Individual variability and sex-related differences in the growth of *Diplodus annularis* (Linnaeus, 1758)

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Running title

Individual growth variability in short life-span fishes

Abstract

Variability and changes in the individual life-history parameters of fishes are frequently overlooked, and it is assumed that all individuals mature, spawn, grow, and die at the same rates over their lifespans. Here, the variability in the individual growth of the rudimentary hermaphrodite *Diplodus annularis* (Linnaeus, 1758) is described using a Bayesian approach. This approach enables the inference of individual growth curves, even in a species of a relatively short lifespan, and revealed a biphasic growth pattern for this species. Conventional von Bertalanffy growth failed to fit the individual back-calculated lengths-at-age data well. A generalization of this model is proposed for accommodating one change in the growth rate at some moment of the lifespan of this species. This novel five-parameter model (L_{∞} , k_0 , k_1 , t_0 and t_1 , i.e., size at infinite age, initial and final growth rate, age at size zero and age at the change of growth rate) represents the different allocation of energy to somatic growth or reproduction, prior to and post sexual maturity. Moreover, between-sex growth differences are described; juvenile fish display similar growth rates in both sexes, but mature females have lower growth rates than males. The detailed description of the growth of the *D. annularis* shown here can provide adequate input for future implementation of population dynamics models that take into account individual variability (e.g., IBMs, individual-based models). These models could facilitate the management of a species targeted by recreational fishery.

Keywords

Back-calculation, Bayesian inference, biphasic growth, *Diplodus annularis*, energy allocation, rudimentary hermaphrodites

Introduction

Fisheries biologists and managers have traditionally focused the management of exploited stocks by means of models that incorporate growth descriptions as well as other variables such as age and size distributions, survival, reproductive potential and recruitment (e.g., Haddon, 2001). The growth parameters are explicitly incorporated into traditional population dynamics models used for establishing sustainable exploitation levels of fish stocks (Beverton and Holt, 1957).

However, the conventional growth models (i.e., a single observation per fish) clearly overlook individual variability because they do not include the individual characteristics of exploited fish. Population growth is usually described through mean growth parameters (known as “average” growth; Pilling et al., 2002). Recently, studies reported the relevance of the variability at within-population level to estimate and improve the population growth (see Troynicov and Walker (1999) using stochastic models). Thus, it is unreasonable to assume that all individuals will have the same growth pattern in a wild population (Sainsbury, 1980; Smith et al., 1997). This procedure introduces a bias when life expectation depends on size, as is the case for most size-selective fisheries (faster growing fishes tend to be younger when fished, both in commercial [Jackson et al., 2001; Watson and Pauly, 2001; Pauly et al., 2003] and recreational fisheries [Cooke and Cowx, 2006; Lewin et al., 2006]).

The back-calculation of length-at-age data contained in fish hard parts, such as otolith growth increments, is considered the most realistic method to obtain information prior to capture (Pilling et al., 2002). Fitting the length-at-age data with the aid of Bayesian inference has allowed for estimating the individual von Bertalanffy trajectories and their variability at the population level (Pilling et al., 2002; Helser and Lai, 2004; Helser et al., 2007). However, instead of using the conventional von

Bertalanffy model based in three parameters, several authors recently proposed an extension that accommodates for one change of growth rate at some moment of the lifespan to account for the different distribution of the energy for reproduction versus somatic growth along the lifespan (Day and Taylor, 1997; Lester et al., 2004; Charnov, 2005; Charnov, 2008; Quince et al., 2008a; Quince et al., 2008b). The growth rate (k) would not be a meaningful parameter if these life-history phases are not considered (Charnov, 2008). Day and Taylor (1997) suggested that the somatic growth trajectory should be specified by two different equations; one for the prior-maturity period (i.e., the entire energy supply is devoted to somatic growth) and one for the post-maturity period (i.e., most of the energy supply is devoted to reproduction). This growth pattern is known as biphasic somatic growth (Quince et al., 2008a; Quince et al., 2008b).

Here, we describe the individual growth of *Diplodus annularis* (Linnaeus, 1958), commonly known as annular seabream. This species is a small Sparid that inhabits the Mediterranean and Black Sea coast, the Atlantic from the gulf of Biscay to Gibraltar, and the Madeira and Canary Islands (Bauchot, 1987). It is a demersal species, common in the bottoms covered by seagrass beds at 0 to 50 m in depth (Bauchot, 1987). It has been catalogued as a rudimentary hermaphrodite (Buxton and Garratt, 1990). The 50% of the female population reach sexual maturity before males (100 mm versus 90 mm; Matic-Skoko et al., 2007). Until now, population growth parameters have been estimated using the conventional population von Bertalanffy curve (Gordoa and Moli, 1997; Pajuelo and Lorenzo, 2001; Matic-Skoko et al., 2007). This conventional version of this model does not fit well with the fast growth experienced by juveniles when they are 1 or 2 years old (Gordoa and Moli, 1997).

In the Balearic Islands (NW Mediterranean), this species has low commercial interest and is classified as byproduct or bycatch by the artisanal fleet (data from the

Department of Fisheries, Balearic Island Government). Due to this historic low commercial interest in this species, no specific management plan for *D. annularis* has been developed anywhere. In contrast, this species is one of the main targets of recreational fishery (Morales-Nin et al., 2005) and it has been recently reported that this species is vulnerable to the impact of some recreational angling activities (Alós et al., 2008).

The main goal of this study is to describe the individual growth pattern of *D. annularis* and its intra-population and sex-related variability. Information about the growth at an individual level should facilitate future implementation of individual-based models (IBMs) focused on elucidating the effects of recreational fisheries on the population dynamics of this species.

Materials and methods

Sampling methods and study area

Experimental fishing sessions were conducted at the Cabrera National Park located on the south coast of Mallorca Island (NW Mediterranean, Fig. 1). This site was selected for two main reasons. First, because recreational angling activities are not allowed (sanctuary area since 1991), the abundance of old individuals is higher than in other open-access sites. Old individuals improve the fit of individual growth trajectories (see results). Second, sites displaying the adequate bottom characteristics for *Diplodus annularis* (i.e., bottom dominated by *Posidonia oceanica* beds and placed between 10 and 20 m deep) are abundant. A total of 423 individuals were caught between March 13th and August 31st 2007 in this area. These individuals were sampled twice a month using hook-and-line methods with conventional recreational gear. All individuals were measured (total length in mm). Sagittal otoliths were extracted and gonads were dissected. This sample was used for describing the distribution of age and size of the

population and the individual growth pattern, as well as for testing for the existence of sex-related differences.

When a strong relationship between otolith length and fish body length exists (as is the case for *D. annularis*, see Results), it is possible to infer the body size of a fish at younger ages from the width of the annual increments recorded in the otoliths (Pilling et al., 2002). After evaluating the strength of the relationship between otolith size and fish size with a additional second sub-sample (see below), we measured the width of both annual increments and the marginal increment (i.e., the last increment) using a photograph of each left otolith. The images were captured using a video camera (LEICA© M165C and Allied vision technologies© Marlin F080B). Typically, opaque and translucent increments are seen alternating outward from the nucleus (i.e., the growth center of the otolith). The succession of one opaque band and one translucent band was considered one annual increment. The $x_i y_i$ coordinates of the nucleus, the coordinates of all the annual increments along a predefined growth axis, and the coordinates of the otolith edge (Fig. 2) were recorded using TPSdig software (available at <http://life.bio.sunysb.edu/morph/>; Rohlf, 2007). The width of the increments was computed simultaneously for all individuals from these coordinates using a Microsoft Excel macro. In order to avoid uncertainties of assigning a year fraction to the width defined by the last increment and the total otolith size, only full annual increments were considered to fit individual growth trajectories.

The additional second sub-sample mentioned above was composed of 2,462 individuals caught at several sites in the south of Majorca Island during three sampling years (2006-2008). The sampling methods include hook-and-line fishing with a monthly periodicity and a set of individuals caught with small trawl gear to improve the sample size of younger classes. The total fish length (± 1 mm) and the sampling date were

recorded for each individual caught. The additional purpose of the second sub-sample, as well as improving the regression between fish and otolith size, was the validation of the aging method, i.e., the evaluation of the periodicity of annuli formation. The two validation methods used here assume that the formation of opaque increments (faster growth) begins (roughly) simultaneously for all individuals (usually, in spring) and increase in width until a new increment (the following spring) is generated. Thus, if and only if the putative annual increments are annual, the monthly percentage of individuals with an opaque border (or, in the second method, the averaged width of the last increment after normalization by the radius of the otolith) follows, at the population level, a periodic sinusoidal-like curve from spring to spring (Gordoa and Moli, 1997; Pajuelo and Lorenzo, 2001; Morales-Nin and Panfili, 2005).

Sagittal otoliths were used for age determination and for measuring otolith radius and increment widths in both sub-samples described above. Whole otoliths were immersed in a glycerine-ethanol (1:1) solution to improve the visualization of annual increments. Each otolith was examined twice by a single reader, with an interval of 2-3 months between readings. When the two readings of the same otolith differed, a third reading was conducted. If this third reading was inconclusive, the otolith was discarded and considered unreadable.

Regarding the sex-determination of each individual (i.e., *D. annularis* did not show any sexual dimorphism) gonads were removed from all individuals and immediately fixed in 3.6% buffered formalin. A middle portion of the fixed gonads was extracted, dehydrated, embedded in paraffin, sectioned at 3 μ m and stained with hematoxylin-eosin for microscopic analysis using a Leica DM RE (Digital Microscope series RE). Consistent with the point of view of rudimentary hermaphrodites, also called

“late” gonochorism (Buxton and Garrat, 1990), fish were considered male when functional testes were found and female when functional ovaries were present.

Individual growth model

The back-calculated length-at-age data obtained from the otoliths were fitted to a non-linear mixed effects model adapted to longitudinal data (Pilling et al., 2002; Helser and Lai, 2004; Helser et al., 2007; Zhang et al., 2009). For these purposes, the response variable y_{ij} consisted of the distances from the nucleus to the j annual increment, where $j = 1$ to t full annual increments per otolith, and $i = 1$ to N otoliths (or fish). Among different possible non-linear models to fit individual growth trajectories, most of the recently published analyses use the von Bertalanffy growth model (VBGM; Jones, 2000; Pilling et al., 2002; Helser and Lai, 2004; Helser et al., 2007; Edeline, 2007; Zhang et al., 2009). This model is based on three parameters: t_0 , a growth rate (k , which is constant throughout the lifespan of the individual) and an asymptotic length (L_∞). The conventional form of this model is:

$$y_{ij} = L_{\infty i} * (1 - \exp(-k_i * (t_j - t_{0i}))) + \varepsilon_{ij}, \text{ where } i = 1 \text{ to } N \text{ (fish) and } j = 1 \text{ to } t \text{ (years)}$$

where y_{ij} is the size of the fish i at the age j , $L_{\infty i}$ is the asymptotic size at infinite age, k_i is the growth rate, t_{0i} is a correction term allowing that the fish i has some specific size at time = zero, and ε is a normally distributed error.

Charnov (2008) suggested that reproductive effort should negatively affect growth rate. The hypothesized differences in growth rates between juvenile and mature individuals are described by the so-called biphasic growth curves (Quince et al., 2008a; Quince et al., 2008b). This model is intended to correct for the absence of energetic costs linked to reproduction before sexual maturation (or the small energetic cost during

the first few years after maturation). Here, we propose a generalization of the conventional three-parameter VBGM model that allows for a change in the growth rate at a specific moment t_j of the life span of an individual of *D. annularis*. This alternative growth model based on five parameters is:

$$y_{ij} = L_{\infty i} * (1 - \exp(-k_{0i} * (t_j - t_{0i}))) + \varepsilon_{ij}, \quad \text{for } t_j < t_1$$

$$y_{ij} = L_{\infty i} * (1 - \exp(-k_{0i} * (t_{1i} - t_{0i}) - k_{1i} * (t_j - t_{1i}))) + \varepsilon_{ij}, \quad \text{for } t_j > t_1$$

where k_{0i} and k_{1i} are the growth rates before and after the moment of the change (t_{1i}). The full model is fully detailed in Appendix 1.

The parameters of these two growth models were determined for each individual using a Bayesian approach. Bayesian inference, although it is not free of technical problems, has recently become popular in improving the fit of the individual growth trajectories of fishes (Pilling et al., 2002; Helser and Lai, 2004; Helser et al., 2007; Zhang et al., 2009). This inference method emphasizes the inclusion of a priori information. A convenient algorithm (Markov Chains Monte Carlo; MCMC) moves iteratively around the values of the parameters that best fit the data. The distributions of these iterations directly give the probability distributions of the parameters. We adopted specific strategies to improve the convergence of MCMC chains. First, multi-normal distributions of the parameters (as suggested by Pilling et al., 2002; Helser and Lai, 2004; Helser et al., 2007) were discarded because this approach implied severe convergence problems. Thus, independent normal distributions of each one of the parameters were assumed as priors. Simulations done using data generated by correlated growth parameters (and using between-parameter correlation values similar to those obtained by Pilling et al. (2002) showed that the use of independent distributions (three

or five, depending on the VBGM) assures a very good recovery of the actual values of the parameters. This strategy allowed us to simplify the model and explore a posteriori correlations between parameters. Second, t_0 was considered fixed (i.e., all individuals from the population have the same value). This strategy was proposed by Zhang et al. (2007) and greatly alleviates convergence problems because it considerably reduces the number of parameters to be estimated. Again, the outcome of this approximation was accepted because simulated data with a variability level similar to that reported by Pilling et al. (2002) showed that it has a very small impact on all the other parameters estimated.

We used semi-informative priors. They were based on the reasoning that all individuals of the same sex were sampled from a common normal distribution (Mean=0, tolerance ($1/\text{square root of sd}$) = 10^{-6}). However, normal distributions were constrained to be within the interval of 2 to 6 mm for L_∞ (length on the otolith scale), and from 0 to 1 for the growth rates (ks). These values were based on the previous literature reported for this species (Gordoa and Moli, 1997; Pajuelo and Lorenzo, 2001; Matic-Skoko et al., 2007). The parameter t_1 (change in the growth rate) was not constrained at all (flat prior). Priors for between-sex differences were assumed to be uniform distributions: 2 to 6 mm (length on the otolith scale), 0 to 7, and 0 to 0.4 were used for L_∞ , t_1 and growth rates, respectively. Variance was assumed to be invariant to age and gamma-distributed (flat prior). In all cases, a posteriori distributions were much narrower than a priori distributions.

The units for L_∞ are in mm (distance from the otolith center to the border, following the growth path). However, in order to make an easier interpretation, in some graphs, the scale was translated to fish size (TL) using the linear relationship between otolith size and fish size.

Three MCMC chains were run using randomly chosen initial values for each individual (within a reasonable interval), and convergence criteria were checked by visual inspection of the sample history for each parameter estimated. A different number of iterations depending of the VBGM (Beg = 1200 in the 3-p based and Beg = 2500 in the 5-p based) were not considered prior to convergence of the MCMCs. Autocorrelation was also checked, and thinning (in the case of VBGM 3-p, no thinning was needed, and in the VBGM 5-p, only one out of five consecutive values was kept) was adopted to assure independence of values within each chain. The number of iterations was selected for each run to obtain at least 2700 valid values for the 3-p VBGM and 1600 for the 5-p VBGM after convergence and thinning. Runs of each model lasted approximately 3000 s and 9900 s, respectively. Models were implemented using the library BRugs of the R-package (<http://www.r-project.org/>) known as OpenBugs (<http://mathstat.helsinki.fi/openbugs/>).

Results

Age and size distributions

The annuli from the sagittal otolith of *Diplodus annularis* were easily and clearly identifiable (Fig. 2). From the first sub-sample (i.e., the individuals for back-calculating length-at-age; n = 423), 372 (87.9%) were successfully aged and analyzed. With respect to the second sub-sample (n = 2,462), a total of 2,242 (91.1%) otoliths were successfully aged. The sex ratio of the first sub-sample was 1.17 females per male. The total length of the females varied from 92 mm to 209 mm with an average ($\pm$ S.D.) of 147.8 ($\pm$ 21.3) mm. Males varied from 84 mm to 193 mm with an average of 138.6 ($\pm$ 20.5) mm. The ages varied from 0 to 9 years with an average of 3.83 ($\pm$ 1.6) years for the females, and from 0 to 8 years and an average of 3.31 ($\pm$ 1.5) years for the males. Figure 3 shows the distribution of observed values by the classes of age and size

structure of males and females. Size- and age-frequency distributions for each sex (Fig. 3) are clearly in agreement with the rudimentary hermaphrodite reproductive strategy hypothesis.

Aging validation

The marginal increment evolution confirmed that *D. annularis* follows a periodic sinusoidal-like curve from spring to spring. Thus, annual periodicity of putative annual increments is assumed for this species. The annual variations in the percentage of translucent last increments for different ages are shown in Fig. 4 and the marginal increment widths are shown in Fig. 5. Individuals sampled with translucent marginal increment rose 100% during the winter months, coinciding with the slow growth season. At the beginning of March, the number of individuals with opaque marginal increment increased (Fig. 4). During May, June and July percentages of individuals with opaque marginal increment raised up the 100% coinciding with the warm season (Fig. 4). Results also showed how young individuals presented a shorter opaque marginal increment than older individuals (i.e., 2-3 vs. 4-5 years old, Fig. 4). At the end of summer (i.e., from August to September), the percentage of otoliths with opaque last increments decreased and the translucent last increments increased again 100% in the winter (Fig. 4). This pattern was confirmed by studying the averaged marginal increment ratio. This ratio was small in summer and increased until the initiation of a new opaque band (Fig. 5). During the period of May to March (i.e., when initializing the opaque band), between-individual variability was high, since individuals finalizing the translucent (i.e., with large marginal increments) band and initiating the opaque band (i.e., with short marginal increments) were sampled together (Fig. 5).

Individual growth patterns

The linear regression between the fish total length and the otolith size showed a very good relationship (Fig. 6, $r^2 = 0.88$), suggesting that otoliths can be used as a reliable proxy of somatic size in order to reconstruct ontogenetic growth trajectories. Preliminary runs to fit the individual growth trajectories of the 372 individuals from the first sub-sample showed poor performance of the Bayesian approach, due to the fact that young individuals (1 or 2 years old) were fit with difficulties. Thus, estimation of individual growth parameters was reduced to 166 females and 141 males 3 years old or older. The results obtained after fitting individuals 4 years old or older were qualitatively the same as those obtained with 3 years and older individuals. Therefore, hereafter, only the results corresponding to the analyses of 3 years old and older individuals were used to describe the individual growth pattern and its variability.

The fit of the length-at-age data in a non-linear hierarchical mixed effects model based on the conventional three-parameter VBGM (L_∞ , t_0 and k) did not provide a good fit of the data (Fig. 7). This model showed a systematic error in the prediction of the fast growth experienced during the first two-three years of the lifespan of *D. annularis*. Related to this, conventional VBGM also implies an important overestimation of the old ages. As a consequence, L_∞ was also dramatically underestimated (Table 1 and Fig. 8). In fact, old individuals displayed an estimation of their L_∞ lower than the observed total length at the moment of catch. Observed and predicted sizes for a specific individual are shown in Fig. 7. The distribution of the residuals proved that this bias was systematic for most of the individuals and suggested that a change in the growth when individuals were around 2 or 3 years old could exist (Fig. 7). This fact motivated the use of an alternative version of the VBGM that allows for one change of growth rate. The five-parameter version better accommodated the fast growth during the younger years and provided better estimations of size at old ages (after “ t_1 ”; see M&M). The residuals of

this alternative VBGM model did not show severe age-related biases, and they were closer to zero (Fig. 7). Moreover, the results of the estimation of the L_{∞} were more robust and logical from the biological standpoint (Table 1 and Fig. 8). These two facts support the use of only the second model in the next section for describing individual and sex-related variability.

Individual and between-sex growth variability

The mean, standard deviation and Bayesian credibility interval obtained for males and females are shown in Table 1. The 95% credibility interval for L_{∞} for females varied between 211.3 and 232.3 mm, with a mean of 219.3 mm. Males varied from 208.1 to 213.9 mm, with a mean of 210.2 mm (Table 1 and Fig. 8). The small overlap between these intervals indicated that the asymptotic length is larger for females than for males (9.1 mm, Fig. 9).

The Bayesian means of t_0 were similar for both sexes, with a large overlap of the Bayesian credibility intervals (Table 1). The estimate was -0.17 for females and -0.16 for the males. Regarding the parameter t_1 (i.e., the time where the change in the growth rate was produced), the 95% credibility interval varied from 1.2 years to 3.2 years for the females and from 1.2 years to 2.9 years for the males. The means were 2.2 years for the females and 2.1 years for the males (i.e., females matured slightly later than males, but credibility intervals overlapped considerably).

The individual means of the initial growth rate (k_0) ranged from 0.21 year⁻¹ to 0.38 year⁻¹ for females and from 0.2 year⁻¹ to 0.39 year⁻¹ for males. Note the large variability of this parameter. Nevertheless, mean k_0 s are very close for males and females, and Bayesian credibility intervals largely overlap (Table 1 and Fig. 9). Regarding k_1 , all estimated individual values were lower than k_0 , thus showing a decrease in the growth rate at a specific moment of the life span of *D. annularis* (at t_1).

The individual means ranged from 0.09 year⁻¹ to 0.19 year⁻¹ for females and from 0.09 year⁻¹ to 0.28 year⁻¹ for males. Females presented a lower mean k_1 than males (Fig. 9). Therefore, after the change in the growth rate, females grow more slowly than males.

Correlations between the growth parameters were low in most cases. First, the growth rates (i.e., k_0 and k_1) did not show any tendency for either females ($r^2 = 0.02$) or males ($r^2 = 0.09$). Therefore, the growth after the change in the growth rate was not dependent on the initial rate. The time of change in the growth rate seemed independent of the initial growth rate, both for females ($r^2 = 0.03$) and males ($r^2 = 0.14$). Finally, it has been suggested that the relationship between L_∞ and growth rate should reflect a trade-off between somatic growth and reproduction. Consequently, there is a general assumption that these parameters should be negatively correlated at the individual level. Here, L_∞ and growth rates presented a clear relationship, both for k_0 (females, $r^2 = 0.33$ and males, $r^2 = 0.33$; Fig. 10) and k_1 (females, $r^2 = 0.31$ and males, $r^2 = 0.11$; Fig. 10). However, in contrast with the cases reported based on conventional VBGM, the slopes of the regressions were positive in all cases (Fig. 10). Thus, individuals with fast growth (before and after the change in the growth rate) become the individuals with larger L_∞ .

Discussion

Growth is one of the most important biological characteristics when coping with population dynamics and management issues of exploited fishes. However, the most common approach used to describe population growth is as an average of a common von Bertalanffy growth model, thus ignoring individual variability. Recent trends in fishery science highlight the importance of fitting individual growth curves from length-at-age data (Wang and Ellis, 1998; Troynicov and Walker, 1999; Pilling et al., 2002). Description of individual variability is more easily provided using Bayesian inference. This novel approach allows for obtaining robust results, even when short temporal

series are available (i.e., short lifespan). Indeed, this kind of inference has recently revealed the high individual variability exhibited by the individuals from some populations and how it impacts population dynamics (Wang and Ellis, 1998; Helser and Lai, 2004; Helser et al., 2007).

In the present study, we describe the individual growth pattern of a small Sparid, *Diplodus annularis*. This species has low commercial value, but it is an important target species for local recreational anglers. As recommended by Pilling et al. (2002), we fitted the individual trajectories using a non-linear random effects model. This type of model is commonly used for the estimation of individual growth parameters and seems to behave better (Pilling et al., 2002; Helser and Lai, 2004; Helser et al., 2007). The reason for this enhanced behavior is that these types of models incorporate each individual data set but combine these individual data with the population average (Pilling et al., 2002).

The growth of fishes has historically been described using the von Bertalanffy curve based on three parameters, namely the t_0 , the growth rate (k), which is assumed to be constant throughout the life span of the fish, and an asymptotic length (L_∞). This model has usually been applied at the whole population level (i.e., a conventional one fish-one data approach) and, most recently, at the individual level (i.e., individual growth trajectories). The results for the species analyzed here show poor success of this model to fit and predict the individual back-calculated data. Previous research on the growth of this species at the population level (i.e. one fish one datum) anticipated that the conventional von Bertalanffy model would not fit the growth of this species well (Gordoa and Moli, 1997). This failure may be associated with the fast growth during the first 1-2 years of life. Specifically, residuals (observed minus predicted size) showed a systematic bias depending on age. Consequently, the conventional three-parameter

model resulted in a dramatic underestimation of the L_{∞} . In fact, most of the large and old fish sampled showed a Bayesian mean of the L_{∞} lower than the size at capture. This bias has been already noted at the population level (Gordoa and Moli, 1997). Thus, the values obtained for this parameter were unrealistic from the biological standpoint. The main cause of this failure seems to be the assumption that the growth rate (k) is constant during the lifespan.

Here, we use an alternative five-parameter growth model based on the assumption that *D. annularis* changes its growth rate at some moment during the lifespan. Therefore, we proposed an individual growth model based the conventional von Bertalanffy curve during the first years of life (i.e., with a growth rate k_0). This period is characterized by a fast growth, and fits the early ages of an individual of *D. annularis* very well. Then, at around 2-3 years of age, fish experience a decrease in growth with a smaller growth rate, k_1 . This five-parameter model (t_0 , t_1 , k_0 , k_1 , and L_{∞}) better fits the individual growth of *D. annularis*. This model accommodated the fast growth in early life stages and fitted the decrease in growth rate after the age of change well. This alternative model allowed for better estimates of the parameters, with lower variability, and was more realistic from the biological standpoint. In fact, the previously reported values of L_{∞} estimated at the population level ranged from 203.7 mm to 239.5 mm (Gordoa and Moli, 1997; Pajuelo and Lorenzo, 2001; Matic-Skoko et al., 2007), and the Bayesian means estimated from the conventional von Bertalanffy growth model were 159.3 mm and 151.7 mm for the females and males, respectively. However, using the conventional growth model, the Bayesian mean values obtained rose the 220 mm for both sexes.

A non-constant growth rate is a relatively novel topic in the research involving fish and fisheries at individual growth level. A general assumption exists that there is a

trade-off between the allocation of the energy required for somatic growth and reproduction (Lester et al., 2004; Charnov, 2008). This is based on the assumption that the growth rate of fishes (k) is proportional to the reproductive effort (Charnov, 2008). Several authors proposed a “biphasic” growth curve to correct for the lack of the energetic cost of reproduction after maturation (Day and Taylor, 1997; Lester et al., 2004; Charnov, 2008; Quince et al., 2008a; Quince et al., 2008b). Recently, Quince et al. (2008b) recommended that this kind of model should be used to fit the growth of fishes that present a differential pattern related to sexual maturity.

In the case of *D. annularis*, the existence of a change in the growth rate at the moment of sexual maturity seems to explain the individual growth pattern of this species well. First, this species matures at 100 mm in females and 90 mm in males (Matic-Skoko et al., 2007). Assuming that the individuals analyzed here mature at similar sizes, this implies that they mature during the 2nd or 3rd year of life. This figure agrees with the distribution of the Bayesian mean t_1 for the population (i.e., the age of the change in the growth rate). Thus, the parameter t_1 could relate the trade-off previously assumed between the somatic growth and reproduction. Consequently, the individual growth pattern of this species is characterized by an allocation of the energy to somatic growth during the first years of life (fast growth) and, after that, a redistribution of the energy to reproduction with a cost in somatic growth, and in consequence, a decrease in the growth rate.

Moreover, there were differences in the growth pattern between sexes. Females change the growth rate slightly later than males, and females mature at larger sizes than males. *D. annularis*, along with other members of the family Sparidae, is catalogued in the Mediterranean area as a rudimentary hermaphrodite (Buxton and Garrat, 1990; Matic-Skoko et al., 2007). This reproduction style includes an immature hermaphrodite

gonad prior to maturity of the individual; after that, the individual progresses to either a functional female or male (Buxton and Garrat, 1990). It is reasonable to assume that the growth in immature individuals of *D. annularis* (i.e., immature hermaphrodites) is similar for functional females and males. Results obtained here agree with this statement (i.e., k_0 from males and females are very similar). In contrast, post-maturity growth was different between functional females and males, since females grow less than males. This result is explained by the likely fact that energy costs associated with gamete production are different between sexes (costs related with testes maturation are probably negligible compared with those of ovarian maturation; (Adams et al., 1982; Wootton, 1985).

In addition to between-sex differences, it was expected that the relationship between L_∞ and growth rate at the individual level would be negative since it is considered a trade-off between somatic growth and reproduction. In fact, Pilling et al. (2002) reported the first reliable confirmation for this negative correlation, which was recently supported by Helser et al. (2007). However, when we fitted the alternative five-parameter von Bertalanffy model, the relationship between growth rates (k_0 and k_1) and the asymptotic length (L_∞) became positive in both sexes. Both the five-parameter growth model proposed here and all biphasic growth models explicitly allow for explaining the energy demand imposed by reproduction (Lester et al., 2004; Charnov, 2008; Quince et al., 2008a; Quince et al., 2008b). In accordance with this theoretical framework, the individuals of *D. annularis* with high growth rates (both before and after sexual maturation) displayed large asymptotic length since their growth is faster and the demand imposed by reproduction is already explicitly included in the growth curve. This assumption, although it seems biologically and ecologically sound and agrees with previous research in this topic, needs further research 1) involving multiple populations

(i.e. increasing the range of the growth parameters), 2) increasing the spatial scale (i.e. (i.e. to increase individual variability), and 3) providing qualitative descriptions of the reproductive potential (e.g., fecundity) at the individual level.

Other interesting topic for further research is disentangling the seasonal patterns of the individual growth. Fishes displays seasonal oscillations since they grow faster in warm seasons. The first approaches to the seasonal growth were published by Ursin, 1963. After that, number of authors have been published different kind of models to coping with the seasonal growth (e.g. Pitcher and Macdonald, 1973; Cloern and Nichols, 1978; Pauly et al., 1992). Thus, further research in the individual growth of this species must emphasize in 1) determinate the moment of the change in the growth rate inside the year and its variability and 2) include a sinusoidal curve in the biphasic growth model adopted in the present Bayesian approach allowing seasonal oscillation.

In conclusion, the approach adopted here allows for the accurate description of the individual growth patterns of *D. annularis* on several scales. Combining the Bayesian approach, non-linear mixed effects models, and the biphasic growth pattern revealed that this species showed a change in the growth rate during its lifespan. The existence of biphasic growth is well explained by assuming differential allocation of the energy to either somatic growth or reproduction. This model has been successfully implemented for this short lifespan species and could be used to disentangling the individual growth patterns for other coastal species and to improve the knowledge for long live species. Moreover, we demonstrated the differences in growth between females and males in a rudimentary hermaphrodite never previously described. The knowledge of individual variation is the input of, for example, individual-based models (Martinez-Garmendia, 1998) that are intended to elucidate the biological significance and the expected outputs of growth variability on population dynamics. The ultimate

goal for explicitly incorporating growth knowledge into management models must be to establish sustainable exploitation levels of this recreational target species.

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Table 1
Summary statistics for the population Bayesian means of the growth parameters for the
Cabrera Archipelago using the conventional (3 parameters based) and the alternative (5
parameters based) von Bertalanffy growth model. For each estimated parameter, the
mean, standard deviation (SD), median and, lower and upper 2.5 percentiles of the
posterior distribution are shown for both sexes. Means of L_{∞} are expressed in otolith
scale and in total length (in brackets) in mm, k , k_0 and k_1 as years⁻¹, and t_0 and t_1 as
years.

		Bayesian credibility intervals				
	Parameters	Mean	S.D.	2.50%	Median	97.50%
Conventional 3-p VBGM						
Females						
	<i>Mean (L_{∞})</i>	3.33 (159.3)	0.03	3.27	3.33	3.39
	<i>Mean (t_0)</i>	-0.12	0.02	-0.16	-0.12	-0.08
	<i>Mean (k)</i>	0.45	0.01	0.43	0.45	0.47
Males						
	<i>Mean (L_{∞})</i>	3.19 (151.7)	0.03	3.12	3.19	3.25
	<i>Mean (t_0)</i>	-0.07	0.03	-0.12	-0.07	-0.03
	<i>Mean (k)</i>	0.47	0.01	0.44	0.47	0.49
Alternative 5-p VBGM						
Females						
	<i>Mean (L_{∞})</i>	4.46 (219.3)	0.07	4.34	4.45	4.60
	<i>Mean (t_0)</i>	-0.17	0.02	-0.20	-0.17	-0.13
	<i>Mean (t_1)</i>	2.21	0.07	2.06	2.21	2.35
	<i>Mean (k_0)</i>	0.29	0.01	0.28	0.29	0.31
	<i>Mean (k_1)</i>	0.15	0.01	0.14	0.15	0.17
Males						
	<i>Mean (L_{∞})</i>	4.29 (210.2)	0.07	4.17	4.28	4.43
	<i>Mean (t_0)</i>	-0.16	0.02	-0.20	-0.16	-0.12
	<i>Mean (t_1)</i>	2.12	0.10	1.92	2.12	2.32
	<i>Mean (k_0)</i>	0.30	0.01	0.28	0.30	0.31
	<i>Mean (k_1)</i>	0.17	0.01	0.16	0.17	0.19

Figure captions

Figure 1

Map showing the sampling site of the first sub-sample (black star) located inside the National Park of the Cabrera Archipelago, south coast of Mallorca Island (NW Mediterranean). The second sub-sample of individuals was sampled at several sites in the south of Majorca Island (black points) including Palma Bay, Cape of Regana and the waters of Cabrera Channel.

Figure 2

Image of different sagittal otoliths of 3 years old individuals sampled during different months to view the marginal increment (MI) annual evolution; (A) January, (B) March, (C.a) May with translucent MI, (C.b) May with opaque MI (i.e., 4 years old fish), (D) July, (E.a) September with opaque MI, (E.b) September with translucent MI and (F) November.

Figure 3

Frequency percentages of the observed ages and fish total length resulted from the population of the National Park of the Cabrera Archipelago. Frequencies are structured by sexes.

Figure 4

Monthly percentages of otoliths with translucent marginal increments from the individuals of *Diplodus annularis* sampled. Figure shows the 2 years old (n = 241), 3 years old (n = 435), 4 years old Age (n = 218) and 5 years old individuals (n = 114).

26 Figure 5
27 Mean and standard deviation of Marginal increment ratio (MIR) for the 3 (n = 435) and
28 4 years old individuals (n = 218).

29

30 Figure 6
31 Lineal simple regression between the otolith radius (mm) and fish total length (mm).
32 The samples successfully aged from the first and second sub-samples were included in
33 the regression (n = 2614).

34

35 Figure 7
36 Individual growth trajectory for an individual of *Diplodus annularis* 8 years old
37 obtained from the observed data, from fitting the conventional three-parameter von
38 Bertalanffy growth model (VBGM) and from fitting the five-parameter VBGM.

39

40 Figure 8
41 Frequency distribution of the individual Bayesian means of the asymptotic lengths (L_{∞})
42 resulted from the VBGM based in 3 or 5 parameters. Results have been structured by
43 sexes.

44

45 Figure 9
46 Bayesian confidential intervals (lower and upper 2.5 percentiles) for the growth
47 parameters L_{∞} , k_0 , k_1 and t_1 obtained from the posterior distribution of the Bayesian
48 means for each sex.

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50 Figure 10

Linear simple regression between the individuals means of the parameters L_{∞} and growth rates (i.e., k_0 and k_1) for each sex. L_{∞} is represented in otolith scale (mm).

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