First evidence on the growth of hatchery-reared juvenile meagre *Argyrosomus regius* released in the Balearic Islands coastal region

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ABSTRACT

The success of restocking (releasing hatchery-reared juveniles in the wild) depends on the capacity of phenotypes that are already adapted to captivity to readapt to the natural environment. Changes in growth rate after release can be monitored to determine whether released fish are adapting well to the natural environment or failing to adjust to wild conditions. Nevertheless, it is not known whether released individual fish experience a shift in growth rate. Alternatively, the fish showing long-term survival could be those that were already larger before release. This question is relevant for the maximization of stocking success because certain phenotypes (those with a better probability of readapting) could be selected for release. This study compared the somatic growth of released and recaptured meagre, *Argyrosomus regius*, with control (captive) meagre belonging to the same cohort. Recaptures that had spent less than 3 months at liberty showed the same length-at-age as the control fish, but the length-at-age of many recaptured fish that had spent more than 3 months at liberty was greater than expected. The otolith radius of the growth mark corresponding to the first year of life (i.e., when all fish were still in captivity) was significantly greater for fish that had spent more than 3 months at liberty, indicating that these meagre were larger and had a higher growth rate when they were released. Moreover, the analysis of daily otolith growth before and after release showed that most of the recaptured meagre that had spent less than 3 months at liberty grew an equal or lesser amount in the wild than before release. In contrast, most of the recaptures that had spent more than 3 months at liberty showed a higher growth rate after release. Therefore, results are discussed in light of the combined effect of differential survival and increased growth, although the low sample size requires interpreting the results carefully.

Keywords

Argyrosomus regius, restocking, somatic growth, differential survival, daily otolith increment

1. Introduction

The meagre, *Argyrosomus regius* (Asso 1801), is widely distributed along the Eastern Atlantic coast (from Norway to Congo) and in the Mediterranean (Chao, 1986). *A. regius* is one of the world's largest sciaenid fish, reaching more than 180 cm in total length and 50 kg in weight (Quéméner, 2002; Quéro and Vayne, 1987). It is a fast-growing species, especially during the first 5 years of life, and its growth shows wide variation (González-Quirós et al., 2011). The reported asymptotic length at infinity (L_∞) ranges from a total length of 171.9 cm (Gulf of Cádiz; González-Quirós et al., 2011) to 210 cm (Mauritanian coast; Tixerant, 1974), although these variations could be influenced by the different methodology used in the estimates.

Despite its rapid growth and high fecundity (Gil et al., 2013), meagre is considered a highly vulnerable species because fish form large spawning aggregations and produce conspicuous sounds when migrate to shallow waters with substantial fishing effort during the reproductive season. Furthermore, the spawning habitats of the species (river mouths and lagoons) often suffer serious environmental degradation (Quéro and Vayne, 1987; Sadovy and Cheung, 2003). This reproductive behavior, coupled with the general worldwide tendency to overfish top predators (Christensen et al., 2003), including adult and juvenile meagre specimens (Quéméner, 2002), and the lack of basic biological information about meagre, have raised concerns about the status of *A. regius* stocks. In Mediterranean waters, meagre populations have suffered an alarming decline (Quéro and Vayne, 1987) and have disappeared from the Balearic Islands (Western

Mediterranean), where the species is considered to be in critical danger (Mayol et al., 2000).

A restocking program, based on releasing hatchery-reared fish, is being conducted by the Balearic government to promote the recovery of the wild meagre stock. More than 10,000 tagged juveniles have been produced and released since 2008, and some of these fish have been recaptured and returned by professional and recreational fishermen (Gil et al., 2014).

Adaptation to natural habitats and natural food resources is critical for the survival of released juveniles. The success of the stocking program depends on the ability of the released fish to adapt. Therefore, it is desirable to evaluate how well the released fish perform in a natural environment to decide whether the releases should be continued as is or if changes should be made in the release strategy (Blankenship and Leber, 1995; Paulsen and Støttrup, 2004; Tomiyama et al., 2011).

A period of growth stagnation has been observed immediately after the release of hatchery-reared fish (Tomiyama et al., 2011), in which the released fish have shown lower growth than the wild fish (Finstad and Heggberget, 1993). The reason of this is a poor feeding effectiveness after release because juveniles must learn to capture live prey in sufficient numbers to sustain growth and survive (Ellis et al., 2002; Ersbak and Haase, 1983; Munakata et al., 2000). Therefore, monitoring any change in growth rate after release may serve to indicate whether released fish are adapting to the natural environment or are failing to adjust to wild conditions.

Growth in fish has been shown to exhibit phenotypic plasticity in response to environmental and anthropogenic (typically, fishing) effects (Alós et al., 2010a; Alós et al., 2010b; Helser and Lai, 2004; Sinclair et al., 2002). The two most important environmental factors affecting fish growth are food level and water temperature

(Weatherley and Gill, 1987). Moreover, the different growth rates observed in the same cohort may involve phenotypic selection, as faster-growing individuals may have a higher or lower probability of survival (Takahashi et al., 2012). The survival advantage of the larger or more rapidly growing members of a cohort is due to an improved resistance to starvation, decreased vulnerability to predators and better tolerance of environmental extremes (Beamish et al., 2004; Sogard, 1997; Takahashi et al., 2012). However, these fish may also be more vulnerable to fishing mortality (Brunel et al., 2013; Swain et al., 2007). Also, a fast growth rate has been shown to correlate positively with aggression (Lahti et al., 2001), and high levels of aggression are associated with risk taking behavior and reduced ability to avoid predators (Araki et al., 2008; Berejikian, 1995).

Body length (i.e., length-at-age) has been used to assess the effects of environmental variables on growth rate (Brunel et al., 2013). Another method for analyzing the growth rate of fish is to use the growth marks produced in the otoliths (Barber and Jenkins, 2001; May and Jenkins, 1992; Suthers and Sundby, 1993; Suthers, 1996), only when there is a strong relationship between the otolith length and the fish body length. However, before applying otolith microstructure analysis, the periodicity of formation of the growth marks should be validated. The daily periodicity of putative daily microstructures has been demonstrated for meagre over a wide age range (from 2 months to 2 years old; Morales-Nin et al., 2010). In certain species, in addition to species-specific ontogenetic changes, other factors may affect the width of the daily growth marks in the otolith (McCormick and Molony, 1992; Molony and Sheaves, 1998). For example, the feed regime and starvation may have substantial effects on increment widths in juvenile fish (Campana, 1983; McCormick and Molony, 1992; Molony and Sheaves, 1998; Rice et al., 1985).

The objective of this study was to evaluate the adaptation of released meagre by analyzing their growth pattern. Specifically, the growth of released and control (i.e., still-captive) meagre were compared, and the observed differences could be attributed to increased growth after release or to differential survival into the same released cohort. The first hypothesis to be tested was that although fish may even experience a decrease in growth immediately after release, the growth rate after an adaptation period may be even more rapid than the average growth rate of the same cohort in captivity. The other hypothesis was that some of the released fish, with high growth rate, would be expected to show improved survival. Therefore, this study examined 3 types of evidence to test the presented hypotheses, analyzing the somatic or the otolith growth. Specifically, recaptured fish that had spent different amounts of time at liberty were analyzed in terms of 1) size-at-age, 2) estimated size when they were 1 year old and 3) daily growth rate before and after release.

2. Materials and methods

2.1. Sample collection

2.1.1. Released and recaptured meagre

Approximately 3,000 *A. regius* juveniles per year have been produced and reared with techniques developed at the Laboratori d'Investigacions Marines i Aqüicultura (LIMIA, Balearic Government; Pastor and Grau, 2013). The reproduction was obtained, once per year, by hormonal induction of wild broodstock captured in Cádiz Bay (Pastor and Grau, 2013). The obtained larvae were reared under controlled conditions and fed with rotifers and *Artemia* sp. The juveniles were transferred to sea cages (5.5 m diameter) where they were kept at low density and fed with commercial pellets (Skretting®, Burgos, Spain; Pastor and Grau, 2013), until reaching the release length.

Prior to release, all of the meagre juveniles were measured (total length, L_T), weighed and marked externally with T-bar tags (Floy® T-Bar Anchor FF-94 and FD-94 tags with identification code and a phone number) and internally with an alizarin bath (Morales-Nin et al., 2010). After marking, the fish were moved to the release site in a boat equipped with an aerated tank. Different release sites (Gil et al., 2014) on the coast of Mallorca Island were selected (Fig. 1). *Returned meagre* are defined as those released specimens that have been recaptured by commercial (with trammel nets) or recreational (with fishing rods) fishermen along the entire Mallorca coast and have been returned to the lab by the fishermen or purchased at fish markets (Table 1). Returned fish were stored at -20 ºC. After defrosting, these fish were measured (total length and weight), and the otoliths were extracted for subsequent preparation. Returned fish were identified through the code of the external tag or by the age or alizarin mark observed in the otolith when fish had lost the external tag because had spent long time at liberty. Note that the identification of the returned fish by the age was possible because the wild meagre specimens disappeared in this locality some decades ago.

2.1.2. Control meagre

The control group was composed of 1,366 specimens of meagre born in 2007 and reared with the same methodology as that used for the released fishes. These specimens remained in sea cages (5.5 m diameter) at low density and were fed with commercial feed pellets (Skretting®) following the recommended food rations. The basic sampling involved measuring the length and weight of control fish at known ages (from 0.7 to 4 years old). The sampling dates and sample sizes are detailed in Table 2. Note that the released fish were also considered to represent control fish before they were released.

2.2. Otolith preparation and observation of daily and annual marks

The left sagittal otoliths of 32 recaptured meagre, born in 2007 and released on February 2009, were embedded in epoxy resin and were cut transversely using a diamond-edged precision saw. The otoliths of the other 4 recaptured meagre of this cohort released on February 2009 were discarded because were damaged during the preparation process. Thin sections (300 µm) containing the core (i.e., the center of the otolith) were mounted on glass slides using thermoplastic glue (Crystalbond® 509) and were ground on silicon carbide grinding papers of decreasing grain size (European P-Grade 800 to 2,400) and polished with 0.3 µm alumina until the nucleus was reached and daily increments were observable. A previous study has demonstrated the daily periodicity of the putative daily growth marks (DGMs) in the otoliths of *A. regius* from 2 months to 2 years old (Morales-Nin et al., 2010).

Transverse thin sections were analyzed using a DMRA2 Leica microscope at x400. Four digital calibrated images were taken along a predefined radius using a Leica camera. The use of areas shared between images allowed the images to be manually combined into a single image. Previous pilot analyses had demonstrated that combining 4 images at the magnification scale used (or 400-500 µm) ensures that an area from the otolith edge to a date clearly prior to the release date would be covered. A reading session consisted of counting and measuring all DGMs along the radius included in the 4 images (hereafter *reading radius,* Fig. 2). For this purpose, a commercial image analysis package especially developed for otolith reading (Age&Shape 2.1.1, Infaimon®, http://www.infaimon.com/) was used. Two reading sessions were completed for each otolith. The reading radius was manually selected and its location was nearly, but not exactly, the same for the two sessions. We used the following reading protocol: first, the image analysis system automatically selected a preliminary list of points located at all identified DGMs based on sharp changes in the luminance profile. Then, these positions were interactively modified by the reader, who was able to not only change the exact position of any point but also delete and/or insert new points. All of the reading sessions were completed by the same reader, who was blind to the identity of the fish. The order in which the otoliths were read was random, and an interval of several days elapsed between the two reading sessions for the same otolith. Precision of the readings was estimated by coefficient of variation (as defined by Chang, 1982).

To determine the relationship between otolith size and fish body size, 102 thin transverse sections from 35 recaptured meagre that had experienced contrasting (i.e., short or long) periods of release (32 of them from 2007 cohort and 3 of them from 2008 cohort released on February 2009 and on November 2009, Table 1), 8 control meagre from 2007 cohort and 59 control-reared meagre used in a previous experiment (Morales-Nin et al., 2010) were processed to determine the otolith radius (O_R, mm; distance from the core to the edge following the *sulcus acusticus*). Body size (L_T) of these specimens ranged from 12.7 to 79.1 cm. The radius was measured by applying ImageJ software to calibrated images of the sections. In addition, the radius from the core to the first annual mark was measured for the 32 recaptured meagre from 2007 cohort, in order to estimate differential survival in the recapture meagre. The interpretation of annual growth marks followed the protocol proposed by Prista et al. (2009).

2.3. Data analysis 1: Size-at-age

The growth of meagre, as is typical for any ectothermic organism, is strongly influenced by seasonal factors such as the temperature, light and food supply (e.g., Adolph and Porter, 1996; Alcoverro et al., 1995; Böhlenius et al., 2006; Coma et al., 2000; Pauly, 1990). A formal model comparison between the seasonal Somers' model and the non-seasonal (conventional) von Bertalanffy model was carried out, and the Bayesian DIC value was worse for the conventional model than for the seasonal model. Therefore, the length-at-age relation of the control meagre was adjusted to the growth model proposed by Somers (1988), which is a version of the conventional Von Bertalanffy (VB) growth model that incorporates seasonal growth oscillations (García-Berthou et al., 2012):

$$L_t = L_\infty(1-\exp(-K(t-t_0)-S_t+S_{t0})+\varepsilon_t \qquad (1)$$

where

$$S_t = (CK/2\pi)\sin(2\pi(t-t_S)),$$

$$S_{t0} = (CK/2\pi)\sin(2\pi(t_0-t_S)) \text{ and}$$

$$\varepsilon_t \sim \text{Normal}\,(0, sd_{L_t}),$$

L_∞ is the length at asymptotic infinite age; K is the rate of approach to the asymptotic length (Schnute and Fournier, 1980); t_0 is the theoretical age at which the length would be zero; C modulates the amplitude of the seasonal growth oscillations; and t_S is the time between t_0 and the inflection point of the first sinusoidal growth oscillation.

The parameters of this model were estimated using a Bayesian approach on the length-at-age data from the control fish (see Supplementary material 1). A non-informative normal distribution (zero mean and tolerance = 10^{-6}) for K and a uniform distribution for C, t_0 and t_S were assumed as priors. C was constrained to be within the interval (0, 1) (García-Berthou et al., 2012), and t_S was constrained to be between 1 and 365 days. Prior distribution for L_∞ was assumed to have a 155± 54 cm (mean and S.D.), as estimated from a large number of cultured fish (unpublished data). This distribution includes 171.9 cm, as estimated by González-Quirós et al. (2011).

Three chains were run using randomly selected initial values for each parameter within a reasonable interval, and conventional convergence criteria were checked. The number of iterations was selected for each run to obtain at least 1,000 valid values after convergence and thinning. The models were implemented with the library *R2jags* (http://cran.r-project.org/web/packages/R2jags/R2jags.pdf) of the R package (at http://www.r-project.org/), which uses the samplers implemented in JAGS (http://mcmc-jags.sourceforge.net/).

The observed length-at-age of the 36 recaptured meagre from 2007 cohort was visually compared with the expected length-at-age estimated from control meagre of the same age to determine whether the recaptures followed the same pattern as the control fish. In addition, we tested for a possible difference in the growth pattern between the recaptures that had spent less than 3 months at liberty and those that had spent more than 3 months through the comparison of their residuals (i.e. observed length minus expected length for a control fish of the same age) using a randomization procedure. In this procedure, the expected distribution of the F statistic under the null hypothesis was emulated by 10,000 bootstrap resamples. The threshold of 3 months at liberty was selected because released meagre appear to return to good biological condition and to shift to a more piscivorous diet after spending approximately 3 months at liberty (Gil et al., 2014). Visual inspection (see Results) suggests that the meagre recaptured after more than 3 months have a different growth pattern than control meagre and recaptures that had spent less than 3 months at liberty. Therefore, two additional analyses were completed to test whether the observed differences were due to (1) the differential survival of individuals with different growth rates or (2) increased growth in the natural environment.

2.4. Data analysis 2: Differential survival

Possible differences in survival depending on the growth rate variability of fish from the same cohort were examined by analyzing the size of the recaptures at the first year of age, i.e., when all of them were in the same lab-controlled rearing conditions. Specifically, we tested whether the specimens with a higher growth rate (or, equivalently, fish with a larger size-at-age because all fish were born and released on the same dates) had a higher probability of survival in the natural environment. This objective was achieved by analyzing the otolith radius corresponding to the age of one year (i.e. radius at the first annual growth ring) of 32 returned meagre (those from the 2007 cohort; 1 to 961 days at liberty). The otolith size at one year was compared between the specimens that had spent less than 3 months at liberty and those that spent more than 3 months. Significant differences between groups in the otolith size corresponding to an age of one year were tested using a one-way ANOVA. A probability (*P*) of <0. 05 was chosen as the critical level for rejection of the null hypotheses. Previously, homogeneity of variances and normality of residuals were examined using a Bartlett test and a Shapiro test, respectively, presenting both an accepted P-value of >0.05. Statistical power was estimated using a bootstrapping procedure (i.e., resampling a large number of times from the observed data; Manly, 1997) and it was very close to the conventionally accepted value of 0.8.

Note that it is possible to infer the body length of a fish at younger ages from the width of the annual increments recorded in the otoliths (Pilling et al., 2002) only if there is a strong relationship between otolith length and fish body length. A total of 102 meagre specimens (range L_T 12.7-79.1 cm) were used to analyze this relationship.

2.5. Data analysis 3: Comparing growth before and after release

Possible growth changes experienced by a fish between the period before release and the period after release were analyzed for a subsample of the recaptured fish. Daily growth marks (DGMs) along the reading radius of 9 recaptured meagre from the February 2009 release (2007 cohort) that spent different times at liberty were analyzed.

Two reading sessions at (nearly) the same reading radius were completed for each fish. At each reading session, distances of all the growth marks from an unambiguous landmark to the otolith edge were recorded (see details above). However, the identification and measurement of DGMs involve several sources of uncertainty linked to the preparation of otoliths, the observation of structures a few microns in size (e.g., Fey et al., 2005; Zhang et al., 1991) and the interpretation of these structures (i.e., identification, enumeration and measurement of DGMs; Morales-Nin and Panfili, 2002). A failure to identify one or more daily increments (*skipping*) implies the overestimation of the average growth rate and the underestimation of age. In addition, a given landmark can be identified in only one of the two reading sessions. Therefore, the two sessions are rarely well aligned, in the sense that the i^{th} identified marks in the first session does not necessarily correspond to the i^{th} identified growth mark in the second session.

After this alignment step, the two distances of the same growth mark were averaged (note that none, i.e., skipping, or only one distance may be available for some growth marks), and the width of the growth increments were calculated. The log-transformed width of the daily growth increments (*GI*) appear to be related with age and the temperature (see Supplementary material 2), excepting for some clear outliers. We propose that abnormally large *GI* correspond to mark skipping (i.e., after skipping two or more marks, the resulting *GI* is larger than expected). Therefore, the linear relationship between *log*(*GI*) and age (*Age*) and temperature (*Temp*) we propose is a mere empirical model intended only at estimating a reliable expected value and at identifying skipping.

This expected value ($GI.hat_i$) may differ between before and after releasing. At captivity, it would be:

$$\log(GI.hat_i) = \beta_0 + \beta_1 Age_i + \beta_3 Temp_i + \log(\delta d_i)$$

After release, it would be:

$$\log(GI.hat_i) = \beta_0 + \beta_1 (Age_R - DAL) + \beta_2 (Age_i - (Age_R - DAL)) + \beta_3 Temp_i + \log(\delta d_i)$$

where β_0, β_1, β_2 and β_3 are the parameters of the linear combination, δd_i is the number of days corresponding to the ith growth increment (δd_i Є {1, 2, 3, 4, …}) and Age_R is the age at the releasing. Note that Age_R and Age_i are not absolute age but the number of days from the otolith landmark where the reading session started. The number of days the fish have been at liberty (*DAL*) is known.

The currently observed values of $log(GI_i)$ are assumed to be normally distributed with mean $log(GI.hat_i)$ and standard deviation given by:

$$sd_i = SD\sqrt{\delta d_i}$$

where *SD* is the standard deviation when $\delta d_i = 1$ day.

The number of days δd_i is assumed to be randomly sampled from a multinomial distribution with a probability vector given by:

$$v_{(i,j)} = p(1-p)^{\delta d_i - 1}$$

where p is the probability of skipping and n_i the number of days between two actually detected, consecutive DGMs.

This method allowed us to estimate the values of the parameters β_0, β_1, β_2, β_3 and Age_R and to detect differences between the growth rate before and after release (if $\beta_1 \neq \beta_2$). The parameters of this model were estimated using a Bayesian approach. A non-informative normal distribution (zero mean and tolerance = 10^{-6}) for βs, a uniform distribution between 0 and 1 for p, and an uninformative gamma distribution for SD were assumed as priors. Three chains were run using randomly selected initial values for each parameter within a reasonable interval, and conventional convergence criteria were checked. The number of iterations was selected for each run to obtain at least 1,000 valid values after convergence and thinning. The models were implemented with the library *R2jags* (http://cran.r-project.org/web/packages/R2jags/R2jags.pdf) of the R package, which uses the MCMC samplers implemented in JAGS (http://mcmc-jags.sourceforge.net/). The R scrip used (including a copy of the alignment algorithm; Palmer et al., submitted) is provided as supplementary material.

3. Results

3.1. Somatic growth of control and recaptured meagre

The data from the control meagre were successfully fitted by the proposed model (Fig. 3). The length-at-age data for the recaptured meagre that had spent less and more than 3 months at liberty were added to the growth curve fitted to the control fish (Fig. 3). Almost all of the recaptures that had spent less than 3 months at liberty had a length within the 95% Bayesian credibility interval of the expected length-at-age of fish of the same age but reared in captivity (i.e., control fish). In contrast, the length-at-age of many (4 of 10 fish) of the recaptured fish that had spent more than 3 months at liberty were outside (larger than) the corresponding credibility intervals (Fig. 3). The probability that 4 of 10 fishes were sampled outside the 95% credibility interval was smaller than 0.001. Also, note that some of these fish reached a given size more than one year before than their brothers cultured at captivity did.

The residuals (observed length minus expected length for a control fish of the same age; Fig. 4) for the recaptured meagre that had spent more than 3 months at liberty were significantly greater than those for the recaptured fish that had spent less than 3 months at liberty ($P < 0.001$). Therefore, the recaptured meagre that had spent more than 3 months at liberty were larger than expected. This pattern may be the result of differential survival of the largest specimens, of increased growth in the wild, or both.

3.2. Differential survival

Fish body length and otolith radius from 102 meagre specimens followed a positive linear relationship (Fig. 5; $r^2 = 0.94$), suggesting that otolith length can be used as a reliable proxy for somatic length. For this reason, the otolith radius at the first year was used to compare the estimated body length of recaptured fish that had spent less and more than 3 months at liberty. This comparison showed that the recaptures that had spent more than 3 months at liberty showed an otolith radius at the first year that was significantly larger ($F_{1,30} = 6.17$; $P < 0.05$) than that for the recaptures that had spent less than 3 months at liberty (Fig. 6).

3.3. Increased growth after release

The mean estimated precision (coefficient of variation) of the meagre otolith reading was 6.5%. The method used in this study allows the skipped DGMs to be estimated.

Therefore, the release date can be located from the readings of the otolith radius, and the growth of the otolith before and after release can be compared (Fig. 7). Note that the pattern obtained from this analysis is observable in addition to the effects of temperature on growth because temperature was added to the model as a covariable. The number of skipped DGMs identified suggests that to ignore skipping would produce an overestimate of the averaged growth rate and an underestimate of the age. A few probable sub-daily growth marks were also identified in several fish, but the small number of these marks indicates that it is implausible that they affected the growth rate estimates.

This method failed to converge for meagre which had spent a few days at liberty because the high among-day variability in growth prevents the reliable estimation of the growth rate after release. In addition, a result of the complex process of otolith preparation was that DGMs were not interpretable for several other otoliths. Therefore, only 9 meagre otoliths could be properly analyzed (Fig. 7, Supplementary material 3). The range of days at liberty for these 9 otoliths was from 35 to 422 days. The difference between the estimated growth rate before and after the release was variable, suggesting that certain meagre grew more in the wild but that the growth of others was less than or similar to the amount of growth in captivity (Table 3). Interestingly, most of the meagre that had spent less than 3 months at liberty (*n* = 4) showed a growth rate in the wild similar to or lower than the growth rate before release, and just one of the meagre (R24, Table 3) presented a higher growth rate in the wild. Instead, most of the meagre that had spent more than 3 months at liberty (*n* = 3) showed a higher growth rate in the wild than in the previous reared condition, and only one fish (R27, Table 3) had a lower growth rate. However, the low number of otoliths for which reliable growth rates have been obtained prevents a proper statistical comparison of the general trends found for all fish.

4. Discussion

A high growth rate in released fish may indicate that they have adapted well to wild conditions and have good prospects of survival. Satisfactory growth cannot be achieved if released fish are unable to obtain sufficient prey. For this reason, the estimation of the post-release growth performance of returned fish is an indirect way to evaluate the effectiveness of restocking (Tomiyama et al., 2011; Wada et al., 2010).

However, the length-at-age of returned fish has little value in itself as an indicator of the adaptation of fish to the wild. Control fish of the same age maintained in captivity furnish a good reference value for comparison because wild specimens are not available in this locality. However, the growth of meagre appears to depend on not only age but also environmental factors. The growth model proposed by Somers (1988), which incorporates seasonal growth oscillations (García-Berthou et al., 2012), was chosen to fit the length-at-age data on meagre specimens maintained in captive rearing conditions. Thereby, the strong influence of seasonal factors, such as temperature, light and food supply, on meagre growth was included in the model of growth. The growth rate of meagre decreases substantially if the temperature is less than 16 ºC (El-Shebly et al., 2007; Quéméner, 2002). This pattern of decreased growth at lower temperatures has also been observed in mulloway *Argyrosomus japonicus*, in which high growth has been reported at warmer temperatures (Taylor et al., 2009). Therefore, the incorporation of seasonal oscillation in the growth model has allowed us to obtain more reliable estimates of length-at-age and to compare them with those currently observed for the returned fish.

The returned meagre were those provided by the fishermen or purchased at fish markets by us for biological analyses. Although a great effort was made to inform fishermen about the meagre restocking program and the information of more than 400 recaptured meagre were reported by them (Gil et al., unpublished results), a low number of samples was available for the growth analysis limiting statistical comparisons. Although clear trends in growth of recaptured meagre were observed, the conclusions of the study should be interpreted with caution. Mainly in analysis from DGMs, it should be emphasized that reliable estimates of the growth rate before and after release have been obtained for a relatively small number of fish, and the sample size should be increased. In future experiments, it would be desirable to increase the sample sizes in order to corroborate the results observed in this study. Moreover, most of the recaptured meagre were caught by commercial fishermen with trammel nets, and certain fishing selectivity could exist (Swain et al., 2007); however it was assumed to be independent of size, or at least nearly independent for the size range analyzed because this gear capture a wide range of size and its size selectivity is low (Erzini et al., 2006).

The returned specimens showed that at least some meagre remained around the coastal areas of Mallorca Island for at least 2-3 years (Gil et al., unpublished results). The growth performance of returned fish is high. Depending on the cohort, fish can grow from a size of 43.2 cm at release to 77 cm after 1.8 years at liberty or from a size of 34.2 cm at release to 79.1 cm in 2.6 years. The length-at-age of the returned meagre was compared with that of the control fish, and differences between specimens that had spent less and more than 3 months at liberty were observed. The recaptured meagre that had spent less than 3 months at liberty presented lengths-at-age similar to or even lower than those expected for the control meagre. This result is consistent with the results reported by Gil et al. (2014), based on the condition index, stable isotopes and stomach contents, which demonstrate that released meagre need several months (approximately 3) to adapt to wild conditions. This adaptation period appears to be variable and species-specific, but the same growth stagnation has been observed in Japanese flounder (*Paralichthys olivaceus*) for several days after release (Tomiyama et al., 2011). In contrast, comparisons of growth rates between wild and reared turbot (*Psetta maxima*) showed similar growth patterns, indicating that the reared fish were able to adapt rapidly to natural conditions (Paulsen and Støttrup, 2004).

Most of the returned meagre that had spent more than 3 months at liberty showed a higher growth rate than that expected from control fish of the same age. This result suggests that fish may increase their growth in the wild. The use of methods such as otolith microstructure can reveal changes in growth rate associated with the process of adaptation to the natural environment. The otolith represents an integration of the entire growth history of a fish (Burke et al., 1993). Several studies have demonstrated that it is possible to estimate the growth rate by measuring increment widths (Campana and Neilson, 1985; Hovenkamp and Witte, 1991; Stunz et al., 2002). The two key assumptions for using the growth marks on the otolith to estimate somatic growth are that 1) the distance between increments must be proportional to the somatic growth occurring between the corresponding dates and 2) the periodicity at which marks are deposited must be verified (Campana and Neilson, 1985). These assumptions have been verified for both annual (González-Quirós et al., 2011) and daily growth marks (Morales-Nin et al., 2010) in meagre. Food level directly influences otolith growth (Barber and Jenkins, 2001; Jenkins et al., 1993; Paperno et al., 1997). For example, significantly higher otolith growth has been observed in fish fed a high food ration at 18 ºC and 12 ºC (Barber and Jenkins, 2001). However, daily increment deposition during starvation can be observed for a certain time (Campana, 1983) because body fat reserves may provide sufficient energy for otolith growth (Jobling, 1980; Marshall and Parker, 1982). This point is important because the low stomach contents and low condition index observed in meagre juveniles (Gil et al., 2014) immediately following release may imply a relatively long starvation period during which the (otolith) growth rate is expected to be small but positive.

The comparison of the growth rate estimated from DGMs between the periods before and after release in recaptured meagre in the Balearic Islands showed consistent variations in growth. The growth of returned meagre that had spent less than 3 months at liberty was similar to or even slower than their previous growth in captivity. This finding is consistent with the view that the fish were still in an adaptation period. Interestingly, however, most of the recaptured meagre that had spent more than 3 months at liberty and, therefore, should be considered well adapted to wild feeding showed an increased growth rate after release. However, the low number of analyzed otoliths prevented us from conducting a statistical comparison that confirmed the observed trends in the recaptured meagre. Some of the otoliths were unreadable because of processing, and some otoliths were useless because the time spend after release was too short to be analyzed by the model. Besides, the otoliths of meagre older than 3 years had to be discarded from the daily growth study because these fish were mature, and the periodicity of ring formation in these otoliths could be different than in immature fish (Campana, 2001). Another reason to discard the otoliths of older fish was that the closest to the edge increments could be below the resolving power of the light microscope; because several authors have noted a general decrease of increment width with age (Morales-Nin, 2000).

We propose that this shift in growth rate may be related to a corresponding shift from a diet based on invertebrates to a more piscivorous diet. This statement is supported by not only the diet shift observed in returned fish (Gil et al., 2014) but also the finding that a semi-moist fish-based diet produces a better growth rate than diets based on any commercial pellets (unpublished data). Similarly, wild 110 g meagre juveniles reared in sea cages reached 1,850 g in only 8 months if fed with fresh fish (Pastor et al., 2002). However, feeding a long number of fish with fresh or semi-moist diet would involve economic and management disadvantages (Kim and Shin, 2006; Kubitza and Lovshin, 1997). Hence, although it is probable that more energy must be invested in catching fish in the wild, the high efficiency of meagre when consuming fish suggests that well-adapted fish (fish recaptured after more than 3 months at liberty) grew better than the control meagre maintained under the rearing conditions and fed with commercial pellets.

In another species, *P. olivaceus,* the increase in growth observed after a release-related period of growth stagnation (Tomiyama et al., 2011) was attributed to compensatory growth (Ali et al., 2003). Compensatory growth is a phase of accelerated growth occurring when favorable conditions are restored after a period of growth depression. The original growth trajectory is restored, and fish may achieve the same length-at-age as conspecifics experiencing favorable conditions at any time (Ali et al., 2003).

In addition to the increased growth rate of well-adapted fish (i.e., those that had spent more than 3 months at liberty), the otolith radius when fish were one year old (i.e., when all fish were still being reared in captivity) showed that those well-adapted fish were also larger at the release date in comparison with fish that had spent less than 3 months at liberty. This result suggests that fish that are larger at the release date may adapt better to wild conditions, growing faster and surviving better than smaller fish. The hypothesis that natural mortality would depend on size has been considered as the most likely option, although other processes could be intervening in the results. Therefore, fish length should have a major impact upon the recapture rates (and presumably survival) of released juveniles (Leber, 1995) due to the greater impact of predation on smaller organisms (Ray et al., 1994; Tsukamoto et al., 1989). A higher survival rate in more rapidly growing fish (i.e., high-quality fish) has also been observed in *P. olivaceus* (Tomiyama et al., 2011) and *A. japonicus* (Taylor et al., 2009). However, this pattern may be reversed or at least modulated over the long term if fishing mortality is the principal source of mortality because fisheries-induced evolution tends to select smaller-sized fish (Brunel et al., 2013). The focus of the current study was only the short and critical period during which released fish must adapt to dramatically different conditions or die.

In conclusion, a higher than expected length-at-age was observed in released meagre that had spent several months at liberty, but this growth pattern could be observed only for survivors, i.e., those fish that appeared to have successfully adapted to wild conditions and survived. These long-time survivors were the largest members of the cohort. Their large size implies not only a lower vulnerability to predation but also a greater competence in obtaining food and, therefore, a greater adaptability to wild conditions. The relationships between the fish quality, post-release growth and survival of released juveniles imply that stocking effectiveness could be improved by selecting specific phenotypes during juvenile production (Tomiyama et al., 2011). Therefore, improvements in the production protocols and in the release strategies could enhance the adaptation of the released juveniles and increase their potential survival after release.

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