ICES Journal of Marine Science
Vol. 63, Issue 9 , November 2006, Pages 1674-1681
http://dx.doi.org/10.1016/j.icesjms.2006.07.007

Evidence of underestimation of European hake growth in the Bay of Biscay, and its relationship with bias in the agreed method of age estimation

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Abstract:

In 2002, a pilot experiment on hake tagging was carried out using methodology specifically developed to catch and handle fish in good condition. By the end of 2005, 36 hake and five tags had been returned to the laboratory (a 3.1% return rate) with a maximum time at liberty of 1066 days. The somatic growth of the recoveries proved to be twofold higher than that expected from published von Bertalanffy growth functions for the species in the Bay of Biscay. The growth underestimation was related to age overestimation, as demonstrated by two independent analyses. The first was based on a blind interpretation of marked otoliths conducted independently by two European experts involved in the routine age estimation of hake. The result shows that the age estimates were neither accurate (inconsistent with oxytetracycline mark positions) nor precise. The second approach compared the predicted otolith growth with the observed growth, and the discrepancy between the two data sets was large. Both types of analyses invalidate the internationally agreed age estimation method and demonstrate a need for further research. Although based on limited data, the study highlights the need to improve biological knowledge of the species in order to improve assessment and management advice. It also strengthens the argument for age validation.

Keywords: age; age estimation method; age validation; European hake; growth; *Merluccius merluccius*; otolith; tagging

Introduction

European hake (*Merluccius merluccius*) are distributed widely over the northeast Atlantic shelf, from Norway to Mauritania, with greatest density between the British Isles and south of the Iberian Peninsula (Casey and Pereiro, 1995). For several decades, it has been targeted by demersal fisheries, being landed either as a target or as incidental catch using a variety of gear, including bottom trawl, net, and longline.

Two stocks of European hake are considered by the International Council for the Exploration of the Sea (ICES) for assessment purposes. The northern stock is distributed north of the Cape Breton Canyon, which separates the waters of France from those of Spain in the southeastern Bay of Biscay, and the southern stock is south of this physical barrier. Total annual landings of European hake declined from about 120 000 t in the early 1960s to a current level of some 50 000 t (ICES, 2005). In recent years, assessments have raised concern about the state of the stocks, and in 2004 a Recovery Plan was implemented by the EU Commission (EC Regulation No 811/2004). Spawning-stock biomass declined from the mid 1980s to the beginning of the 1990s, and has since remained low, although there has been signs of a slight recovery since 2000. Recruitment declined during the 1990s.

The stock assessment model currently used by ICES is an age-based sequential population model (Extended Survivors Analysis, XSA; Darby and Flatman, 1994), a model that has proved useful in establishing a diagnosis on stock status. However, the current assessment has several limitations and shortcomings, including scientific misgiving about growth rate, which obviously impacts the age distributions of the catch and abundance indices used in the age-structured model.

The debate about whether hake is a fast- or a slow-growing species has been going on since the 1930s (Hickling, 1933; Belloc, 1935). Studies since those days in various areas have reported very different growth estimates for hake in both the Northeast Atlantic (Bagenal, 1954; Guichet *et al.*, 1973; Robles *et al.*, 1975; Decamps and Labastie, 1978; Iglesias and Dery, 1981; Lucio *et al.*, 2000a; Piñeiro and Sainza, 2003) and the Mediterranean (Aldebert and Recasens, 1996; Morales-Nin and Aldebert, 1997; Garcia-Rodriguez and Esteban, 2002). It is important to assess whether such diversity is biologically meaningful or whether it reflects bias in the estimation methods.

In most studies, growth functions are provided, using otoliths to estimate age. Errors in age estimation can be caused by accuracy and/or precision issues (Campana, 2001). Accuracy refers to the closeness between measurements (here, the age estimates) and their actual (true) values. Precision (also referred to as repeatability or reproducibility) pertains to the closeness of a set of repeated observations to each other (here, several readings of the same otolith). Hake otoliths are difficult to interpret and the age estimation method has not been validated, although progress has been made recently regarding precision (Piñeiro and Sainza, 2003). To address this, a pilot experiment was carried out in 2002 in the northern Bay of Biscay, and this resulted in the development of a suitable tagging method for this reputedly very fragile species (de Pontual *et al.*, 2003). Here we report on the somatic and otolith growth of the hake recovered from that tagging work, and compare both with what would have been expected according to current knowledge of the species in the Bay of Biscay. We also examine the accuracy and precision of the internationally agreed age estimation criteria (here called the agreed age-estimation method). Questions raised by this analysis are then discussed.

Methods

For a detailed description of the tagging method, the reader is referred to de Pontual *et al.* (2003). Basically, the innovative aspects of that method concern both the capture method (trawling with a codend specially designed to minimize mortality), and the handling method. The tagging process consists of measuring hake total length (TL) to the centimetre below, inserting a T-bar tag (Floy Tag® FD–94 Anchor tag) at the base and in front of the second dorsal fin, and injecting the fish with Terramycine®, a veterinary solution of oxytetracycline (OTC), at a dose of 60 mg kg^{-1}. The individual OTC dose was adjusted using the weight–length relationship $W = 5.13\times10^{-6}L^{3.0744}$ (Dorel, 1986). As this antibiotic deposits a fluorescent mark on growing calcified structures, it is conventionally used for age validation (see Wright *et al.*, 2002).

Analysis of somatic growth

Recaptured tagged fish were stored frozen until subsequent processing. Prior to otolith extraction, they were measured and weighed, and sex was recorded if possible, i.e. for fish returned ungutted.

To our knowledge, all hake growth models are based on the von Bertalanffy growth function (VBGF), as rearranged by Beverton (1954) and Beverton and Holt (1957):

$$L_t = L_\infty \, (1 - e^{-K(t - t0)}) \,, \qquad (1)$$

where L_t is the predicted length at time t, L_∞ the asymptotic maximum length reached when t tends to infinity, K the Brody growth coefficient, and t_0 is the hypothetical time at which length is assumed to be zero.

The growth expected for a given period, for instance, the time elapsed between tagging and recapture, can be derived from Equation 1 as follows:

$$L_2 - L_1 = (L_\infty - L_1) \, (1 - e^{-K\,(t2 - t1)}), \qquad (2)$$

where L_2 and L_1 are the lengths at recapture and tagging, respectively, and t_2 and t_1 are the corresponding dates of catch and tagging (i.e. t_2–t_1 is the time interval between catch and tagging). Equation 2 was therefore used to compute the growth predicted by the VBGF (L_∞ and K) as previously published, so allowing comparison of observed and predicted growth.

We then fitted the VBGF to the tagging data in order to obtain relationships of length at age, which were used for various comparisons.

Otolith growth analysis and age estimation

Otolith extraction was performed under clean conditions, as required for chemical analysis. The left and right sagittae were stored in clean polypropylene vials and stored in a dessicator awaiting further treatment. For this study, we systematically used the left sagittae (an arbitrary choice for standardization). The otoliths were weighed to the nearest µg, then embedded in epoxy resin. Transverse sections (TS) through the core were made with a precision saw, embedded on a glass slide with epoxy resin, and finally ground and polished using a polishing machine. Impurities were removed by rinsing the TS in an ultrasonic bath with Milli Q water. The remaining anterior and posterior otolith parts were kept for subsequent use.

The TSs were observed under a compound microscope equipped with three light sources (transmitted, reflected, and UV). We used TNPC software (Fablet and Ogor, 2005) to acquire calibrated numerical images and to make appropriate otolith measurements. For each otolith, images were digitized under all three light modalities.

Otolith analysis was carried out in two different ways: first, we used an interpretation exercise using the agreed age estimation method, i.e. following the specific interpretation criteria described in Piñeiro and Sainza (2003); second we compared observed and expected otolith growth. The blind interpretation of marked otoliths was carried out independently by two European experts involved in the routine age estimation of hake. No information was provided to them except for the date of fish recapture. The experts were asked to store interpreted images with positions of the reading axis, false rings (FR), and winter rings (WR), for subsequent comparisons.

Otolith growth analysis was carried out by first fitting an otolith growth model to data (size of ventral radius by age group) acquired during the 2002 international exchange of European hake otoliths (Anon., 2002). It is worth noting that this data set was obtained using the agreed age estimation method. The otolith growth model was fitted using monthly data. The conversion of age groups to age data was performed using catch dates and considering 1 January as the birthdate. In this study, we considered the observed otolith growth of tagged fish to be the ventral radius at recapture (Rv2 = nucleus to otolith edge) minus the ventral radius at tagging (Rv1 = nucleus to OTC mark). This observed otolith growth was compared with the expected otolith growth using the same approach as for somatic growth analysis. The otolith analysis took place in June 2003, and subsequent recoveries were used for somatic growth analysis only.

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Results

With respect to previously published data (de Pontual *et al.*, 2003), the recovery rate has increased slightly. We now have 41 recoveries (36 fish returned to the laboratory plus 5 tags sent without the fish to which it was attached), corresponding to a recapture rate of 3.1%. Time at liberty varies from 1 to 1066 days.

Somatic growth

Fish that had spent fewer than 20 days at liberty had a nil or even negative somatic growth rate. Therefore, growth analysis was performed excluding recoveries for which L_2–$L_1 \leq 0$. For combined sexes, the growth rate was estimated at 0.038 ± 0.004 cm d^{-1} (mean ± 1 s.d.; $n = 20$). The growth rates of 0.029 ± 0.006 ($n = 7$) and 0.039 ± 0.005 cm d^{-1} ($n = 8$) for males and females, respectively, did not differ significantly (*t*-test, $p = 0.269$).The growth rate, when restricted to recoveries that had at least one summer and one winter at liberty, was estimated to be 19.82 ± 1.49 cm y^{-1} ($n = 6$).

Figure 1 illustrates the results of a more thorough analysis that compared the observed growth with that predicted by current growth models. Observed and expected growth coincides for fish that had been at liberty less than ca. 50 days. Thereafter, growth is about twice as high as expected according to Equation 2 and using the values of L_∞ and K parameters published by ICES (1993) and Lucio *et al*. (2000a) for European hake of the northern stock in the Bay of Biscay (see Table 1). Although few returns had a long time at liberty, they do provide a strikingly consistent data set with relatively small individual variability, and faster growth of fish tagged at relatively smaller length (see, e.g., fish tagged at 21 and 23 cm on Figure 1).

Fitting VBGF parameters on sex-combined data (L_2–$L_1 > 0$, $n = 20$) with a non-linear regression model provided the estimates for model 1 of $L_\infty = 89.9$ cm (66.8–112.9 cm asymptotic 95%CI, $r^2 = 0.959$) and $K = 0.362$ (0.176–0.549 asymptotic 95%CI). The correlation between K and L_∞ estimates was –0.977. This good correlation and the scarcity of data are the main reasons for the large confidence intervals. In order to obtain a better estimate of K, we set L_∞ to 110 cm, a value that is included in the model 1 CI and that corresponds to the estimate of Lucio *et al.* (2000a). For model 2, K was estimated at 0.250 (0.225–0.276 95%CI, $r^2 = 0.955$). This value is twofold higher than the value of K estimated by Lucio *et al.* (2000a; Table 1). Figure 2 provides a graphic comparison between our estimated growth models and the available reference models. Models 1 and 2 are very close in the size range of recoveries (maximum length 67 cm). However, we consider model 2 (referred to as the "new VBGF" hereafter) to be more reliable than model 1, because L_∞ is probably larger than 90 cm, and because of the reduced CI on K.

Fitting the von Bertalanffy growth fucntion onto data separated by sex was not feasible if both L_∞ and K were estimated. A very large CI was obtained for males ($n = 7$), and no convergence at all for females ($n = 8$). We therefore fixed the L_∞ values as those of Lucio *et al*. (2000a), respectively 80 cm and 110 cm for males and females, which led to an estimated K of 0.436 (0.336–0.536 95%CI, $r^2 = 0.976$) for males, and 0.261 (0.204–0.319 95%CI, $r^2 = 0.902$) for females. A graphic presentation of the results compared with reference material is given in Figure 3.

According to these estimates, the ages at first maturity could well be 1+ and 2+ for males and females, respectively, on the basis of known sizes at first maturity in the Bay of Biscay ($L_{50} = 37.8$ cm and 48.8 cm for males and females, respectively; Lucio *et al.*, 2000a).

Age estimation and otolith growth

The first approach to otolith analysis consisted of the blind interpretation exercise based on the agreed age estimation method. The precision of the age estimates ($n = 33$) provided independently by two European expert readers was quite low, agreement being just 48.5% (Figure 4a). This poor precision was highlighted by comparing the annotated images, which revealed inconsistencies between numbers and positions of WRs and FRs identified by the two experts. Figure 4a shows a cross-comparison of estimates provided by the two. The recoveries aged between 1 and 4 years by expert A were aged between 2 and 5 years by expert B. The discrepancies between estimates did not exceed one year except in the case of 9% of the fish (2 fish aged 4 years by expert A were aged 2 years by expert B, and 1 fish aged 2 years by expert A was aged 5 years by expert B; Figure 4a).

The important outcome of this analysis is evidence that the agreed age estimation method leads to inaccurate estimates of age. Figure 5 shows an otolith of a hake that had been at liberty for less than 1 year (301 days) after tagging. Considering the position of the OTC mark, it is clear that macrostructures interpreted as WRs were actually FRs. The fish first aged 4+ years was then aged 2+ years. The inconsistency between otolith interpretation by experts and the OTC mark position was observed in all fish displaying significant otolith growth (i.e. sufficient time at liberty). A prospective interpretation exercise guided by the OTC mark position was undertaken. The age range provided by the new interpretation (referred to as new age in Figure 4b) was 1–2 years, whereas the range of the mean ages provided by the blind reading was 2–4 years. In all cases but one, the new interpretation provided younger ages than the rounded mean ages estimated from the blind interpretation exercise (Figure 4b). Estimates also shifted towards younger ages (Figure 4c) when they were derived from the new VBGF (model 2).

The second approach to analysing marked otoliths consisted of comparing observed with predicted otolith growth. In order to obtain an otolith growth model based on the agreed age estimation method, we tested three methods of fitting otolith growth data (size of ventral radius vs. fish age) acquired during the 2002 international otolith exchange for European hake. The von Bertalanffy otolith growth model turned out to be better than the linear and power models ($r^2 = 0.924$, $r^2 = 0.879$, $r^2 = 0.907$, respectively; $n = 99$). Otolith growth was estimated as follows:

$$\mathrm{Rv} = 5.018 * (1 - e^{(-0.168(t+0.80))}), \qquad (3)$$

where Rv is the otolith ventral radius (in mm) and t the age (in years).

This model was used to compute expected otolith growth following the argument used to analyse somatic growth (see Equation 2). Figure 6 is a comparison of expected and observed otolith growth; there is great discrepancy between the two data sets. Otolith growth was measurable on fish that had a very short time at liberty, and the discrepancy between expected and observed growth occurred for early recoveries. Although individual variability is quite high, the observed otolith growth is, overall, more than twice as high as expected from the otolith growth model of Equation 3. This is further evidence that the agreed age estimation method gives biased age estimates for hake.

Discussion

Somatic growth

For the first time since research on hake started in the 1920s, observed growth data are available for comparison with estimations. Two hake tagging experiments were reported before our pilot study. Lucio *et al.* (2000b) reported 3 recaptures from 151 released tagged fish, but only one fish was retrieved after a very short time at liberty. An interesting pioneer experiment also succeeded with the recovery of just one tagged fish after 255 days at liberty (Belloc, 1935). The fish lengths at tagging and recapture were respectively 28.9 cm and 40.6 cm, corresponding to a growth rate of 16.7 cm y^{-1}. From his single observation, Belloc (1935) said that hake was a fast-growing species, contradicting the slow-growth hypothesis of Hickling (1933), who estimated the species growth rate at 8.9 cm y^{-1}. The disagreement between these authors could not be explained by geographic area because both studies took place off the south coast of Ireland. Numerous studies have since reported very different hake growth patterns for areas between Ireland, the British Isles (Bagenal, 1954; Guichet *et al.*, 1973), and Morocco (Goñi and Piñeiro, 1988), including the Bay of Biscay (Decamps and Labastie, 1978; ICES, 1993; Lucio *et al.*, 2000a) and off the Iberian Peninsula

(Robles *et al.*, 1975; Iglesias and Dery, 1981; Piñeiro and Sainza, 2003). We focused our comparative analysis on data published by ICES (1993) and Lucio *et al.* (2000a), in order to restrict comparisons to the Bay of Biscay.

Negative growth rates observed in some fish that spent a very short time at liberty may be the result of shrinkage following freezing, as has been observed for other species (Armstrong and Stuart, 1997; Al Hassan *et al.*, 1999), and/or the consequence of poor precision of measurement at sea (always to the centimetre below). Stress induced by capture and tagging is likely to lower the somatic growth rate for some time, as observed here for fish that had been at liberty for less than ca. 50–80 days (see Figure 1). However, our results clearly show that the growth rate of hake that spent sufficient time at liberty diverges by a factor of 2 from previous estimates. They provide direct evidence for the fast growth hypothesis defended by Bagenal (1954), who used *in toto* otolith readings, and Pineiro and Pereiro (1993), who examined the modal progression of size frequency. Interestingly, they also confirm the recently published study on 0-group hake from the Bay of Biscay and the Celtic Sea, which states that the mean length of juvenile hake at the end the first year of life was 23.8 cm (Kacher and Amara, 2005). Those authors based their estimate on counts of otolith micro-increments, assuming a daily rhythm of deposition. Marked otoliths have allowed us to validate this hypothesis (work in progress). According to the VBGF fitted to our tag-recapture data, the length at age 1 would be 24.3 cm (sexes combined, model 2), very close to the estimate of Kacher and Amara (2005). Different growth rates in males and females have been extensively reported (Casey and Pereiro, 1995; Piñeiro and Sainza, 2003). The non-significant *t*-test comparing the growth rates of males and females may be questionable because it considered fish that were tagged at different sizes and that had spent different times at liberty. The VBGF fitted on sex-based data (Figure 3) may change our perception, assuming that the L_∞ values given by Lucio *et al.* (2000a) are correct. However, these models remain tentative because of the maximum sizes of the recovered hake (67 cm and 49 cm for males and females, respectively), and the insufficiency of the data. Nevertheless, hake probably mature much younger than previously believed, whatever the sex, a finding that will undoubtedly have a substantial impact on the understanding of the population dynamics of the species.

The VBGFs derived from the tagging data (sexes combined or separate) need to be refined, and interannual variability linked to environmental conditions and/or density-dependence has to be investigated. We might have other alternative growth models from our data, for instance deciding on L_∞ from historical data or from the maximum reported length of 140 cm (Cohen *et al.*, 1990). However, our data do not support the hypothesis of a very high L_∞ (see the CIs of model 1), but they do support the L_∞ value given by Lucio *et al.* (2000a). Moreover, recent findings on fisheries-induced rapid evolution of key life-history traits in harvested populations (Olsen *et al.*, 2004) inclines one to be cautious when using historical data. More data are obviously needed. Some should be provided in the near future, perhaps from large-scale tagging surveys carried out in 2004 and 2005 in the northern Bay of Biscay. Recent mark-recapture studies from several research institutes should also produce valuable information on the geographic variability in hake growth rates. Waters off the Iberian Peninsula, the southern Bay of Biscay and the Mediterranean (Gulf of Lions and the Balearic Isles) have been under consideration until now. For the first area, the preliminary results of a pilot tagging experiment carried out in 2004 indicate that the fast-growth hypothesis of hake could also be valid for the southern stock.

Age estimation and otolith growth

The analyses performed on marked otoliths clearly show that age overestimation is the reason for growth underestimation. This is an important issue, because the annual assessment of hake stocks by ICES requires that reliable age-length keys (ALK) be provided annually by different countries. Regarding hake, considerable effort has been made to improve the precision of age data through successive international reading exercises and workshops. This goal has been partially achieved, and experts have recently agreed on criteria that provide acceptable precision for ages up to 5 years (Piñeiro and Sainza, 2003), i.e. ages of up to 2–3 years in the context of faster growth shown here. However, those authors emphasized the difficulty in interpreting ring patterns, which are particularly complex in hake otoliths, and the need to validate the agreed interpretation criteria.

Our results clearly show the unsuitability of these criteria. Both precision, which was assessed by a cross-comparison of estimates provided by two independent experts, and accuracy, which was assessed by analysing the consistency of the ages provided by the experts with the oxytetracycline mark positions, have turned up questionable results. Poor precision (Figure 4a) is inconsistent with the progress previously achieved in international workshops and exchanges. It is worth pointing out too that the experts involved in our marked otolith interpretation were considered as the most experienced in the international comparison. The percentage agreement they achieved during the last international exchange (Anon., 2002) was 68%, when computed on the size range of the recoveries. Poorer precision may at least partly result from the fact that fish length was not provided, although one expert usually exploits this extra information during his routine annual hake age estimation. Access to this information may well have improved precision. In fact the use of auxiliary data can reduce errors as well as introduce bias (Morison *et al.*, 2005). Specific validation studies are necessary to assess accuracy (see review by Campana, 2001). For European hake, all previous attempts have proved unsuccessful, so our results point to progress on this topic. Results reported in Figure 4b, 4c, and 5 lead to a conclusion that the agreed age estimation method provides overestimated age and underestimated growth. From a more general perspective, such results highlight the fact that precision management in the absence of accuracy cannot, under any account, guarantee data quality.

Otolith growth analysis (Figure 6) provides further evidence of biased age estimates for hake. Interestingly, results show that otolith growth is measurable on very quick recoveries, even on the dorso-ventral axis where growth is relatively compressed. Therefore, the hake otolith continues to grow even though somatic growth has seemingly ceased, perhaps because of stress. This observation may illustrate the possible uncoupling of otolith and somatic growth under particular conditions (Mosegaard *et al.*, 1988, Folkvord *et al.*, 2000). The relatively high individual variability may be explained by several factors, including length at capture, season, and environmental conditions, such as the temperature that fish actually experience.

Validated data are currently insufficient to develop an alternative robust age estimation method for European hake. Data expected from recent tagging experiments should help to achieve this goal, but attention must be focused on drawing up a typology of macrostructures and on understanding their biological meaning, as well as on understanding the mechanisms (environmental and endogenous) that control their deposition.

The results of the present study raise concern over the production of potentially inaccurate ALKs for stock assessment and management advice. The impact of biased age estimates on the European hake stock assessment conducted in ICES is currently under investigation, and it may well be considered as critical by managers, the consequence of both the recent concern about the state of Atlantic stocks and in the context of an international commitment to exploit stocks to their maximum sustainable yields by 2015 (UN, 2002).

Besides being a contribution to knowledge of Atlantic hake, our results have a more generic interest, because they strengthen the argument for age validation. This point needs to be stressed, because uncertainty in age estimation in a number of ICES stocks is well recognized.

Acknowledgements

We thank Jacques Labastie (Ifremer, La Rochelle, France) for participating in otolith interpretation, and André Ogor (Ifremer, Lasaa, Brest) for technical support. Thanks are also due to P. J. Wright (Fisheries Research Services, Marine Laboratory, Aberdeen, United Kingdom) and an anonymous referee for their valued comments on an early draft of this paper.

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Figure legends

Figure 1. Comparative analysis of observed somatic growth and growth predicted by ICES (1993) and Lucio *et al.* (2000a) von Bertlanffy growth functions for hake in the Bay of Biscay. Numbers above the points indicate fish lengths (in cm) at tagging.

Figure 2. Comparison of a sexes-combined von Bertlanffy growth function of hake in the Bay of Biscay (ICES, 1993; Lucio *et al.*, 2000a), and the same function fitted from recapture data (in model 1, both K and L_∞ were estimated, whereas in model 2, L_∞ was set to 110 cm).

Figure 3. The von Bertlanffy growth function fitted from recapture data for male and female hake and the corresponding function given by Lucio *et al.* (2000a). Fitting was performed fixing L_∞ values to those given by Lucio *et al.* (2000a): 80 cm and 110 cm for males and females, respectively.

Figure 4. Results of marked otolith interpretation analyses. (a) Blind reading: a cross-comparison of age estimates (in years) provided by experts A and B. (b) Comparison of the rounded mean ages given by the experts and ages subsequently assigned using the oxytetracycline mark position to guide interpretation. (c) Comparison of the rounded mean ages given by experts and the ages predicted using the new von Bertlanffy growth fucntion (L_∞ = 110 cm, K = 0.250)

Figure 5. Transverse section of a marked otolith (#1356) observed under reflected light. (a) Blind interpretation (age 4+ years); (b) new interpretation (age 2+ years). Blue indicates the false ring (FR) described by Piñeiro and Sainza (2003), red the winter rings (WR), and yellow the oxytetracycline (OTC) mark. The fish was recaptured 301 days after tagging (TLcap: 30 cm, TLrecap 49 cm). PUBLISHER – REPRODUCE THIS FIGURE IN COLOUR

Figure 6. Comparative analysis of the expected otolith growth and the observed otolith growth with respect to time at liberty. Otolith growth (ΔRv) is the distance (in µm) from the oxytetracycline mark to the edge, measured on the ventral radius. Numbers above the points indicate fish lengths (in cm) at tagging.

Running headings

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Table 1. Von Bertalanffy growth parameters fitted from recapture data with respect to reference models for hake from the northern stock of the Bay of Biscay. See Equation 1 for the significance of the parameters.

Author	Sex	K	L_∞ (cm)	t_0 (years)
ICES (1993)	Combined	0.073	127.5	–1.130
Lucio *et al.* (2000a)	Combined	0.124	110.0	–0.452
	Males	0.181	80.0	–0.724
	Females	0.122	110.0	–0.619
This study	Combined	0.362	89.9	–
This study ($L\infty$ fixed)	Combined	0.250	110	–
	Males	0.436	80	–
	Females	0.261	110	–

Figure 1

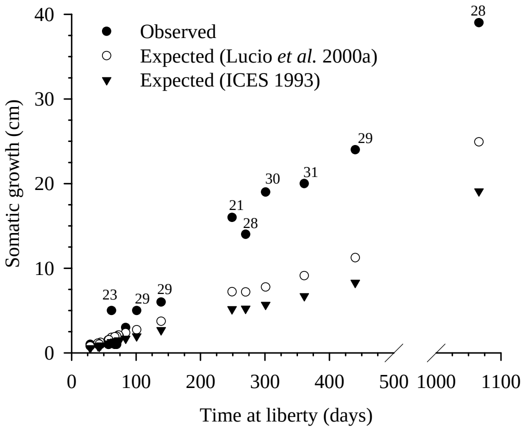

Figure 2

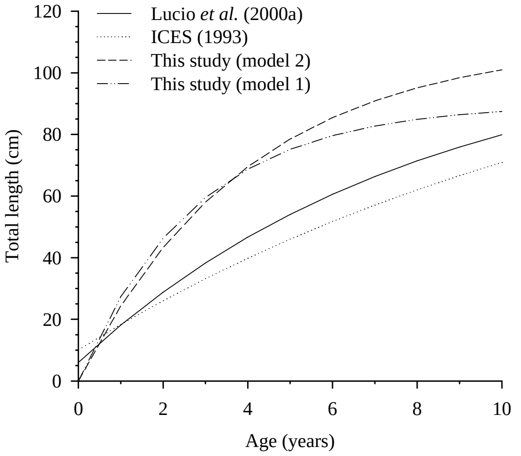

Figure 3

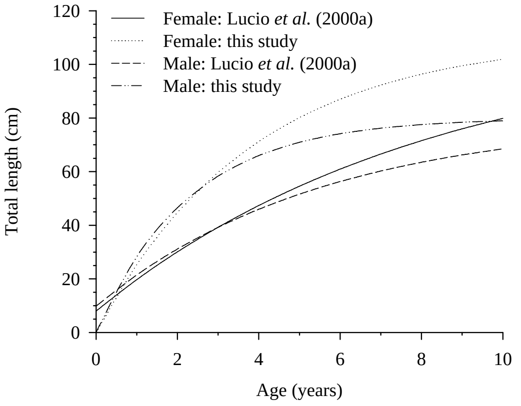

Figure 4.

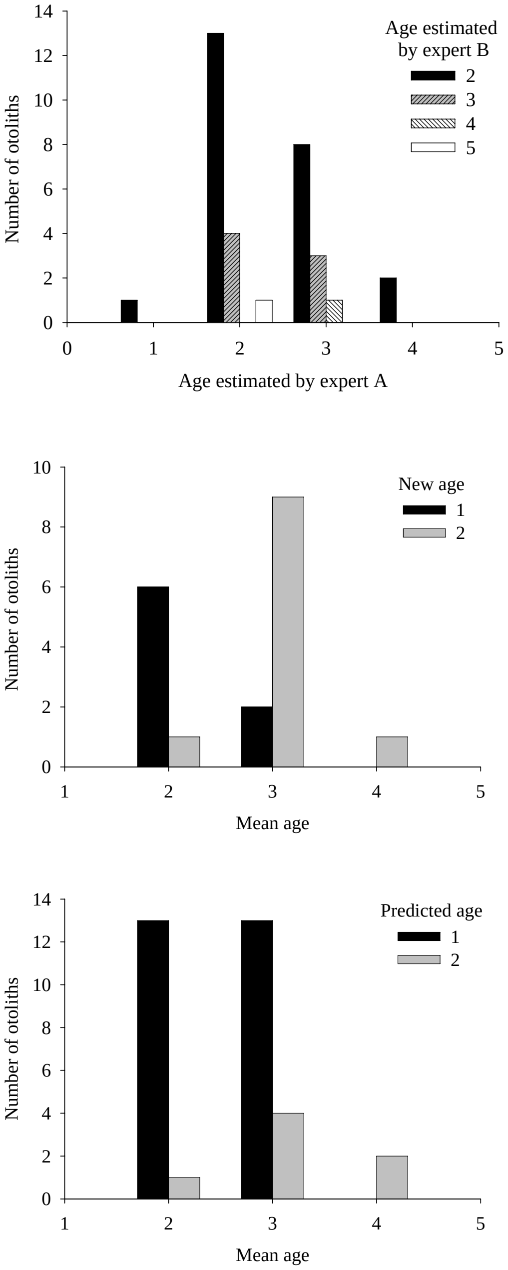
14
12
10
8
6
4
2
0
Number of otoliths
0
1
2
3
4
5
Age estimated by expert A
Age estimated
by expert B
2
3
4
5
10
8
6
4
2
0
Number of otoliths
1
2
3
4
5
Mean age
New age
1
2
14
12
10
8
6
4
2
0
Number of otoliths
1
2
3
4
5
Mean age
Predicted age
1
2

Figure 5

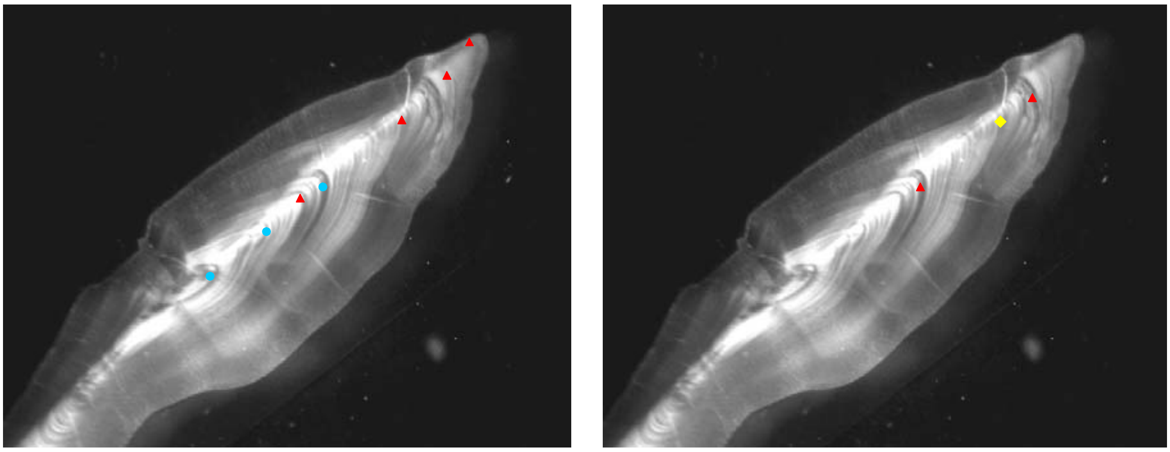

Figure 6