiment, $n = 485$ ; 9 growth profiles (P1 to P9)																
P1	9	7	4	10	3	6	4	6	9	7	7	12*	6	9	–	100
P2	4	4	10	6	16*	10	6	10	6	6	8	6	4	4	–	100
P3	6	6	19*	13	6	6	13	0*	13	6	0*	0*	6	6	–	100
P4	5	11	3	6	3	11	12	7	4	6	10	7	6	7	–	100
P5	7	8	5	5	5	3	5	5	8	8	7	8	14*	10	–	100
P6	12*	7	5	7	5	5	5	12*	7	12	7	0*	10	7	–	100
P7	6	8	10	5	13	2	5	5	10	10	6	8	10	5	–	100
P8	3	3	11	6	9	14*	9	11	5	3	8	6	5	8	–	100
P9	7	4	11	14*	7	4	7	4	11	7	4	11	4	7	–	100
Deaths %	11	3	0	0	0	0	0	0	0	0	0	0	0	0	–	
Theoretical %	6.4	7.0	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	7.2	–	
'Lipid' experiment, $n = 748$ ; 6 growth profiles (L1 to L6)																
L1	10	5	4	8	4	9	7	7	6	4	8	9	7	7	6	100
L2	5	11*	7	5	5	5	6	8	5	8	5	6	8	8	8	100
L3	8	8	6	9	9	4	6	7	7	10	5	6	7	3	9	100
L4	4	0*	9	4	8	8	6	6	11	6	11	8	6	9	6	100
L5	6	6	9	7	7	8	7	7	6	5	9	5	4	7	6	100
L6	6	6	6	2	10	5	7	4	10	10	4	9	10	5	6	100
Deaths %	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	
Theoretical %	6.7	6.7	6.7	6.6	6.7	6.7	6.7	6.7	6.7	6.6	6.7	6.7	6.7	6.7	6.7	

Tank 1 to Tank 15 (T1 to T15); \* size significantly different from theoretical size ( $\chi^2 < 0.05$ ).

## 4. DISCUSSION

### 4.1. Growth profiles shape

The growth profiles were curvilinear in both experiments, though the initial fish mean weights were different (approximately 90 and 240 g in experiments 1 and 2, respectively). They differed in their linear components, and no significant differences in their quadratic component were observed, but this is most probably due to its strong variability (high coefficient of variation of root mean square error). According to Moreau (1987), fish growth curves are sigmoid, and a

Von Bertalanffy growth function was widely used in the long term (over a few years) length–growth studies. The duration of our experiments was 90 and 105 days, respectively for experiment 1 and 2. A curvilinear relationship, with growth acceleration over time and no inflexion point, is not inconsistent with a sigmoid model when considering such duration of the experiments.

### 4.2. Initial weight and growth profiles

At similar *SGR*, some growth profiles show significantly different  $W_i$ , or conversely, some growth pro

files with similar  $W_i$  (adjusted) show significantly different  $SGR$ . This result confirms that an homogeneous initial weight among individuals does not lead to similar specific growth rates, as has been shown in the case of trout and salmon (Gardeur et al., 2001).

#### 4.3. Sex and growth profiles

There is an important effect induced by gender, since a higher  $SGR$  was observed when the ratio of males was low. The correlation between the  $SGR$  and the ratio of males was  $-0.96$  ( $n = 9$ ) and  $-0.82$  ( $n = 6$ ), respectively in experiments 1 and 2. Thus, our study confirms the occurrence of sexual growth dimorphism in sea bass, as has been previously observed. According to Bruslé and Roblin (1984), testicular or ovarian differentiation is observed in sea bass, reared in artificial conditions, when the standard length reaches 86 to 130 mm. The initial sexual maturity of males is reached by 50% of individuals at 23 months (standard length between 187–197 mm) and for 100% at 33 months (standard length between 276–316 mm). In the case of females, maturity occurs later and is only completed at the end of the third year. At the onset of experiment 1 and 2, the standard lengths were respectively  $190 \pm 9$  and  $264 \pm 10$  mm for the males and  $192 \pm 10$  and  $269 \pm 10$  mm for the females. During the period of sexual maturity (April, experiment 1) 30 to 83% of males were mature. At the end of experiment 2 (December) all the females were in stage 2 of the Barnabé scale (Barnabé, 1986). One might conclude, for the two experiments, that sexual growth dimorphism appears in a population of mature males and immature females.

Sexual growth dimorphism is obviously an important factor to take into consideration in the case of growth studies. However, males and females were present in every growth profile, and with a similar ratio of males, significantly different  $SGR$  were observed. Factors other than sex should be taken into consideration in the study of variability among growth profiles.

#### 4.4. Social interaction and growth profiles

The strong correlation between the  $SGR$  and the  $CV_{SGR}$  among growth profiles reflected the aggregation of individuals into groups within which the highest growth performance is regular over time. According to different authors (McCarthy et al., 1992; Jobling, 1995; Alanärä et al., 1998) the  $SGR$  or the  $CV_{SGR}$  can be considered as significant indicators of social ranking within a group: dominant fish display high  $SGR$  and low  $CV_{SGR}$ . This hypothesis is supported by Jobling and Baardvik (1994), who showed that jumpers have lower  $CV$  values in feed intake over time. Conversely, dominated fish display low  $SGR$  and high  $CV_{SGR}$ . As for our results, the P7, P2, P3, P4, P1, L4 and L3 growth profiles had high  $SGR$  and low  $CV_{SGR}$ . These growth profiles represented 36% of the fish in both experiments and were mainly composed of 'jumpers' among which the females were more numer-

ous. The P6, P9, L6 and to a lesser degree the P5 and P8 growth profiles had lowest  $SGR$  with greatest  $CV_{SGR}$ . These growth profiles were composed of dominated individuals, among which the males were more numerous. Jobling (1995) suggested that this kind of growth could result from adverse rearing conditions. Nevertheless, in our conditions, each growth profile was found in almost every group. The individuals were subjected to the same environmental conditions, and the data were adjusted according to the treatment and the tank effect.

#### 4.5. Intrinsic individual growth potential and growth profiles

A low  $SGR$  coupled with an intermediate  $CV_{SGR}$  could also be genetically determined, as previously suggested (Sunde et al., 1998; Wang et al., 1998). The number of individuals in each growth profile does not seem to be randomly distributed in each tank, especially in experiment 1. Since the data were adjusted for the treatment and the tank effects, this default of randomisation may be due to an uncontrolled factor of variability, which could reflect the variability in intrinsic individual growth potential.

### 5. CONCLUSION

This study led to the description of the variability of individual growth curves in relation to initial weight level, slope and sex ratio at two different stages of development.

The differences in growth performance were due at least in part, to sexual growth dimorphism. This individual variability is worth taking into account when individual data are available in order to improve statistical significance of growth studies. However in some cases, the variability in growth cannot be related either to the sex of the fish, nor to its initial weight or to social interactions such as dominance. It is suggested that this variability is probably also caused by the individual genetic growth potential, and particularly by the individual potential for protein catabolism (Carter et al., 1993), or by differences in appetite.

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