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**ASSESSING NATURAL MORTALITY OF BAY OF BISCAY ANCHOVY FROM
SURVEY POPULATION AND BIOMASS ESTIMATES**

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Abstract: The closure of the anchovy fishery in the Bay of Biscay between 2005 and 2010 due to low biomass levels provided an opportunity to estimate natural mortality using data from egg (DEPM) and acoustic surveys implemented for the assessment of this population since

1987. Assuming that natural mortality (M) is constant over time and that catchability in both surveys is equal for all ages, M could be estimated using log-linear models on the series of surveys of population numbers at age, and seasonal integrated stock assessments. The analysis suggests M values of around 0.9 for a common natural mortality at all ages. However, we found firm evidence that natural mortality at ages 2 and older (M_{2+}) is markedly higher than at age 1 (M_1), which indicates senescent mortality, a possibility suggested a long time ago for this type of short-lived species.

Keywords: Anchovy, natural mortality, senescence, Engraulidae.

Résumé: La fermeture de la pêche de l'anchois du Golfe de Gascogne entre 2005 et 2010, en raison de la faible biomasse du stock, a été une opportunité pour estimer la mortalité naturelle à partir de données de campagnes halieutiques issues de l'observation de la présence d'oeufs (DEPM) et de mesures acoustiques, utilisées pour l'évaluation de cette population depuis 1987. En considérant que la mortalité naturelle est constante au cours du temps et que la capturabilité des deux campagnes est identique pour tous les âges, la mortalité naturelle peut être estimée par des modèles log-linéaires appliquées aux séries temporelles de nombres aux âges issues des campagnes, et par des modèles d'évaluations de stock prenant en compte la saison. L'analyse suggère des valeurs de M autour de 0.9 comme mortalité naturelle courante à tous les âges. Cependant, nous avons des éléments forts indicateurs que la mortalité aux âges 2 et plus (M_{2+}) est remarquablement plus forte qu'à l'âge 1 (M_1) ce qui suppose un signe de mortalité sénescence, une possibilité qui a déjà été évoquée il y a longtemps pour ce type d'espèce à vie courte.

Mots clés: clupéidés (Clupeidae), Mortalité Naturelle, Senescence, Engraulidae, évaluations des stocks

1. Introduction

Natural mortality (M) is a key population parameter scaling the population abundance and fishing mortality estimates in standard (age-structured) assessment methods (Hilborn and Walters 1992; Quinn and Deriso 1999; Gislason *et al.* 2010). However, it is difficult to estimate because of the risk of confusion between natural (M) and fishing (F) mortality, or between M and survey catchability at age (Vetter 1988; Quinn and Deriso 1999; Cotter *et al.* 2004; Wang *et al.* 2009). For this reason, the common approach is to apply a constant M value (Hilborn and Walters 1992; Gislason *et al.* 2010; Jorgensen and Holt 2013). Such value is often guessed according to the life span of the species. On other occasions, M is based on published empirical relationships between M and life history parameters valid for comparable groups of species and environments (Beverton 1992; Pauly 1980; Hoening 1983; Hewit & Hoening 2004). And sometimes it broadens to include size or age-dependent mortality as well (Caddy 1991; Lorenzen 1996; Charnov *et al.* 2001; Charnov and Gillooly 2004; Gislason *et al.* 2008, 2010).

In evolutionary theory, it is often suggested that the extrinsic mortality rate, attributable to external factors like disease or predation, is the major factor that shapes the evolution of life history (and indirectly, of senescence) through fitness optimization (Williams' hypothesis – 1957- in Williams *et al.* 2006; Woodhead 1998; Reznick *et al.* 2002; Charnov *et al.* 2001; Jorgensen and Holt 2013). Natural mortality of fish will change throughout the successive life stages, from very high values in the egg, larval and juvenile stages to medium or low values across their mature life span, before increasing again during senescence (Chen and Watanabe 1988; Charnov *et al.* 2001). Several biochemical mechanisms have been proposed to explain the progressive deterioration of the physiological condition of organisms over time associated

70 with senescence, such as the mutation accumulation theory or the antagonistic pleiotropy
71 theory (see reviews and discussions in Woodhead 1998; Williams *et al.* 2006; Golubev 2009).

72 Increasing mortality associated with senescence occurs at older ages (Vetter 1988; Woodhead
73 1998; Reznick *et al.* 2002; Gislason *et al.* 2010), and this is presumed to be particularly
74 noticeable in short-lived clupeoids (Beverton 1963). Measurements of senescent mortality, as
75 part of natural mortality, are difficult to obtain in the wild due to the many errors affecting the
76 observation of populations (Quinn and Deriso 1999; Gislason *et al.* 2010). Nevertheless,
77 various fish senescence patterns have been reported, ranging from the abrupt senescence of
78 salmon and eels (Woodhead 1998) or of some gobies (Caputo *et al.* 2002) to the gradual
79 senescence of guppies (Reznick *et al.* 2006), *Nothobranchius furzeri* (Terzibasi 2007),
80 gadoids (Sparholt *et al.* 2002; Nielsen *et al.* 2012) or herring (Tanasichuk 2000; Beverton *et*
81 *al.* 2004), and to the very slow or even negligible senescence of rockfish and carps (Reznick
82 *et al.* 2002).

83

84 The Bay of Biscay anchovy (*Engraulis encrasicolus* L.) is a fast growing and short-lived
85 species, fully mature at age 1, and rarely exceeding its third year of life (Uriarte *et al.* 1996;
86 Petitgas *et al.* 2010). In this region, anchovy is prey, along with other small pelagic fish, for
87 piscivorous species such as hake, megrim, sea bass, tunnidae or cetaceans, among others
88 (Preciado *et al.* 2008; Goñi *et al.* 2011; Lassalle *et al.* 2011; López-López *et al.* 2012). The
89 adult anchovy population is monitored yearly by two independent research surveys: an
90 acoustic survey (Massé *et al.* 1996, in press) and an egg survey applying the Daily Egg
91 Production Method - DEPM (Somarakis *et al.* 1994; Motos *et al.* 2005; Santos *et al.* 2011, in
92 press). Both surveys provide estimates of biomass and population numbers at age, which are
93 included in the assessment of this stock carried out by ICES (International Council for the

Exploration of the Sea). A Bayesian two-stage biomass model (Ibaibarriaga *et al.* 2008) is used for this assessment. Until 2004, ICA (Integrated Catch at age Analysis, Patterson and Melvin 1996) was used (ICES 2005). Until 2013, natural mortality rate has been assumed to be constant at 1.2 per year for all ages. This value was inferred in the nineties from direct DEPM estimates of the population at age, assuming that they were absolute and unbiased (Uriarte *et al.* 1996; Prouzet *et al.* 1999). While the Bayesian model presumes constant catchability across ages and surveys, ICA calculated the catchability at age which was 50% higher for age 2 than for ages 1 or 3 (ICES 2005) in both surveys. This was not regarded as a realistic outcome, taking into account the standard designs of both the DEPM and acoustic surveys, which included non-selective fishing gears for adults (capable of catching sizes well below minimum anchovy sizes in spring), and the sufficient spatial coverage of anchovy distribution (ICES 2013). Certainly, an alternative explanation of the findings could be that natural mortality is not constant over age.

Due to recruitment failures since 2001 and subsequent low biomass estimates (ICES 2013), the anchovy fishery in the Bay of Biscay was closed between 2005 and 2010. However, since scientific surveys were still ongoing during its closure, they provided a unique opportunity to estimate the actual natural mortality rate and possible patterns in natural mortality at age. Likewise, this closure allowed comparisons to be made between total mortality rates during the closed period and those in the former period of exploitation, in order to get natural and fishing mortality estimates under the assumption that no major changes in M occurred between both periods (Gulland 1983; Vetter 1988; Cook 1994; Sinclair 2001).

In this paper, several methods for estimating the natural mortality of the anchovy in the Bay of Biscay were applied. First, a direct analysis of the variance (ANOVA) of total mortality rate (Z) derived from consecutive survey estimates of the population in numbers at age was performed, where Z in the closure period was equivalent to the natural mortality rate (M). Next, M was estimated by regression of Z based on an indicator of fishing mortality (F) derived from the ratio of catches to the survey estimates of abundance. Thus, M is calculated from the intercept of Z at zero fishing mortality, which includes information from surveys at other F rates. Finally, an integrated assessment with a seasonal (half-year) separable fishing mortality model was applied to catch and survey data in order to find natural mortality rates and patterns that would optimize data fit, under the assumption of equal survey catchability at age. This approach provides M estimates that best fit with all historical survey information (including the two spring surveys and an acoustic recruitment index started in 2003 – Boyra *et al.* 2013) and the historical catches at age. Therefore the successive methods gradually use a larger amount of information. Furthermore, while the first two approaches assume log-normal errors of the population at age estimates from surveys, the integrated assessment will in addition allow for multinomial errors.

2. Materials and Methods

2.1. Surveys

Estimates of population numbers at age are available from the acoustic (PELGAS –Ifremer-Massé *et al.* 1996, in press) and DEPM (BIOMAN–AZTI- Somarakis *et al.* 1994; Motos *et al.* 2005; Santos *et al.* in press) surveys carried out yearly in May since 1987 and 1989, respectively (ICES 2013). DEPM surveys since 1987 and acoustic surveys since 2000 have reported population at ages 1, 2 and 3+ (with 3+ referring to fish of age 3 and older), while earlier acoustic estimates have reported total biomass and, only occasionally, population numbers at age 1 and 2+ (in 1989, 1991, 1992 and 1997).

In addition, since 2003, an autumn survey has been carried out to provide an acoustic index of juvenile anchovy abundance (Boyra *et al.* 2013). This was used as auxiliary information on the level of recruitment at age 0 in the integrated assessment.

149

2.2. Direct total (Z) and natural (M) mortality estimates.

In a cohort of N fishes at age a in year y ($N_{a,y}$) subject to an annual mortality rate Z , the survivors into the next year will be $N_{a+1,y+1} = N_{a,y}e^{-Z_{a,y}}$.

Let $U_{a,y,s}$ denote the number of individuals at age a in year y estimated from survey s . Provided this index is proportional to the true population abundance (N) by a catchability coefficient (Q), and subject to a log-normal observation error common to all ages ($U_{a,y,s} = Q_{a,s}N_{a,y}e^{\varepsilon'_{s,y}}$), then the log of the ratio of successive age classes estimates in consecutive years is an estimate of the total mortality at age a in year y from survey s , $Z_{a,y,s}$ modified by the change in catchability:

$$\hat{Z}_{a,y,s} = \ln \left[\frac{U_{a,y,s}}{U_{a+1,y+1,s}} \right] = \ln \left[\frac{N_{a,y} \cdot Q_{a,s} \cdot \exp(\varepsilon'_{s,y})}{N_{a+1,y+1} \cdot Q_{a+1,s} \cdot \exp(\varepsilon'_{s,y+1})} \right] = Z_{a,y} + \ln \left[\frac{Q_{a,s}}{Q_{a+1,s}} \right] + \varepsilon_{s,y}$$

We refer to this as a Z estimate. Z estimates are further split into the natural and fishing mortality components:

$$\hat{Z}_{a,y,s} = \ln \left[\frac{U_{a,y,s}}{U_{a+1,y+1,s}} \right] = F_{a,y} + M_{a,y} + \ln \left[\frac{Q_{a,s}}{Q_{a+1,s}} \right] + \varepsilon_{y,s} \quad \text{Equation 1}$$

Three Z estimates are derived: Z_{1+} , from ages 1+ to 2+; Z_1 , from age 1 to 2; and Z_{2+} , from ages 2+ to 3+. Notice that Z_{1+} will generally be closer to the Z of the most abundant age classes (in this case, age 1). Since surveys are carried out at spawning time in May, Z estimates refer to mortality rates from May to May. These estimates rely on two assumptions: 1) catchability is similar over age, and 2) survey observation errors follow log-normal distribution and are of similar average magnitude in both surveys.

Consistency of the Z estimates by survey depending on fishing or closure periods was tested by analysis of variance. Year, survey type (DEPM or acoustic), age (1 or 2+) and fishing period (closed or open fishery) were taken as factor variables, under the terms **Year** and **Survey** and **Old** and **Fishing**, respectively.

We first tested, using ANOVA, the consistency of Z estimates by survey across years for all ages

$$\hat{Z}_{a,y,s} = Year_y + Survey_s + [Old] + \varepsilon \quad (\text{Model A1, Equation 2})$$

Old is in brackets because it only applies in the joint analysis of Z_1 and Z_{2+} . As the year factor will cover the inter-annual variability in Z due to either natural (ecological) or fishing causes, the former analysis should serve to assess whether or not the Z estimates provided by the two surveys are consistent. This was checked by testing the statistical significance of the **Survey** factor and, for the analysis by age, of the **Survey** * **Old** first order interaction.

182

183 Next, we tested the effect of closure on the overall and age-dependent Z values, which during
184 the closure period, will be our direct estimate of the natural mortality rate (M):

185
$$\hat{Z}_{a,y,s} = \text{Fishing} + \text{Survey}_s + [\text{Old}] + \text{Interactions} + \varepsilon \quad (\text{Model A2, Equation 3})$$

186 As before, **Old** only applies when analyzing Z_1 and Z_{2+} together, but not when dealing with
187 Z_{1+} . Interactions are the potential first and second order interactions of the former variables,
188 which were initially checked. Finally, ε is assumed to be a normal random variable with
189 constant variance common to all ages, years and surveys.

190

191 **2.2 Natural mortality estimates from linear models**

192

193 In order to make use of the whole dataset for the estimation of M through a linear model, an
194 indicator of the fishing intensity for each year was obtained from the ratio of the catches
195 between surveys and the mean abundance of the cohort between surveys. This follows from
196 the catch equation:

197
$$F_{a,y} = \frac{C_{a,y}}{N_{a,y}} = \frac{C_{a,y}}{N_{a,y,s} \cdot (1 - e^{-Z_{a,y,s}}) / Z_{a,y,s}} = \frac{C_{a,y}}{U_{a,y,s} \cdot (1 - e^{-Z_{a,y,s}}) / Z_{a,y,s}} \cdot Q_s = RC \cdot Q_s \quad \text{Equation 4}$$

198 where the coefficient of proportionality of the Relative Catches over survey estimates (RC) to
199 F equals the catchability coefficient of the surveys (assumed constant across ages) (Q_s). If
200 RC can be estimated then it can be used to calculate M from Equation 1, as the intercept of the
201 linear model. However, the problem with this approach is that the fitted Z will appear in the

independent covariate (RC). In order to avoid this, we considered two alternative formulations of RC and checked the sensitivity to them:

$$RC_{Survey2} = \frac{C_{a,y}}{(U_{a,y,s} + U_{a+1,y+1,s})/2} \quad \text{Equation 5}$$

$$RC_{Joint2} = \frac{C_{a,y}}{\sum_s (U_{a,y,s} + U_{a+1,y+1,s})/4} \quad \text{Equation 6}$$

The first RC estimator provides an estimate by survey ($RC_{Survey2}$) using as denominator the arithmetic mean of the abundances provided by the survey at the beginning and end of the Z estimate period. The second estimator RC_{Joint2} provides a single joint indicator of fishing intensity for each year from both surveys together, by taking as denominator the average population provided by both surveys during the same period. In the latter case the analysis will be restricted to the years when both surveys were carried out in parallel, so that the two Z_s estimates of the year will be linked by the same RC_{Joint} estimate.

In all cases, the catches considered are those between May 15 of year y and May 15 of year $y+1$, for the ages a and $a+1$ in each respective year. Catches at age (in numbers) with their mean weights are reported by season in ICES until the closure of the fishery in 2005 (ICES 2005) and, more recently, in WGHANSA reports (ICES2013).

The following linear model was statistically tested for the different potential significant coefficients:

$$\hat{Z}_{a,y,s} = M_{a,y,s} + F_{a,y,s} + \varepsilon_{a,y} = M + [Old_a] + Q_s \cdot RC_{a,y} + Survey + Interact + \varepsilon_{a,y,s}$$

(Model B, Equation 7)

222 With M (natural mortality) being the intercept either at age 1 (M_1) or for all ages together
 223 (M_{1+}) - depending on the subset of data being analyzed - Old is now a dummy variable, being
 224 0 for age 1 and 1 for age 2+. This term will indicate the increase of natural mortality in fish of
 225 age 2+ relative to M at age 1 (M_1), for the joint analysis of Z_1 and Z_{2+} . RC accounts for the
 226 Relative Catches between surveys of the respective age a in year y , and coefficient Q_s
 227 accounts for proportionality of RC to fishing mortality F . $Survey$ is a dummy variable, being
 228 0 for DEPM and 1 for acoustics, and this term will reflect any potential effect of the acoustic
 229 survey relative to the DEPM on Z estimates. $Interact$ are the potential first and second order
 230 interactions of the former variables, which were initially checked.

231 For the joint analysis of Z by age (Z_1 and Z_{2+}), our assumption about catchability, constant
 232 across age and necessary to estimate Z , implies that the first or second order interactions
 233 referring to the slope changing by age are not significant as the slope coefficient is the
 234 catchability of the survey. Secondly, the intercepts reflecting M are population parameters
 235 which should be similarly estimated by the surveys. As such, first order interactions of
 236 intercepts with surveys should not be significant. Therefore, the only interaction which could
 237 be significant is that of the slopes by survey, which would correspond with the common
 238 assumptions in most assessments of different catchabilities by survey. We will refer to the
 239 two-slope model as the one allowing different slopes on $RCSurvey_2$ by survey (but with
 240 constant slopes across ages), while we will refer to the single slope model as the one forcing a
 241 common slope for both surveys.

242

243 For the ANOVA analysis associated to all analyses above Type III errors were used.

244

245 2.3 Natural mortality estimates from integrated assessments

246 Finally, an integrated catch at age analysis with a seasonal (half-yearly) separable fishing
247 mortality model was applied to the catch and survey data currently used by ICES for the
248 assessment of this fishery (ICES 2013): Catches in tons and at age on a half-yearly basis,
249 spring surveys; Acoustic and DEPM estimates of total biomass (tons) and populations at age
250 (numbers); and finally, an acoustic survey on juveniles (JUVENA Survey index, started in
251 2003, which is used to tune the recruitment at age 1 with a power catchability function). The
252 purpose, as before, was to check what levels and patterns of natural mortality at age optimize
253 an integrated assessment, under the assumption of equal catchability at all ages in the surveys.
254 Natural mortality by age was applied either to a calendar year, going from January to
255 December or from July to June (the latter was checked because the main surveys are carried
256 out in May, i.e. closer to July than to January). The model was fitted using two different
257 approaches: the first one assumes, as before, that observations (catches or survey estimates in
258 biomass and by age) are subject to log-normal errors and the objective function is a direct
259 minimization of a weighted sum of squared residuals (WSSQ fitting - like in ICA analysis -
260 Patterson and Melvin 1996); the second approach is similar to the former one except that it
261 assumes that all age disaggregated data (catches and population at age estimates) are subject
262 to multinomial errors and hence are entered as percentages at ages 1, 2 and 3+. In the latter
263 case, model fitting is achieved by maximization of the log-likelihood (using log-likelihood
264 ratios - LLHR fitting). Given the general agreement in both surveys in terms of percentages at
265 age, and the poorer agreement in terms of biomass trends (ICES 2013), it seems that the
266 multinomial approach for indexes at age is probably a suitable way to deal with the type of
267 errors associated with survey observations. Details of the model's fitted objective functions
268 are given in Appendix A. The two modeling approaches were run in Microsoft Excel, using
269 Solver for objective function optimization. Convergence was verified using different starting
270 parameter values and likelihood of fitted models was calculated (see Appendix). Confidence

intervals for natural mortality estimates were obtained using the profile likelihood method. Based on the likelihood ratio test, the 95% confidence interval around the joint optimum of $\hat{M}1$ and $\hat{M}2+$ is defined as the pairs of $M1$ and $M2+$ which satisfy the following inequality:

$$\ln(L(\hat{\theta}, \hat{M}1, \hat{M}2+) - \ln(L(\hat{\theta}, M1, M2+)) \leq \frac{1}{2} \chi^2_2(.95) \quad \text{Equation 8}$$

Where $L(\hat{\theta}, \hat{M}1, \hat{M}2+)$ represents the likelihood at the optimum of $M1$ and $M2+$ and every other parameter ($\hat{\theta}$), and $\ln(L(\hat{\theta}, M1, M2+))$ is the likelihood for any selected alternative of fixed $M1$ and $M2+$ parameters (for the optimum of the remaining parameters - θ). And $\chi^2_2(.95)$ is the 0.95 percentile of the Chi-square with 2 degrees of freedom (i.e. 5.9915). Confidence intervals for $M1+$ were also deduced from Equation 8 applied to a single M parameter and Chi-square with 1 degree of freedom.

In order to compare the different fitted models, we used the corrected Akaike's Information Criterion (AICc), estimated as:

$$AICc = -2 \cdot \ln(\text{likelihood}) + 2 \cdot K + (2 \cdot K \cdot (K+1)) / (n-K-1), \quad \text{Equation 9}$$

with K being the number of parameters and n being the number of observations.

285

2.4 Sensitivity analysis

Sensitivity to some observations, that looked noisy at first sight and might have become too influential for the particular methods applied, was tested by including and excluding such data (when excluded we will refer to the subset of data). For raw data direct analysis during the closure period (2005-2010), the 2005 and 2006 survey data resulted in negative Z estimates between them, indicating that either 2005 estimates were too low or 2006 estimates too high.

292 As for the linear models, years with high RC values (above 0.8) were considered unlikely to
293 be actually happening (due to the difficulty of producing such a fishing impact) which led us
294 to suspect some noisy, excessively low biomass estimates from the surveys during those
295 years. In addition, years 2011 and 2012 were checked for sensitivity as they resulted in
296 extremely different Z estimates by survey due to a large discrepancy in the 2012 biomass
297 estimates (ICES 2013). For the integrated assessment, analyzing sensitivity to the
298 inclusion/exclusion of the 2012 survey biomass estimates was considered sufficient (the year
299 of maximum biomass divergence – ICES 2013).

300

301 Furthermore, we tested the sensitivity of our results to a maximum potential level of errors in
302 age determination from otoliths. Even though the current ageing method is perceived to be
303 unbiased (Uriarte *et al.* in press), the actual level of error is unknown. Using expert advice, a
304 maximum of a 5% level of ageing errors among contiguous age groups (from ages 1 to 3+)
305 was evaluated. Larger errors were considered unlikely and were not compatible with data.
306 Determination of age 0 was considered fully accurate. In addition, given the low percentage
307 of age 3 in surveys and catches, age 2 errors were considered to occur more often with age 1
308 (in 80% of cases) than with age 3 (only 20%). The tested matrix for age determination error
309 (**E**) is shown in **Table 1**. Given a vector with the observed (assigned) age composition **A**
310 (1*4) of a survey or catches, the corrected estimates of the age composition **C** (1*4) are
311 deduced in matrix notation as:

$$312 \qquad \qquad \qquad \mathbf{C} = \mathbf{A} \cdot \mathbf{E}^{-1} \qquad \qquad \qquad \text{Equation 10}$$

313 Corrections were not allowed to reduce the size of any age class below 20% of its original
314 value (before correction) and *ad hoc* changes were applied to ensure those minimums (by
315 restoring enough numbers from the contiguous age class in proportion to the removals

316 produced on the original amount so as to still allow 20% of the starting amount). As for the
317 catches, corrections were applied to international catches separately over three periods: before
318 surveys (January – mid-May), after surveys (mid-May - June) and in the second half of the
319 year.

320

321 3. Results

322 a) Direct Z and M estimates (Model A)

323 The series of Z estimates by survey show a large inter-annual variability (**Figure 1**). Z
324 estimates did not differ statistically between surveys ($p>0.95$ for Z1+ and $p>0.12$ for the Z by
325 age, Model A1). During the 2005-2009 closure, Z estimates (proxy of M1+) were markedly
326 lower on average (0.81, CV=13%) than during fishing periods (1.66, CV=9%) (**Figure 2**;
327 **Table 2**). Parallel differences between fishing periods were noticed for the Z by age (**Table 2**)
328 (with $p[\text{Fishing}]<0.002$, from Model A.2), and were consistently shown for both surveys
329 (with non-significant interactions of *Fishing* by *Survey*, $p>0.6$).

330 Natural mortalities deduced from Z estimates by age during the fishing closure period
331 (proxies of M1 and M2+) were slightly affected by the omission of the 2005 and 2006 noisy
332 estimates and turned out to be $M1=0.66$ (CV=11%) and $M2+=1.63$ (CV=19%) (**Table 2**).
333 Such big difference in Z by age was consistently shown in both surveys (**Figures 1 & 2 and**
334 **Table 2**) in the time series (Model A.1) and for the two fishing periods (Model A.2) (with
335 $P(\text{Old})<0.0001$ and $p(\text{Old}*\text{Survey})>0.2$ in both models).

336

337 b) Natural mortality estimates from linear models (Model B)

338

339 M estimates (intercepts) did not differ statistically between surveys, neither in the case of Z1+
340 ($p[\text{Survey}] > 0.6$) nor by ages Z1 and Z2+ ($p[\text{Survey}] > 0.3$ and $p[\text{OLD} * \text{Survey}] > 0.25$) for any
341 RC index or subset of data. Therefore the requisite for the joint analysis of the Z from both
342 surveys using this model was verified.

343

344 As regards total mortality (Z1+), the two-slope model on RCSurvey2 (**Figure 3**) resulted in
345 M1+ of 1.05 (CV=19%) (**Table 3**), though the slopes were not significantly different
346 ($p=0.283$). This estimate was very close to the mean of the individual M1+ estimates from the
347 surveys, which was 1.14 (CV=26%) for the DEPM and 0.953 (CV=26%) for the acoustic
348 (**Table 3**). Forcing a common slope for both surveys on RCSurvey2 made the single slope
349 model significant and resulted in a M1+ of about 1.15 (with a CV of 15%). The RCJoint2
350 estimator results in a M1+ of 0.885 (CV=20%). Removal of the suspicious Z1+ values
351 corresponding to RCSurvey2>0.8 and Year>2011 globally improved the fitting while leading
352 to a reduction of M1+ estimates (**Table 3 and Figure 3**). In summary, if the complete dataset
353 pointed towards an M1+ range of between 0.88 and 1.15, the analysis of the subset of data
354 reduced those values to a range between 0.78-0.92, with RCSurvey2 pointing towards higher
355 M1+ than RCJoint2.

356

357 Analysis of Z by ages (Z1 and Z2+) revealed significant differences in the intercepts (M) by
358 age ($P[\text{Old}] < 0.001$) for any RC index. In the case of RCSurvey2, the two-slope model
359 (**Figure 4**) pointed to M1=0.94 and M2=1.79, with CVs around 17% and 14%, respectively
360 (**Table 4**). These estimates were close to the mean of individual survey estimates (**Table 4**)
361 but the slopes by survey were not significantly different ($p=0.437$). The single slopes model

became fully significant and resulted in very similar values. Using RCJoint2 (**Table 4** and **Figure 4**, bottom panels) resulted in slightly lower M1 (at 0.82, CV=23%) and rather similar M2 (at 1.73, CV=17%).

Working with the subset of data (**Figure 4b** and **Table 4b**) improved the overall fittings and again led to a reduction of M estimates. For the two-slope model on RCSurvey2, the values decreased to 0.78 for M1 (CV= 25%) and to 1.46 for M2+ (CV=20%), and achieved very similar values in the single slope model. For the RCJoint2, the use of the subset of data reduced M1 to 0.58 (CV=35%) and M2 to 1.57 (CV=19%). In summary, the complete dataset resulted in M1 in the range 0.82-0.94 and M2+ around 1.73, whilst analysis restricted to the subset of data reduced those estimates to M1 within the range 0.58-0.78, and M2+ in the range 1.40-1.57, with RCSurvey2 pointing towards higher M1 than RCJoint2.

C) Natural mortality estimates from integrated assessments

Optimization for a single overall natural mortality (M1+, common for all ages) including all input data resulted in M values of around 1.15 and 1 for the WSSQ and LLHR optimizations, respectively (**Table 5a**). In all cases, the response surface was rather flat around the optimum (± 0.1), being basically guided by the age-structured survey indexes, followed by the catches at age information and finally, to a lesser extent, by the biomass survey indexes - which in fact favored slightly lower M1+ optimums (around 0.7-1.1) (**Figure 5a**). In all cases, the small contribution of JUVENA favored M1+ values at or above the synthetic optimum. The sensitivity of these results to the omission of the 2012 survey estimates was negligible, with optimums differing by less than 1% (not shown for simplicity).

Optimization of natural mortality by ages (M1 and M2+) for a Jan-Dec calendar year suggested, for both objective functions, that the lower the M1 the better the fitting achieved, though improvements gradually reduced, being minimal below 0.7 (**Figure 5b**) with optimum M1 around 0.15-0.3 and M2+ around 1.35-1.45 (**Table 5b**). Applying a July-June calendar year provided optimums for both objective functions of around 0.7 for M1 (**Figure 5c** and **Table 5c**) and 1.4-1.5 for M2+ (see joint confidence intervals by models in **Figure 6a&b**). Results are basically guided by the age-structured survey indexes which provide a rather parallel response, whilst all other inputs are non-informative (almost flat) (**Figures 5b & c**). Compared to the assessments assuming a single natural mortality (M1+), the assessments allowing M at age to be estimated (M1/M2+) get a better fitting (higher likelihood - **Figure 6**) and lower Akaike's Information Criterion (**Table 5**). These results were insensitive to the omission of the 2012 survey estimates (not shown).

The M at age estimates obtained by the integrated models for the July-June calendar year are consistent with those produced by the direct and linear models previously reported (**Figure 7**).

D) Sensitivity to Ageing Errors

Inclusion of 5% ageing errors did not affect the compatibility of Z1+ estimates by survey, neither in the raw data analysis ($P=0.97$), nor in the log-linear models ($P=0.71$). This compatibility also applied to the analysis of Z by age where all terms with *Survey* were not significant either. Therefore the joint analysis of both surveys was again statistically supported.

408 Consideration of a 5% ageing error raised up the M1+ estimates by about 0.14 in direct and
409 lineal model analyses, resulting for the subset of data all M1+ in the range of 0.94-1.08
410 (**Table 2 and 3**). Incorporation of this ageing error into the integrated models leads to minor
411 increases of the original M1+ estimates (by about 0.04), resulting in poorer fits and larger
412 AICc than for uncorrected data (**Table 5**).

413 By age, consideration of a 5% ageing error meant that paired raw Z1 estimates were still on
414 average below those of Z2+ for both surveys over the whole period (**Table 2b**) (paired t-test
415 $p=0.0295$), and more intensively during the closure period ($p=0.0146$).

416 The correction for a 5% ageing error reduces the differences of M between age by increasing
417 M1 estimates by about 0.2 and 0.3-0.4 in the direct and lineal model analysis, respectively,
418 and by reducing M2+ by a lesser extent (by about 0.08- 0.16). Nevertheless, M1 remains
419 invariantly below M2+, even though statistical significance is sometimes lost (**Table 3**). Both
420 integrated models, when considering a 5% ageing error, also obtained a reduction of the
421 differences of M by age by increasing M1 and reducing M2+, but to a larger extent for the
422 January to December calendar year. Nevertheless, M1 remains invariantly below M2+.
423 Certainly, the improvement in fitting achieved by allowing M to change by age is reduced
424 when compared to no ageing errors, but the differences are still significant (even though only
425 at alpha 0.06 for the WSSQ) (**Figure 6**) and the Akaike's Information Criterion improves (is
426 reduced), therefore still endorsing the M by age models over the single M1+ models.

427 Figure 7b shows the general consistency and overlapping of the M at age estimates for the
428 different methods tested before (**Figure 7**).

429

430 4. Discussion

431

432 Estimating natural mortality is one of the main challenges in stock assessment (Vetter 1988;
433 Hilborn and Walters 1992; Gislason *et al.* 2010), and in order to do it, availability of research
434 surveys is essential (Sinclair 2001; Sparholt *et al.* 2002; Zhao *et al.* 2003; Francis 2011). The
435 basic assumption of this paper was that the direct monitoring program running since 1987,
436 through two research surveys (23 DEPM and 18 Acoustic surveys) and the closure of the
437 fishery for 5 years should enable the overall level of natural mortality and its pattern by age to
438 be inferred for the Bay of Biscay anchovy. This was supported by the compatibility of the Z
439 estimates from both surveys and because, in spite of the large variability inherent to the data,
440 Z differed significantly between the open and closed fishing periods, being lower during the
441 latter period and therefore indicative of the natural mortality rates. Moreover, mortality at
442 ages two and older (Z2+) was significantly higher than at age one (Z1) throughout the time
443 series, suggesting an increasing pattern of natural mortality by age.

444

445 The series of Z estimates have a large inter-annual variability which must be linked either to
446 observation errors in the surveys or to variability in natural and fishing mortality, or both.
447 Observation errors in surveys are evidenced by the fluctuations in Z between consecutive
448 surveys (sometimes reaching negative values) and by the occasional strong divergences of
449 survey estimates (as in 2012). Variability of fishing mortality naturally happens for the
450 fisheries, which tend to stabilize catches when exploiting a highly fluctuating population (like
451 anchovy). Some variability of natural mortality has always been presumed and could be
452 linked to changes in the ecological environment (Vetter 1988; Zwolinski and Demer 2013).
453 For these reasons, we have chosen gradually improved estimators of natural mortality,
454 allowing for increasing data input and, in principle, greater noise filtering.

455

456 The direct and linear models provide a natural mortality for all age groups (M1+) of between
457 0.81 and 1.15, which decreases to 0.78-0.92 after filtering the suspected noise. The integrated
458 models indicate M1+ at about 1.15 for WSSQ and 1.00 for LLHR, i.e., at the upper range of
459 the estimates in the former models. Even though these estimates are not statistically different,
460 there can be several reasons explaining this preference for upper M1+ in the integrated
461 models. Firstly, their results include, in addition to the spring surveys, other auxiliary
462 information which partly favors this upper range of M1+ values, mainly by the recruitment
463 index and to a lesser extent the catches by age. Secondly, it should be pointed out that linear
464 models make inferences of M1+ from the decay between age groups 1+ to 2+, whilst
465 integrated models fit simultaneously the three age classes (1/2/3+) with the same M1+, and as
466 such the former estimates may be closer to the weighted mean of M by age (according to their
467 abundance), while the latter is closer to an arithmetic mean (as residuals by age have equal
468 weights). Hence, weighted M1+ to age class abundance should favor the M1+ at the lower
469 range pointed out before, because M1 is lower, and will serve to better describe the average
470 change of the whole population. In any case, this results in a most likely range going from
471 0.78 (RCJoint2) to 1 (log-likelihood assessment), which corresponds with an annual survival
472 of between 46% and 37%. If a single figure is needed, a rough compromise could be in the
473 middle of the ranges, close to 0.9 for M1+ (annual survival rate of 41%).

474 These results point towards a lower M1+ than the currently assumed value of 1.2, which was
475 calculated in the 1990s on the basis of the DEPM survey alone (Uriarte *et al.* 1996; Prouzet *et*
476 *al.* 1999). Moving to an M1+ of 0.9 would imply a reduction of the average historical
477 estimates of SSB by about 30-35%, and an inverse parallel increase of fishing mortality
478 estimates.

479 This average natural mortality for adult anchovy in the Bay of Biscay is just slightly below
480 the values of 1.08 and 1.34 which result from applying Hoening's equation (1983) (for a
481 T_{max} of 4) and that of Pauly (1980) (for von Bertalanffy growth parameters L_{inf} , K and t_0
482 about 18.05 cm, 0.77 and 0.72, respectively, as fitted to DEPM survey observations and a
483 mean temperature of 16 °C). Nevertheless, these M_{1+} estimates are rather similar to, albeit
484 slightly higher than, the ones reported for short-lived species of similar growth, such as sprats,
485 some *Sardinops* or *Engraulidae* (Beverton 1963, 1992; MacCall 1973; Methot 1989; Iversen
486 *et al.* 1993; Sinovčić 2000), but at a lower level than the ones reported for Peruvian anchovy
487 (Pauly *et al.* 1987), *Anchoa mitchilli* (Neweberger and Houde 1995) and other *Engraulidae* of
488 smaller maximum sizes (Bayliff 1967).

489

490 All the analyses improved by allowing M to change with age: the *Old* factor was retained in
491 the linear models and the likelihood of the integrated models improved significantly when M
492 was estimated by age compared to the single common M_{1+} modeling (Figure 6). This led to
493 the conclusion that M_1 was significantly lower than M_{2+} (Figure 7): On the one hand, the
494 direct Z estimate and the linear models resulted in a range of M_1 from 0.45 to 0.94 when
495 using the full dataset, and a narrower range of about 0.6-0.8 with the most reliable subset of
496 data. This corresponds with an annual survival of about 55%-45% for the 1-year-old group.
497 On the other hand, M_{2+} was consistently about twice the value of M_1 : 1.59 to 1.79 for M_{2+}
498 with the full dataset and 1.4-1.65 for the most reliable subset of data. This corresponds with
499 an annual survival rate of about 25%-19% for ages two and older.

500 Furthermore, integrated assessment indicated M at age consistent with the former results, but
501 only for the July-June calendar, whilst the Jan-Dec calendar year suggested a better fit at a
502 lower M_1 (Figure 7). For the latter modeling, such discrepancy arises from the pronounced

mismatch between the calendar of application of natural mortality by age (January to December) and the calendar between survey observations (from May to May) which have to be fitted. Both integrated assessments from July to June (WSSQ and LLHR) produced almost identical estimates as those from the linear models in RCSurvey2 on the most reliable subset of data. This means that the population modeling context of the integrated assessment, including other auxiliary information, has enabled natural filtering of much of the noise affecting the individual spring survey estimates. In summary, both July-June integrated assessments have captured the pattern of natural mortality at age between survey observations (from May to May) well and are consistent with the former simpler linear models (particularly with those using the reliable subset of data) (Figure 7). Simplifying, they all pointed towards an $M1$ of around 0.70 and $M2+$ of around 1.40 (i.e. survivals about 50% and 25% respectively).

Our data do not allow saying when this additional mortality at age 2 and older happens during the year; however the sharp decrease of the 2 and 3 year-olds is already noticeable in the fishery after spawning, during the second half of the year (ICES 2005, 2013; Uriarte *et al.* 1996). This could have been the result of some permanent emigration of the old (2+) fishes outside of the major fishing grounds, off the Bay of Biscay, but such a possibility has never been proven and it is well known that, every spring, old fishes concentrate again to spawn in the southeast of the Bay of Biscay (Motos *et al.* 1996) where the surveys take place. Therefore, this increasing mortality at age 2 and older is most likely due to either increased vulnerability to predation at older ages or to natural biological mortality, probably reflecting senescence of anchovies at age 2 and older. No major concentration of predators on adults in early summer has been reported. The Bay of Biscay is an area of bottom-up controlling of the upper trophic levels (Lassalle *et al.* 2011), with anchovy being one (and not the main) among several small pelagic and other fishes (such as sardine, sprat, horse mackerel, blue whiting,

etc) connecting the plankton communities to piscivorous species (Sanchez and Olaso 2004; Preciado *et al.* 2008). It contributes to the diets of demersal species such as hake, monkfish, megrim and tunnididae but mainly as juveniles (Guichet 1995; Preciado *et al.* 2008; Lezama-Ochoa *et al.* 2010; Goñi *et al.* 2011, 2012; López-López *et al.* 2012), whilst in adult anchovy it seems that some demersal fishes (John dory and hake, etc) and cetaceans prey routinely all year around (Preciado *et al.* 2008; Mahe *et al.* 2007; Lassalle *et al.* 2012; Meynier *et al.* 2008). Therefore, by discarding any ecological higher predation on adults, we tend to think that senescence might be occurring at the age of two and older, in accordance with the expectation of observable senescent mortality affecting short-lived cupleoids (Beverton 1963).

538

We hypothesized that this anchovy population may suffer from “reproductive stress” inducing increased mortality, particularly after its second spawning event. It is known that the large energy cost of reproduction can induce some varying rates of mortality due to “reproductive stress”, as shown for cod (Hutchings 2005), or in extreme cases, of semelparous species like Pacific salmon *Oncorhynchus*, which reproduces and dies, whereby dramatic hormonal changes induce starvation that causes intestine deterioration by necrosis and inflammatory processes during spawning migration (McBride *et al.* 1986). Examples of mortality associated to reproductive stress in short-lived species are common, as in invertebrates (squids and shrimps – Caddy *et al.* 1996) and fishes such as *Aphia minuta* (an extremely short-lived goby where apoptosis of enterocytes is related to post spawning mortality – Caputo *et al.* 2002), capelin *Mallotus villosus* (Vilhjálmsen 1992; Gjørseter 1998) and in the short-lived gadoid Norway pout (Nielsen *et al.* 2012). Anchovy in the Bay of Biscay invests much energy in reproduction having one of the highest spawning frequencies among the Engraulidae, capable of increasing slightly with size and age (Uriarte *et al.* 2012), which results in a very high daily

fecundity (Santos *et al.* in press). Many of the 1-year-old fishes lay down a spawning check at the end of the spawning season (in early summer) (Petitgas and Grelletier 2003; Uriarte *et al.* 2002, in press) being probably indicative of the limiting condition of many anchovies after spawning (Pecquerie *et al.* 2012). While they have reached about 88% of their maximum attainable growth (18.3 cm) by the age of 2, spawning starts earlier and probably lasts longer than at age 1, with a likely increase in the number of batch-spawning events during the spawning season (Motos *et al.* 1996; Motos 1996; Pecquerie *et al.* 2009), in accordance with the indications for other Engraulidae (Parrish *et al.* 1986; Claramunt *et al.* 2007; Cubillos and Claramunt 2009). On average, 2-year-old anchovies do not resume opaque edge formation in otoliths until mid-June, beyond the mid-point of the spawning season (Uriarte *et al.* 2002, in press), this being also indicative that much of the energy of this age group is invested in reproduction during the first half of the year. This reproductive strategy of anchovy may result in some physiological reproductive stress at the end of the spawning season for the age 2+ group, which may explain the increase in natural mortality observed in our analysis. As such, this population of anchovies may have evolved in its fluctuating environment by allowing some non-negligible chances of reproducing over two spawning seasons before senescence. This would enhance the opportunities to overcome single (not repeated) environmentally-induced failures of recruitment. This strategy would place anchovy among capelin, which mostly dies after its first spawning (Vilhjálmsón 1992; Gjøsaeter 1998), and sprats, sardines or sandeels which have progressively longer adult life expectation with several annual reproductive cycles (Cook 1994; Nunes *et al.* 2011; Zwolinski and Demer 2013); ending up with the herrings, which seem to have up to eight reproductive seasons during their life history before increased mortality by senescence shows up (as for Norwegian spring-spawning herring – Beverton *et al.* 2004). To our knowledge, senescence in Engraulidae had only been suggested previously for Northern anchovy (from age 2 and older

578 – MacCall 1973 – based on analysis of catch ratio from catches and surveys) and for the
579 anchovy in the Yellow Sea (from age 3 and older – Zhao *et al.* 2003 – based on analysis of
580 surveys). We suspect that this pattern of increasing mortality by age may be applicable to
581 other Engraulidae, whereby assessments following the usual constant mortality assumption
582 often results in non-understandable big changes in catchability by age in surveys (Giannoulaki
583 *et al.* 2014).

584 In terms of assessment, the new M estimates would impact the average level of spawning
585 biomass approximately in proportion to the reduction in average M. For instance, for LLHR
586 modeling, moving from the single M1+ hypothesis at 1.2 to its optimum at 1.00 would reduce
587 mean biomass by about 27%, while moving further from the optimum M1+ to its optimal
588 mortality by age would result in a minor reduction of about 5%. So once M1+ is set at its
589 optimum, a further change to the optimum M by age does not imply additional major changes
590 to mean biomass estimates. In spite of this, however, this latter change to M by age will
591 probably have implications in any population and fishery projections which might be required
592 for the provision of advice to managers. For instance, for this anchovy old populations
593 (composed mainly of ages 2+) will decay faster (with M around 1.4) than young ones
594 (composed mainly of age 1) (with an M around 0.7-0.8). Therefore, in terms of management
595 moving to unbiased M estimates should also improve the quality of advice as reported for
596 other species (Lee *et al.* 2011; Zwolinski *et al.* 2013). Certainly, the perception of fishing
597 mortality will change inversely to the estimation of biomass levels. Furthermore, as the new
598 M estimates change the perception of cohort dynamics in mass, this will affect the estimation
599 of management-related reference points ($F_{0.1}$, F_{MSY} , etc.).

600

601 These results are partly sensitive to the maximum level of ageing errors put into
602 consideration. Correction of such a 5% ageing error moved the direct and linear model
603 estimates of M1+ and of M1 upwards, while slightly reducing M2+. This was associated with
604 a partial loss of the statistical significance of the difference between M1 and M2+ (Figure 7b).
605 Integrated models were less affected in the M1+ estimates (remaining just slightly above the
606 original optimums), and also showed a reduction of the differences between M1 and M2+
607 (**Table 5**). Nevertheless, integrated assessments show that models allowing M by age
608 estimates achieve better fittings than single M1+ models (with $p < 0.056$ for the WSSQ and
609 $p < 0.000$ for the LLHR) (Figure 6). Therefore, even after consideration of this maximum level
610 of potential ageing errors, the significant increase pattern of natural mortality at age is still
611 supported by integrated assessments. In any case, M estimates will be conditioned by the
612 actual level of ageing errors affecting the observations.

613

614 Certainly, the results depend upon the assumption of the constant catchability of surveys
615 across ages, on which Z estimates rely (an assumption we have proved to be compatible with
616 the data). Sustaining this is not true would be difficult to understand, given the good spatial
617 coverage of the surveys, and would imply that the prevailing null hypothesis should be on the
618 assumption that M is equal across ages. Biologically, this is known not to be true (Vetter
619 1988), even though for simplification this has been the null hypothesis for the assessment of
620 the exploited range of ages of most of the long and short-lived fish resources. Although this
621 has already been questioned and revised for younger ages (Caddy 1991; Abella *et al.* 1997;
622 Gislason *et al.* 2010), it has not been sufficiently revised yet for the inclusion of senescence in
623 the older age classes. And, certainly for short-lived species, senescence should have been
624 presumed to be noticeable not too long after reaching maturity (Beverton 1963). By accepting
625 that the null hypothesis should be that senescence is present, then our analysis shows

626 consistency of the observations with the hypothesis, and we would rely more on the
627 observations of the age structures reported by surveys rather than on doubtful assumptions of
628 constant natural mortality across ages; and finally the assessment can become parsimonious
629 (as in our case with two surveys) in terms of demanding a lesser amount of parameters to
630 infer population size (i.e. lesser amount of catchability at age parameters in comparison to the
631 increased number of natural mortality by age).

632

633 A correct selection of the natural mortality serves to properly scale the assessments around
634 true population abundance values and this becomes particularly relevant in the context of
635 relative indexes of population abundance, and even more for short-lived species. In this paper
636 we have shown that that the overall natural mortality M_{1+} was somewhat below what had
637 been assumed so far, and furthermore, that natural mortality at ages 2+ is higher than at age 1,
638 in line with expectation of senescence. In achieving this conclusion, the continuous
639 monitoring of the population by two parallel and independent methods for many years,
640 including a period of fishing closure, has been essential, as it has provided sufficient contrast
641 for the analysis. The natural mortality issue should be revisited periodically when additional
642 years of survey observations and improvements in our base knowledge become available.
643 Relevant improvements may come from better understanding of survey catchability, or of the
644 accuracy of age determinations for this anchovy, besides, for instance, from monitoring
645 biological and biochemical markers of aging and reproductive stress or from further studies
646 on eco-trophic interactions.

647

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Figure 4: Fitted models for the Z by age (Z1 and Z2+) as a function of the relative catches between surveys, RCsurvey2 and RCJoint2 for the complete set of data (left graphs) and for the subset of data (which removes Z values with RC>0.8 and Years>2010) (right graphs). In all cases dashed lines correspond with age group 2+ and continuous lines with age 1. For the two slopes model the steeper lines correspond with the fitting of the Z estimates from the DEPM series and the flatter lines refer to the fitting of Z estimates from the acoustic series.

Figure 5: Response surfaces (total and partial contribution of the different auxiliary information) for the two objective functions, weighted sum of squares (WSSQ, left panels) and Log-Likelihood Ratios (LLHR, right panels) for a) a range of single natural mortality values (M1+), b), for a range of natural mortality at age 1 (M1), optimizing M2+, with a natural calendar year (January to December) and c) by age as before (case b) but with a calendar year from July to June.

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to June, with information about the MLE estimates for M1 and M2+ (black dot) with their joint 95% confidence region (grey area) and MLE for a single natural mortality common to all ages (M1+) and its 95% confidence limits (black square point and lines along the 1:1 dotted line) for a) no ageing error default case (upper graphs) and b) for an assumption of 5% ageing errors (see text for details).

Figure 7: Comparison of natural mortality estimates by age (M1 and M2+) for the different estimation methods: a) for cases with no ageing errors b) for cases with 5% ageing errors. A 1:1 dotted line is included to check compatibility with the typical assumption of a single natural mortality.

There is one Appendix:

Appendix A: Integrated assessment of the Bay of Biscay

1 Table 1: Matrix of age determination errors

2

3

True Age	Assigned age				Total
	0	1	2	3+	
0	1.00	0.00	0.00	0.00	1.00
1	0.00	0.95	0.05	0.00	1.00
2	0.00	0.04	0.95	0.01	1.00
3+	0.00	0.00	0.05	0.95	1.00

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8 Table 2: Mean Z estimates for Z1+, Z1 and Z2+ by fishing periods and surveys or jointly for the two surveys (pooled surveys), for the raw data (a-
 9 upper tables) and assuming a 5% ageing error (b- bottom tables). The fishery was closed between July 2005 (with only very small catches in 2006) and
 10 December 2009.

a) No Ageing Errors

Data Sources	DEPM Surveys			ACOUSTIC Surveys			Pooled Surveys		
Z Means by periods	Z1+	Z1	Z2+	Z1+	Z1	Z2+	Z1+	Z1	Z2+
N (complete data)	19	19	19	14	13	13	33	32	32
Complete Series	1.48	1.22	2.32	1.30	0.99	1.65	1.40	1.13	2.05
(1987-2012) CV	13%	19%	8%	14%	22%	11%	9%	14%	7%
Fishing Period	1.69	1.47	2.53	1.61	1.38	1.78	1.66	1.44	2.26
(1987-2004 & 2010-12) CV	12%	17%	7%	13%	11%	15%	9%	11%	7%
Closure Period	0.87	0.55	1.73	0.76	0.35	1.44	0.81	0.45	1.59
(2005-2009) CV	21%	53%	19%	17%	106%	14%	13%	50%	12%
Subset Closure Period	0.89	0.62	1.92	0.86	0.70	1.35	0.88	0.66	1.63
(2007-2009) CV	9%	7%	29%	10%	23%	26%	6%	11%	19%

b) 5% Ageing Errors

Data Sources	DEPM Surveys			ACOUSTIC Surveys			Pooled Surveys		
Z Means by periods	Z1+	Z1	Z2+	Z1+	Z1	Z2+	Z1+	Z1	Z2+
N (complete data)	19	19	19	14	13	13	33	32	32
Complete Series	1.79	1.64	2.17	1.56	1.24	1.47	1.69	1.48	1.89
(1987-2012) CV	12%	15%	8%	17%	21%	14%	9%	12%	7%
Fishing Period	2.06	1.95	2.36	1.95	1.68	1.53	2.02	1.85	2.05
(1987-2004 & 2010-12) CV	10%	13%	7%	17%	14%	20%	9%	10%	8%
Closure Period	1.03	0.78	1.66	0.87	0.53	1.38	0.95	0.65	1.52
(2005-2009) CV	18%	35%	20%	16%	76%	15%	12%	35%	13%
Subset Closure Period	1.05	0.85	1.88	0.98	0.92	1.27	1.01	0.88	1.58
(2007-2009) CV	18%	18%	30%	14%	20%	28%	10%	12%	21%

Table 3: Summary results from linear models on overall mortality (Z1+) and estimates of overall natural mortality (M1+) from the intercept of the linear models. a) Upper panel analysis for all data, b) bottom panel analysis for data with RC<0.8 and year<2011. Left two columns estimates by surveys, central three columns pooled surveys estimates by RC indicators, and final three columns pooled surveys estimates for cases assuming 5% ageing errors. Values in red and italics with an asterisk are statistically not significant (with p> 0.05).

CASE Z1+		Estimates by Surveys		Pooled Estimates			Pooled Estimates & 5% Ageing Errors		
RC estimator		RCsurvey2	RCsurvey2	RCsurvey2	RCsurvey2	RCJoint2	RCsurvey2	RCsurvey2	RCJoint2
SURVEY Series		DEPM	Acoustic	Pooled	Pooled	Pooled	Pooled	Pooled	Pooled
Linear model with		Single-Slope	Single-Slope	Two-Slopes	Single-Slope	Single-Slope	Two-Slopes	Single-Slope	Single-Slope
a) Complete set of Data \ N:		19	14	33	33	26	33	33	26
Intercept (= M1+)		1.136	0.954	1.052	1.152	0.885	1.137	1.301	1.001
	CV	26%	26%	19%	15%	20%	20%	15%	23%
RC slope coefficient		0.656*	2.380*	1.991*	0.694	1.633	3.107	1.048	2.188
	CV	69%	55%	62%	49%	33%	44%	36%	32%
Additive Slope component				-0.915*			-1.951*		
	CV			81%			65%		
Model P-Value		0.1636	0.095	0.0837	0.0496	0.0064	0.0119	0.0099	0.0043
R-Squared		11%	21%	15%	12%	27%	26%	20%	29%
b) Subset of Data \ N:		13	12	25	25	22	24	24	22
Intercept (= M1+)		0.762	0.884	0.826	0.920	0.781	0.936	1.078	0.941
	CV	45%	32%	26%	22%	22%	29%	23%	27%
RC slope coefficient		1.787	2.583*	2.804	1.651	1.831	3.829	2.103	2.309
	CV	41%	54%	44%	33%	27%	38%	34%	31%
Additive Slope component				-1.130*			-1.731*		
	CV			96%			75%		
Model P-Value		0.0333	0.0927	0.015	0.006	0.0013	0.014	0.0079	0.0039
R-Squared		35%	26%	32%	25%	41%	34%	28%	35%

Table 4: Summary results from linear models on estimates of Z by age (from Age 1 to 2 and from Age 2+ to 3+), with estimates of M1 and M2+ from the intercepts of the fitted models. a) Upper panel analysis for all data, b) bottom panel analysis for data with RC<0.8 and year<2011. Left two columns estimates by surveys, central three columns pooled surveys estimates by RC indicators, and final three columns pooled surveys estimates for cases assuming 5% ageing errors. Values in red and italics with an asterisk are statistically not significant (with $p > 0.05$).

CASE Z by ages RC estimator SURVEY Series Linear model with	Estimates by Surveys		Pooled Estimates			Pooled Estimates & 5% Ageing Errors		
	RCsurvey2	RCsurvey2	RCsurvey2	RCsurvey2	RCJoint2	RCsurvey2	RCsurvey2	RCJoint2
	DEPM	Acoustic	POOLED	POOLED	POOLED	POOLED	POOLED	POOLED
	Single-Slope	Single-Slope	Two-Slopes	Single-Slope	Single-Slope	Two-Slopes	Single-Slope	Single-Slope
a) Complete set of Data \ N:	38	26	64	64	50	64	64	50
Intercept1 (= M1)	0.951	0.933	0.940	0.900	0.822	1.373	1.319	1.113
CV	23%	26%	17%	17%	23%	12%	12%	19%
OLD (addition for M2+)	0.999	0.644	0.854	0.839	0.908	<i>0.339*</i>	<i>0.313*</i>	<i>0.448*</i>
CV	26%	46%	23%	23%	25%	62%	67%	56%
Intercept2 (= M2+)	1.951	1.577	1.794	1.738	1.730	1.713	1.631	1.561
CV	18%	24%	14%	14%	17%	16%	16%	21%
RC slope coefficient	0.527	<i>0.412*</i>	<i>-0.009*</i>	0.634	<i>0.818*</i>	<i>-0.474*</i>	0.418	<i>0.878*</i>
CV	45%	234%	9593%	31%	64%	172%	33%	62%
Additive Slope component			<i>0.621*</i>			<i>0.873*</i>		
CV			128%			90%		
Model P-Value	0.0002	0.0875	0.1942	0.0000	0.0002	0.0045	0.0026	0.048
R-Squared	39%	19%	15%	35%	30%	15%	18%	12%
b) Subset of Data \ N:	23	22	45	45	40	45	45	40
Intercept1 (= M1)	0.682	0.861	0.780	0.742	0.582	1.091	1.058	0.883
CV	44%	32%	25%	26%	35%	20%	20%	26%
OLD (addition for M2+)	0.754	<i>0.610*</i>	0.684	0.662	0.997	<i>0.261*</i>	<i>0.221*</i>	0.546
CV	41%	54%	32%	33%	23%	93%	110%	48%
Intercept2 (= M2+)	1.436	1.471	1.464	1.403	1.580	1.352	1.279	1.429

RC slope coefficient	CV	30%	29%	20%	21%	19%	24%	25%	24%
		1.748	0.629*	0.748*	1.535	1.710	0.507*	1.413	1.871
Additive Slope component	CV	36%	163%	116%	32%	35%	171%	38%	36%
				0.878*			1.079*		
Model	CV			91%			76%		
	P-Value	0.0044	0.1474	0.1474	0.0002	0.0001	0.0306	0.0115	0.0069
	R-Squared	42%	18%	18%	33%	41%	14%	16%	24%

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24 Table 5: Summary results of the integrated assessments for a) No ageing errors and b) 5%
 25 ageing errors.

	a) No ageing errors		b) 5% ageing errors	
Single M	WSSQ	LLHR	WSSQ	LLHR
Mean M1+	1.148	1.000	1.188	1.044
CV (aprox)	5.4%	4.3%	6%	4%
Objective Function	42.3093	308.5502	50.1018	317.7327
Total LogLikelihood	-88.1095	-490.0735	-126.5522	-491.5557
AIC	362.2191	1166.1470	439.1043	1169.1115
AICc	419.3563	1223.2842	496.2416	1226.2487
M. by ages	M. (January to December)		M. (January to December)	
	WSSQ	LLHR	WSSQ	LLHR
Mean M1	0.172	0.262	0.733	0.582
CV (aprox)	88%	44%	36%	21%
Mean M2+	1.467	1.376	1.326	1.263
CV (aprox)	7.5%	6.1%	9%	6%
Objective Function	38.1907	270.0725	49.1966	64.0470
Total LogLikelihood	-73.1320	-451.5218	-123.5479	-478.6685
AIC	334.2641	1091.0436	435.0958	1145.3369
AICc	392.8215	1149.6009	493.6532	1203.8943
LogLikelihood ratio vs single M	14.9775	38.5517	3.0043	12.8873
Probability of the Ratio	0.0000	0.0000	0.0496	0.0000
M. by ages	M. (July to June)		M. (July to June)	
	WSSQ	LLHR	WSSQ	LLHR
Mean M1	0.700	0.712	0.979	0.853
CV (aprox)	19%	9%	15%	8%
Mean M2+	1.518	1.429	1.351	1.299
CV (aprox)	8.0%	6.4%	9%	7%
Objective Function	38.5194	271.5586	49.2783	305.014
Total LogLikelihood	-74.6555	-452.8735	-123.7316	-478.888
AIC	337.3109	1093.7471	435.4632	1145.7757
AICc	395.8683	1152.3045	494.0206	1204.3331
LogLikelihood ratio vs single M	13.4541	37.1999	2.8205	12.6679
Probability of the Ratio	0.0000	0.0000	0.0596	0.0000

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31 Figure 1: Series of Z estimates by surveys for a) overall ages Z1+ and b) by age groups (Z1
32 and Z2+).

Figure 2: Box-and-whisker plot for Z by age (pooling survey estimates), for a) Overall Z (Z1+), b) Z at age 1 (Z1); c) Z at age 2 and older (Z2+).

Fishing legend: N= No Fishing (Closure period). Y= Fishing period.

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40

Complete set of data

Subset of data

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42

43

Figure 3: Fitted models (Model B1) of total Z estimates (Z1+) as a function of the relative catches between surveys, RCSurvey2 (two and single slope fitting – upper and medium panels) and RcJoint2 (bottom panels), for the complete set of data (left graphs) and for the subset of data (which removes Z values with RC>0.8 and Years>2010) (right graphs).

48 Figure 4

Figure 4: Fitted models for the Z by age ($Z1$ and $Z2+$) as a function of the relative catches between surveys, $RCSurvey2$ and $RCJoint2$ for the complete set of data (left graphs) and for the subset of data (which removes Z values with $RC > 0.8$ and $Years > 2010$) (right graphs). In all cases dashed lines correspond with age group 2+ and continuous lines with age 1. For the two slopes model the steeper lines correspond with the fitting of the Z estimates from the DEPM series and the flatter lines refer to the fitting of Z estimates from the acoustic series.

Figure 5

WSSQ minimization LLHR minimization

a) M1+

b) M1 & M2+ (Jan-Dec)

c) M1 & M2+ (July-June)

Figure 5: Response surfaces (total and partial contribution of the different auxiliary information) for the two objective functions, weighted sum of squares (WSSQ, left panels) and Log-Likelihood Ratios (LLHR, right panels) for a) a range of single natural mortality

73 values ($M1+$), b), for a range of natural mortality at age 1 ($M1$), optimizing $M2+$, with a
74 natural calendar year (January to December) and c) by age as before (case b) but with a
75 calendar year from July to June.

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Figure 6

a) No Errors

WSSQ minimization LLHR minimization

b) 5% Ageing Errors

WSSQ minimization LLHR minimization

Figure 6: Joint likelihood profile contour plots for natural mortality estimates by age (M1 and M2+), deduced from the two integrated assessments based either on weighted sum of squares (WSSQ, left graphs) or on log-likelihood ratios (LLHR right graphs), both based on a calendar

89 year going from July to June, with information about the MLE estimates for M1 and M2+
90 (black dot) with their joint 95% confidence region (grey area) and MLE for a single natural
91 mortality common to all ages (M1+) and its 95% confidence limits (black square point and
92 lines along the 1:1 dotted line) for a) no ageing error default case (upper graphs) and b) for an
93 assumption of 5% ageing errors (see text for details).

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Figure 7:

a) No ageing errors

b) 5% Ageing Errors

Figure 7: Comparison of natural mortality estimates by age (M1 and M2+) for the different estimation methods: a) for cases with no ageing errors b) for cases with 5% ageing errors. A 1:1 dotted line is included to check compatibility with the typical assumption of a single natural mortality

Appendix A to Uriarte et al. submission 16/02/2015 to CJFAS (29/09/2015)

Integrated assessment of the Bay of Biscay:

We applied a Seasonal Integrated Catch at Age analysis (SICA) on a six-monthly basis, fitting different selectivity patterns to the international fleet operating during each half of the year and tuning the population to the abundance indexes available (as used by ICES 2013): the two spring surveys (Acoustic and DEPM index) and a recruitment acoustic survey on juveniles in autumn. Age structure of both catches and spring surveys go up to age group 3+ (grouping ages 3 and older). The survey on juveniles produces a single index at age 0 in the autumn of any year Y which is entered as an indicator of the strength of the recruits at age 1 in January of year Y+1.

Biomass indexes are dealt with as relative indexes proportional to abundance for which no additional catchability is estimated. In addition, in SICA, a Qflat catchability model is implemented for the purposes of this analysis (i.e. forcing catchability at age of the surveys to be equal for all ages).

We have fitted SICA with the Qflat catchability model for the two surveys allowing to optimize for M1+ (a single natural mortality for all ages) or for M1 and M2+ (i.e. one M for age 1 and another for the plus group of ages 2 and older); the latter is essayed in order to find out what natural mortality pattern optimizes the fitting. In practice, as the model is implemented in Excel, a systematic optimization procedure across a range of M1+ or M1 (including the optimization of M2+) was made. Initially a range of M between 0.1 and 1.7, in steps of 0.1, was covered. Later, a

26 systematic 2D mapping around the optimum was carried out in stopes of 0.05. The
27 results show the values of the objective function optimized for the selected range of
28 M1+ or M1 values (the latter also optimized for M2+) in 1D or 2D as required.

29

30 **Operating Model**

31 Population and fishing mortality at age: We applied the typical population survival
32 exponential model (Ricker 1975) with catches following the Baranov (1918)
33 equation, subject to a separable model of fishing mortality by age, year and seasonal
34 (half-year) fishery of the form:

35

36
$$F_{a,y,p} = F_{ref,y,p} \cdot S_{a,p}$$
 Eq A.B.1

37

38 Where $F_{ref,y,p}$ is the fishing mortality in year y and half-year fishery p for the age of
39 reference (ref), which in this study is age 2 ($F_{ref,y,p} = F_{2,y,p}$).

40 $S_{a,p}$ is the selectivity for each age typical of every half-year fishery and relative to the
41 age of reference (age 2), which is fixed at 1 (*i.e.* selectivity value of $S_{2,p}=1$).

42 Catches are modeled up to age 3+ (older ages are negligible) on a half-yearly basis.

43

44 Natural Mortality model: Natural mortality can be set common for all years and
45 ages (by setting a constant M1+) or varying between ages 1 and 2+ by a common
46 factor, as follows:

47
$$M_{2+} = M_1 \cdot Mfactor_{2+}$$
 Eq A.B.2

48 $Mfactor_{2+}$, if included, is estimated and kept constant across years.

49 We checked the sensitivity of applying this factor to age 2 from the beginning of the
 50 year or from July only.

51

52 The modeled average population during the spring period is tuned to the Acoustic
 53 and DEPM spawning biomass and population at age estimates. The tuning indices
 54 were used as relative (i.e. proportional to abundance by a catchability parameter Q).

55

56 Parameters: For an assessment covering the period 1987-2012 (including the first half
 57 of 2013), we would have the following parameters for the 26 years (Y) of data: 4 for
 58 the numbers at ages in the first year 1987 (ages 1-4, because the 3+ plus groups were
 59 modeled as the sum of two age groups --3 and 4+), 26 recruits at age 0 ($N_{0,y}$),
 60 $2*26+1$ for the fishing mortalities at the age of reference (age 2) (one per half year:
 61 $F_{2,y,1}$ and $F_{2,y,2}$ and $F_{2,2013,1}$), 5 selectivities at age (the ages on a half-yearly basis: $S_{1,1}$
 62 $/ S_{3,1} / S_{0,2} / S_{1,2} / S_{3,2}$), 4 Catchability parameters (Q_{Ac} , Q_{DEPM} , and Q & $Power$ for the
 63 Juvenile index), and a minimum of 1 natural mortality (M_{1+}) = $4+26+53+5+4+1=93$
 64 parameters (or 94 if M_1 and M_{2+} were estimated instead of single M_{1+}).

65

66 Objective function: two objective functions were defined, one responding to the case
 67 of assuming log-normal errors in all tuning data, which was based on a sum of
 68 squared log residuals (similar to the Integrated Catch at age Analysis Patterson and
 69 Melvin 1996), and the other for the case where age disaggregated observations (of
 70 catches or from the spring survey abundance indexes) are split in a biomass
 71 component (assuming log-normal error) and in percentages at age (assuming
 72 multinomial errors). In the latter, the objective function was based on the log-
 73 likelihood ratios (similar to the objective function in Stock Synthesis Model SS3 -

74 Methot and Wetzel 2013). Parallel to the minimization of the objective function, the
75 log-likelihoods and the Akaike information criterion (AIC) were estimated for
76 comparison purposes (see below).

77

78 For the analysis assuming log-normal errors of all data catchability of surveys was
79 estimated common (equal) for all ages (flat catchability at age) but independently for
80 each survey, so that a single common catchability by survey is estimated. Both the
81 population in numbers at age and biomass (SSB) indices are used for the fitting.
82 However, the fitting to SSB indices do not require a catchability parameter, because
83 only the population at age estimates derived from the surveys are used to fit the
84 catchability by survey. Modeled SSB as estimated for a survey is just the product of
85 the modeled numbers at age estimates for the survey times the weights at age in the
86 population. In this way, consistency is assured between the catchability at age
87 estimates and SSB estimates for the surveys. In addition, the residual sum of squares
88 between modeled and observed biomass by the surveys contributes to the total fitting
89 even in the years when no age estimates from the surveys were available (as in 1994
90 and 1998 for the Acoustics or in 1996, 1999 & 2000 for the DEPM). In turn, this
91 implies that the years when only a biomass index is provided by a survey do not
92 contribute to the fitting of the catchabilities at age. As such, 14 out of 16 acoustic
93 estimates are used for tuning the catchabilities at age (because the other 2 cruises
94 have no age index). For this same reason, only 19 out of 22 cruises tune the
95 catchability at age for the DEPM.

96

The objective function is a sum of squared log residuals (SSQ) defined for the tuning survey indices of biomass and population at age estimates and for the catches at age and catches in tonnes of the different seasonal fisheries defined above.

100

$$WSSQTotal = SSQCapt_{age} + SSQCapt_{weight} + SSQSurveys_{age} + SSQSurveys_{weight} \quad \text{Eq A.B.3}$$

The SSQ of the catches in tonnes ($SSQCapt_{weight}$) are estimated as:

$$\sum_{1987}^{2013} \sum_{p=1}^2 \lambda_{y,p} \cdot \left(\ln(C_{y,p} / \hat{C}_{y,p}) \right)^2 \quad \text{Eq A.B.4}$$

Where the summation reaches the first half of year 2013 and suffix p refers to the seasonal fishery (i.e. the first or second half of the year). The expected catches in weight are just based on the SOPs (sum of products) of the modeled catches at age and their observed mean weights.

108

In parallel the residuals to the catches at age (in numbers) ($SSQCapt_{age}$) are estimated as:

$$\sum_{ages} \sum_{1987}^{2012} \sum_{p=1}^2 \lambda_{a,y,p} \cdot \left(\ln(C_{a,y,p} / \hat{C}_{a,y,p}) \right)^2 \quad \text{Eq A.B.5}$$

Where modeled catches ($\hat{C}_{a,y,p}$) are simply obtained from the Baranov equation over the half-year period.

114

In addition, for DEPM and Acoustics population at age the estimates, the

$SSQSurveys_{age}$ are

$$SSQSurveys_{age} = \sum_{ages} \sum_{year}^{2013} \sum_s^{surveys} \lambda_{a,y,s} \cdot \left(\ln(U_{a,y,s} / \hat{U}_{a,y,s}) \right)^2 \quad \text{Eq A.B.6}$$

Where the modeled index is estimated as:

$$\hat{U}_{a,y,s} = Q_s \cdot \hat{N}_{a,y,s} = Q_s \cdot \frac{\hat{N}_{a,y,p=1} \cdot e^{-\alpha_v \cdot Z_{a,y,p=1}}}{(\alpha_s - \omega_s) \cdot Z_{a,y,p=1}} \cdot (1 - e^{-(\alpha - \omega) \cdot Z_{a,y,p=1}}) \quad \text{Eq A.B.7}$$

Where, suffix *s* refers to the Acoustic or DEPM surveys, suffix *p=1* refers to the first half of the year period; and *a* and *y* for age and year. *Z* is total mortality and $\hat{N}_{a,y,s}$ the modeled population in numbers at survey time. And $\alpha_s - \omega_s$ are the starting and ending time of the surveys (as fractions of the year). Notice that the survey catchability Q_s is common for all ages. Suffix *a* reaches for acoustics age 2+ until 1999 and subsequently to age 3+ as for the whole DEPM series.

And for the aggregate indices of acoustic or DEPM the $SSQ_{\text{Surveys}_{\text{weight}}}$ equals:

$$\sum_{\text{year}} \sum_v^{2013 \text{ surveys}} \lambda_{y,s} \cdot (Ln(U_{y,s} / \hat{U}_{y,s}))^2 \quad \text{Eq A.B.8}$$

With the modeled index estimated simply as the sum of products of the estimated index by age by its observed mean weight in the population, as: 8

$$\hat{U}_{y,s} = \sum_{\text{ages}} \hat{U}_{a,y,s} \cdot W'_{a,y,s} \quad \text{Eq A.B.9}$$

where no additional catchability parameters appear.

Weighting factors: tuning data and fishery catches at age can be weighted (with the lambda factors, λ): Fitting the catches (in tonnes) of the two halves of the year received equal weighting factors (lambda = 1). Weighting factors for the catches at ages 1 to 3+ were all set equal to 1, but for age 0 it was set equal to 0.01 because these catches are not considered to be actually separable (since they are taken independently of the other ages and are very noisy). Weighting factors for the DEPM and acoustics were set equal to 0.667 as used in ICA; this is made to

discount for correlation across ages in the survey estimates as in the standard ICA implementation. The survey biomass estimates by the model were fitted directly without any differential weighting ($\lambda=1$), therefore acting as a penalty when the total sum of products of the modeled age structured values diverges from the biomass observations.

We carried out a sensitivity analysis to the weighting factors applied to the indexes at age from surveys for which all $\lambda_{a,y,s}$ were set at 1 (not shown in the paper). Such alternative weighting result in negligible changes of the natural mortality estimates, with changes smaller than 3% both in the estimates as in the range of the 95% confidence intervals.

The Log likelihood estimates (LLH) of the fitting to the (o) auxiliary series of (n) observations, each subject to log-normal errors, was simply the sum over the observation series of their respective $LLH_{-Observations}$:

$$LLH_{-Observations} = - \sum_{years_ages} \sum \lambda_{y,a} \cdot \left(\ln(O_{y,a} / \hat{O}_{y,a}) \right)^2 / (2 \cdot \sigma_o^2) - n \cdot \ln(\sigma_o \sqrt{2 \cdot \pi})$$

Eq A.B.10

Whereby the log standard error σ_o by series was taken from the square root of the weighted mean squared residuals for each auxiliary observation series.

For the analysis assuming multinomial errors of the age

All assumptions for the modeling were the same as for the sum of squared log errors, except that for the age structure information from surveys and catches, which are entered as percentages at age (in numbers), subject to multinomial errors. Model fitting is achieved by maximization of the log-likelihood (using log-likelihood ratios).

166

167 The objective function is a sum of log-likelihood ratios defined for the tuning
 168 survey indices of biomass and population at age estimates and for the catches at age
 169 and catches in tons of the different seasonal fisheries defined above.

$$170 \quad L_Total = L_Capt_{age} + L_Capt_{weight} + L_Surveys_{age} + L_Surveys_{weight} \quad \text{Eq A.B.11}$$

171

172 Where log-likelihood ratios for the catches in tonnes ($LCapt_{weight}$):

$$173 \quad L_Capt_{weight} = \sum_{1987}^{2013} \sum_{p=1}^2 \lambda_{a,y,p} \cdot \left(\ln(C_{y,p} / \hat{C}_{y,p}) \right)^2 / (2 * CVc^2) \quad \text{Eq A.B.12}$$

174 Which extends the summation up to the first half of year 2013, with modeled
 175 catches in weight based only on the SOPs (sum of products) of modeled catches.
 176 Suffix p refers to the first or the second half of the fisheries year. The assumed CVc
 177 (equal to log-normal error σ) was 0.1 (i.e. consistent with our assumption of rather
 178 precise catch reporting).

179 The log-likelihood ratios for the observed proportions at age in the catches in
 180 numbers ($LCapt_{age}$) are:

$$181 \quad L_Capt_{age} = \sum_{ages} \sum_{year} \sum_{p=1}^2 x_{y,p} \cdot p_{a,y,p} \cdot \ln(p_{a,y,p} / \hat{p}_{a,y,p}) \quad \text{Eq A.B.13}$$

182 which extends the summation until the first half of 2013. Suffix p refers to the first
 183 or second half of the fisheries year. The modeled proportion of catches by ages ($\hat{p}_{a,y,p}$) is directly deduced from the ratio of catches at age over the total catch in
 184 numbers. The equivalent random sampling size ($x_{y,p}$) of available ages was
 185 assumed to be from 100 individuals of all the series of half-year catches (similar to
 186 sampling levels adopted by default for the surveys).

For the catches at age 0, as they were considered not separable, a likelihood ratio similar to equation A.B.12 above was applied to the observed over expected catches at age 0, assuming a CV_{age0} of 0.25.

191

Similarly, the log-likelihood ratios for the Biomass indexes in tonnes (

$L_Surveys_{weight}$)

$$L_Surveys_{weight} = \sum_{1987}^{2013} \sum_s \lambda_{y,s} \cdot \left(\ln(U_{y,s} / \hat{U}_{y,s}) \right)^2 / (2 * CV_s^2) \quad \text{Eq A.B.14}$$

with the modeled biomass index ($\hat{U}_{y,s}$) is estimated as the sum of products of modeled populations at age times the global (common) catchability across ages of the surveys (given our Qflat model) and their mean weights at age (

$\sum_{ages} Q_s \cdot \hat{N}_{a,y,s} \cdot W'_{a,y,s}$). Suffix s is the survey index (referring to either the Acoustic

or the DEPM). The assumed CV_s (equal to log-normal error) was 0.25 for both

surveys.

201

In addition, the likelihood ratios for the observed proportions at age in the survey estimates ($p_{a,y,s}$) is estimated as

$$L_Surveys_{age} = \sum_{ages} \sum_{year} \sum_s x_{y,s} \cdot p_{a,y,s} \cdot \ln(p_{a,y,s} / \hat{p}_{a,y,s}) \quad \text{Eq A.B.15}$$

205

And the modeled proportion at age estimate of the survey ($\hat{p}_{a,y,s}$) derives from the population at age indexes ($\hat{U}_{a,y,s}$ of equation A.B.7) and is estimated as the ratio of the modeled population at age ($\hat{N}_{a,y,s}$) and the total modeled population (in numbers during survey time).

210

$$211 \quad \hat{p}_{a,y,s} = \frac{\hat{U}_{a,y,s}}{\sum_{ages} \hat{U}_{a,y,s}} = \frac{Q_s \cdot \hat{N}_{a,y,s}}{\sum_{ages} Q_s \cdot \hat{N}_{a,y,s}} = \frac{\hat{N}_{a,y,s}}{\sum_{ages} \hat{N}_{a,y,s}} \quad \text{Eq A.B.16}$$

212

213 Where suffix s is the survey index (to refer either the Acoustic or the DEPM), a and
 214 y stand for age and year respectively.

215 The equivalent random sampling size ($x_{y,s}$) of available ages was assumed to be
 216 100 individuals for the acoustics series whilst ad hoc yearly sizes were estimated for
 217 the DEPM which matched as closely as possible with the yearly reported CVs of the
 218 proportions at ages from this survey series, as currently used for the ICES
 219 assessment (ICES 2014). The ad hoc equivalent sizes for the DEPM ranged from 40
 220 to 500, with a mean of about 140 individuals. A sensitivity analysis was carried out
 221 (not shown) to check the effect of reducing the equivalent sampling size to a
 222 maximum of 66 individuals for all input data series of percentages at age, finding
 223 out only relatively minor effects on the estimates of the natural mortality (by about
 224 2%), though certainly the range of the confidence intervals was increased at
 225 sampling size 66 (by about 20-25%).

226

227 No differential weighting factors for the components of the objective function were
 228 applied for this second modeling of the observations, except for the weighting
 229 factors of the catches at age 0 which were set equal to 0.01 since these catches are
 230 not considered to be separable (this is because they are taken independently of the
 231 other ages and are very noisy).

232 The log-likelihood estimates (LLH) of the fitting to the (o) auxiliary series of (n)
 233 observations each was simply the sum over the observation series (o) of every

234 $LLH_{\text{Observations}}$, which corresponded to either equation A.B.10 for those subject to
 235 log-normal errors (catches in tons, surveyed estimates of total population in biomass
 236 and the recruitment index) or to the following expression for the age disaggregated
 237 observations subject to multinomial errors (catches and populations at age):

$$238 \quad LLH_{\text{Observations}} = \sum_{\text{years}} \ln \left(\frac{x_{y,t}}{x_{y,1}! \cdot x_{y,2}! \cdot x_{y,3+}!} \cdot \hat{p}_{y,1}^{x_{y,1}} \cdot \hat{p}_{y,2}^{x_{y,2}} \cdot \hat{p}_{y,3+}^{x_{y,3+}} \right) \quad \text{Eq A.B.17}$$

239 Whereby the $x_{y,t}$ corresponds to the assumed equivalent random sampling size in
 240 year y for the auxiliary age disaggregated observation, as described above, and the
 241 $x_{y,a}$ to the respective numbers at age as deduced from the observed percentages at
 242 age (as $x_{y,a} = x_{y,t} \cdot p_{y,a}$, rounded) and finally the $\hat{p}_{y,a}$ correspond to the expected
 243 percentages at age according to the modeling, as described above.