Assessing natural mortality of Bay of Biscay anchovy from survey population and biomass estimates

Uriarte Andres [1, *], Ibaibarriaga Leire [2], Pawlowski Lionel [3], Masse Jacques [4], Petitgas Pierre [4], Santos Maria [1], Skagen Dankert [5]

[1] AZTI Tecnalia, Div Marine Res, Herrera Kaia Portualdea Z-G, Pasaia 20110, Spain.
[2] AZTI Tecnalia, Div Marine Res, Txatxarramendi Ugartea Z-G, Sukarrieta 48395, Spain.
[3] IFREMER, Lab Sci & Technol Halieut, 8 Rue Francois Toullec, F-56100 Lorient, France.
[4] IFREMER, POB 21105, F-44311 Nantes 03, France.
[5] Fjellveien 96, N-5019 Bergen, Norway.

* Corresponding author : Andress Uriarte, email address : auriarte@azti.es

Abstract :

The closure of the anchovy (*Engraulis encrasicolus*) fishery in the Bay of Biscay between 2005 and 2010 because of low biomass levels provided an opportunity to estimate natural mortality using data from egg (daily egg production method, 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 ($M2+$) is markedly higher than at age 1 ($M1$), which indicates senescent mortality, a possibility suggested a long time ago for this type of short-lived species.

Résumé :

La fermeture de la pêche de l'anchois (Engraulis encrasicolus) 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 (M2+) est remarquablement plus forte qu'à l'âge 1 (M1) ce qui suppose un signe de mortalité sénescente, une possibilité qui a déjà été évoquée il y a longtemps pour ce type d'espèce à vie courte.

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; Jørgensen 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; Jørgensen 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 1989; Charnov *et al.* 2001). Several biochemical mechanisms have been proposed to explain the progressive deterioration of the physiological condition of organisms over time associated

69   with senescence, such as the mutation accumulation theory or the antagonistic pleiotropy

70   theory (see reviews and discussions in Woodhead 1998; Williams *et al.* 2006; Golubev 2009).

71   Increasing mortality associated with senescence occurs at older ages (Vetter 1988; Woodhead

72   1998; Reznick *et al.* 2002; Gislason *et al.* 2010), and this is presumed to be particularly

73   noticeable in short-lived clupeoids (Beverton 1963). Measurements of senescent mortality, as

74   part of natural mortality, are difficult to obtain in the wild due to the many errors affecting the

75   observation of populations (Quinn and Deriso 1999; Gislason *et al.* 2010). Nevertheless,

76   various fish senescence patterns have been reported, ranging from the abrupt senescence of

77   salmon and eels (Woodhead 1998) or of some gobies (Caputo *et al.* 2002) to the gradual

78   senescence of guppies (Reznick *et al.* 2006), *Nothobranchius furzeri* (Terzibasi 2007),

79   gadoids (Sparholt *et al.* 2002; Nielsen *et al.* 2012) or herring (Tanasichuk 2000; Beverton *et*

80   *al.* 2004), and to the very slow or even negligible senescence of rockfish and carps (Reznick

81   *et al.* 2002).

82

83   The Bay of Biscay anchovy (*Engraulis encrasicolus* L.) is a fast growing and short-lived

84   species, fully mature at age 1, and rarely exceeding its third year of life (Uriarte *et al.* 1996;

85   Petitgas *et al.* 2010). In this region, anchovy is prey, along with other small pelagic fish, for

86   piscivorous species such as hake, megrim, sea bass, tunnidae or cetaceans, among others

87   (Preciado *et al.* 2008; Goñi *et al.* 2011; Lassalle *et al.* 2011; López-López *et al.* 2012). The

88   adult anchovy population is monitored yearly by two independent research surveys: an

89   acoustic survey (Massé 1996; Massé *et al.* in press) and an egg survey applying the Daily Egg

90   Production Method - DEPM (Somarakis *et al.* 1994; Motos *et al.* 2005; Santos *et al.* 2011, in

91   press). Both surveys provide estimates of biomass and population numbers at age, which are

92   included in the assessment of this stock carried out by ICES (International Council for the

93   Exploration of the Sea). A Bayesian two-stage biomass model (Ibaibarriaga *et al.* 2008) is

94   used for this assessment. Until 2004, ICA (Integrated Catch at age Analysis, Patterson and

95   Melvin 1996) was used (ICES 2005). Until 2013, natural mortality rate has been assumed to

96   be constant at 1.2 per year for all ages. This value was inferred in the nineties from direct

97   DEPM estimates of the population at age, assuming that they were absolute and unbiased

98   (Uriarte *et al.* 1996; Prouzet *et al.* 1999). While the Bayesian model presumes constant

99   catchability across ages and surveys, ICA calculated the catchability at age which was 50%

100   higher for age 2 than for ages 1 or 3 (ICES 2005) in both surveys. This was not regarded as a

101   realistic outcome, taking into account the standard designs of both the DEPM and acoustic

102   surveys, which included non-selective fishing gears for adults (capable of catching sizes well

103   below minimum anchovy sizes in spring), and the sufficient spatial coverage of anchovy

104   distribution (ICES 2013). Certainly, an alternative explanation of the findings could be that

105   natural mortality is not constant over age.

106

107   Due to recruitment failures since 2001 and subsequent low biomass estimates (ICES 2013),

108   the anchovy fishery in the Bay of Biscay was closed between 2005 and 2010. However, since

109   scientific surveys were still ongoing during its closure, they provided a unique opportunity to

110   estimate the actual natural mortality rate and possible patterns in natural mortality at age.

111   Likewise, this closure allowed comparisons to be made between total mortality rates during

112   the closed period and those in the former period of exploitation, in order to get natural and

113   fishing mortality estimates under the assumption that no major changes in M occurred

114   between both periods (Gulland 1983; Vetter 1988; Cook 1994; Sinclair 2001).

115

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

138 Estimates of population numbers at age are available from the acoustic (PELGAS –Ifremer-

139 Massé *et al.* 1996, in press) and DEPM (BIOMAN–AZTI- Somarakis *et al.* 1994; Motos *et al.*

140 2005; Santos *et al.* in press) surveys carried out yearly in May since 1987 and 1989,

141 respectively (ICES 2013). DEPM surveys since 1987 and acoustic surveys since 2000 have

142 reported population at ages 1, 2 and 3+ (with 3+ referring to fish of age 3 and older), while

143 earlier acoustic estimates have reported total biomass and, only occasionally, population

144 numbers at age 1 and 2+ (in 1989, 1991, 1992 and 1997).

145 In addition, since 2003, an autumn survey has been carried out to provide an acoustic index of

146 juvenile anchovy abundance (Boyra *et al.* 2013). This was used as auxiliary information on

147 the level of recruitment at age 0 in the integrated assessment.

148

149 **2.2. Direct total (Z) and natural (M) mortality estimates.**

150 In a cohort of N fishes at age a in year y (N_{ay}) subject to an annual mortality rate Z, the

151 survivors into the next year will be $N_{a+1,y+1} = N_{a,y}e^{-Z_{a,y}}$.

152 Let $U_{a,y,s}$ denote the number of individuals at age a in year y estimated from survey s.

153 Provided this index is proportional to the true population abundance (N) by a catchability

154 coefficient (Q), and subject to a log-normal observation error common to all ages ($U_{a,y,s} =$

155 $Q_{a,s}N_{a,y}e^{\varepsilon's,y}$), then the log of the ratio of successive age classes estimates in consecutive

156 years is an estimate of the total mortality at age a in year y from survey s, $Z_{a,y,s}$ modified by

157 the change in catchability:

158 $$\hat{Z}_{a,y,s} = \ln\left[\frac{U_{a,y,s}}{U_{a+1,y+1,s}}\right] = \ln\left[\frac{N_{a,y} \cdot Q_{a,s} \cdot \exp(v'_{s,y})}{N_{a+1,y+1} \cdot Q_{a+1,s} \cdot \exp(v'_{s,y+1})}\right] = Z_{a,y} + \ln\left[\frac{Q_{a,s}}{Q_{a+1,s}}\right] + v_{s,y}$$

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

160 mortality components:

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

162 Three Z estimates are derived: Z1+, from ages 1+ to 2+; Z1, from age 1 to 2; and Z2+, from

163 ages 2+ to 3+. Notice that Z1+ will generally be closer to the Z of the most abundant age

164 classes (in this case, age 1). Since surveys are carried out at spawning time in May, Z

165 estimates refer to mortality rates from May to May. These estimates rely on two assumptions:

166 1) catchability is similar over age, and 2) survey observation errors follow log-normal

167 distribution and are of similar average magnitude in both surveys.

168 Consistency of the Z estimates by survey depending on fishing or closure periods was tested

169 by analysis of variance. Year, survey type (DEPM or acoustic), age (1 or 2+) and fishing

170 period (closed or open fishery) were taken as factor variables, under the terms **Year** and

171 **Survey** and **Old** and **Fishing,** respectively**.**

172

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

174 ages

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

176 **Old** is in brackets because it only applies in the joint analysis of *Z1* and *Z2+*. As the year

177 factor will cover the inter-annual variability in Z due to either natural (ecological) or fishing

178 causes, the former analysis should serve to assess whether or not the Z estimates provided by

179 the two surveys are consistent. This was checked by testing the statistical significance of the

180 **Survey** factor and, for the analysis by age, of the **Survey * Old** first order interaction.

8

181

182   Next, we tested the effect of closure on the overall and age-dependent Z values, which during

183   the closure period, will be our direct estimate of the natural mortality rate (M):

184    $$\hat{Z}_{a,y,s} = Fishing_s + Survey_s + [Old] + Interactions + v$$ (Model A2, Equation 3)

185   As before, **Old** only applies when analyzing Z_1 and Z_{2+} together, but not when dealing with

186    $Z_{1+.}$ Interactions are the potential first and second order interactions of the former variables,

187   which were initially checked. Finally, v is assumed to be a normal random variable with

188   constant variance common to all ages, years and surveys.

189

190   **2.2 Natural mortality estimates from linear models**

191

192   In order to make use of the whole dataset for the estimation of M through a linear model, an

193   indicator of the fishing intensity for each year was obtained from the ratio of the catches

194   between surveys and the mean abundance of the cohort between surveys. This follows from

195   the catch equation:

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

197   where the coefficient of proportionality of the Relative Catches over survey estimates (*RC*) to

198   *F* equals the catchability coefficient of the surveys (assumed constant across ages) (Q_s). If

199   RC can be estimated then it can be used to calculate *M* from Equation 1, as the intercept of the

200   linear model. However, the problem with this approach is that the fitted *Z* will appear in the

201 independent covariate (*RC*). In order to avoid this, we considered two alternative formulations

202 of *RC* and checked the sensitivity to them:

203 $RCSurvey2_{a,y} = \dfrac{C_{a,y}}{\left(U_{a,y,s} + U_{a+1,y+1,s}\right)/2}$ Equation 5

204 $RCJoint2_{a,y} = \dfrac{C_{a,y}}{\sum\limits_{s}\left(U_{a,y,s} + U_{a+1,y+1,s}\right)/4}$ Equation 6

205 The first RC estimator provides an estimate by survey (*RCSurvey2*) using as denominator the

206 arithmetic mean of the abundances provided by the survey at the beginning and end of the Z

207 estimate period. The second estimator *RCJoint2* provides a single joint indicator of fishing

208 intensity for each year from both surveys together, by taking as denominator the average

209 population provided by both surveys during the same period. In the latter case the analysis

210 will be restricted to the years when both surveys were carried out in parallel, so that the two Z_s

211 estimates of the year will be linked by the same *RCJoint* estimate.

212 In all cases, the catches considered are those between May 15 of year *y* and May 15 of year

213 *y+1*, for the ages *a* and *a+1* in each respective year. Catches at age (in numbers) with their

214 mean weights are reported by season in ICES until the closure of the fishery in 2005 (ICES

215 2005) and, more recently, in WGHANSA reports (ICES2013).

216

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

218 coefficients:

219 $\hat{Z}_{a,y,s} = M_{a,y,s} + F_{a,y,s} + v_{a,y} = M + [Old_a] + Q_s \cdot RC_{a,y} + Survey + Interact + v_{a,y,s}$

220 (Model B, Equation 7)

221   With **M** (natural mortality) being the intercept either at age 1 (M1) or for all ages together

222   (M1+) - depending on the subset of data being analyzed - **Old** is now a dummy variable, being

223   0 for age 1 and 1 for age 2+. This term will indicate the increase of natural mortality in fish of

224   age 2+ relative to M at age 1 (M1), for the joint analysis of Z_1 and Z_{2+}. **RC** accounts for the

225   Relative Catches between surveys of the respective age *a* in year *y*, and coefficient $\boldsymbol{Q_s}$

226   accounts for proportionality of **RC** to fishing mortality *F*. **Survey** is a dummy variable, being

227   0 for DEPM and 1 for acoustics, and this term will reflect any potential effect of the acoustic

228   survey relative to the DEPM on Z estimates. **Interact** are the potential first and second order

229   interactions of the former variables, which were initially checked.

230   For the joint analysis of Z by age (Z1 and Z2+), our assumption about catchability, constant

231   across age and necessary to estimate Z, implies that the first or second order interactions

232   referring to the slope changing by age are not significant as the slope coefficient is the

233   catchability of the survey. Secondly, the intercepts reflecting M are population parameters

234   which should be similarly estimated by the surveys. As such, first order interactions of

235   intercepts with surveys should not be significant. Therefore, the only interaction which could

236   be significant is that of the slopes by survey, which would correspond with the common

237   assumptions in most assessments of different catchabilities by survey. We will refer to the

238   two-slope model as the one allowing different slopes on RCSurvey2 by survey (but with

239   constant slopes across ages), while we will refer to the single slope model as the one forcing a

240   common slope for both surveys.

241

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

243

244   **2.3 Natural mortality estimates from integrated assessments**

245   Finally, an integrated catch at age analysis with a seasonal (half-yearly) separable fishing

246   mortality model was applied to the catch and survey data currently used by ICES for the

247   assessment of this fishery (ICES 2013): Catches in tons and at age on a half-yearly basis,

248   spring surveys; Acoustic and DEPM estimates of total biomass (tons) and populations at age

249   (numbers); and finally, an acoustic survey on juveniles (JUVENA Survey index, started in

250   2003, which is used to tune the recruitment at age 1 with a power catchability function). The

251   purpose, as before, was to check what levels and patterns of natural mortality at age optimize

252   an integrated assessment, under the assumption of equal catchability at all ages in the surveys.

253   Natural mortality by age was applied either to a calendar year, going from January to

254   December or from July to June (the latter was checked because the main surveys are carried

255   out in May, i.e. closer to July than to January). The model was fitted using two different

256   approaches: the first one assumes, as before, that observations (catches or survey estimates in

257   biomass and by age) are subject to log-normal errors and the objective function is a direct

258   minimization of a weighted sum of squared residuals (WSSQ fitting - like in ICA analysis -

259   Patterson and Melvin 1996); the second approach is similar to the former one except that it

260   assumes that all age disaggregated data (catches and population at age estimates) are subject

261   to multinomial errors and hence are entered as percentages at ages 1, 2 and 3+. In the latter

262   case, model fitting is achieved by maximization of the log-likelihood (using log-likelihood

263   ratios - LLHR fitting). Given the general agreement in both surveys in terms of percentages at

264   age, and the poorer agreement in terms of biomass trends (ICES 2013), it seems that the

265   multinomial approach for indexes at age is probably a suitable way to deal with the type of

266   errors associated with survey observations. Details of the model's fitted objective functions

267   are given in Appendix A. The two modeling approaches were run in Microsoft Excel, using

268   Solver for objective function optimization. Convergence was verified using different starting

269   parameter values and likelihood of fitted models was calculated (see Appendix). Confidence

270   intervals for natural mortality estimates were obtained using the profile likelihood method.

271   Based on the likelihood ratio test, the 95% confidence interval around the joint optimum of

272    $\hat{M}1$ and $\hat{M}2+$ is defined as the pairs of M1 and M2+ which satisfy the following inequality:

273    $$\ln(L(\hat{,}\hat{M}1,\hat{M}2+)) - \ln(L(\hat{,}M1,M2+)) \le \frac{1}{2}\,t_2^2(.95) \qquad \text{Equation 8}$$

274   Where $L(\hat{,}\hat{M}1,\hat{M}2+)$ represents the likelihood at the optimum of M1 and M2+ and every

275   other parameter $(\hat{})$, and $L(\hat{,}M1,M2+)$ is the likelihood for any selected alternative of fixed

276   M1 and M2+ parameters (for the optimum of the remaining parameters - $\hat{}$). And $t_2^2(.95)$ is

277   the 0.95 percentile of the Chi-square with 2 degrees of freedom (i.e. 5.9915). Confidence

278   intervals for M1+ were also deduced from Equation 8 applied to a single M parameter and

279   Chi-square with 1 degree of freedom.

280   In order to compare the different fitted models, we used the corrected Akaike's Information

281   Criterion (AICc), estimated as:

282   AICc = -2*ln (likelihood) + 2*K + (2*K*(K+1))/(n-K-1),   Equation 9

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

284

285   **2.4 Sensitivity analysis**

286   Sensitivity to some observations, that looked noisy at first sight and might have become too

287   influential for the particular methods applied, was tested by including and excluding such data

288   (when excluded we will refer to the subset of data). For raw data direct analysis during the

289   closure period (2005-2010), the 2005 and 2006 survey data resulted in negative Z estimates

290   between them, indicating that either 2005 estimates were too low or 2006 estimates too high.

291 As for the linear models, years with high RC values (above 0.8) were considered unlikely to

292 be actually happening (due to the difficulty of producing such a fishing impact) which led us

293 to suspect some noisy, excessively low biomass estimates from the surveys during those

294 years. In addition, years 2011 and 2012 were checked for sensitivity as they resulted in

295 extremely different Z estimates by survey due to a large discrepancy in the 2012 biomass

296 estimates (ICES 2013). For the integrated assessment, analyzing sensitivity to the

297 inclusion/exclusion of the 2012 survey biomass estimates was considered sufficient (the year

298 of maximum biomass divergence – ICES 2013).

299

300 Furthermore, we tested the sensitivity of our results to a maximum potential level of errors in

301 age determination from otoliths. Even though the current ageing method is perceived to be

302 unbiased (Uriarte *et al.* in press), the actual level of error is unknown. Using expert advice, a

303 maximum of a 5% level of ageing errors among contiguous age groups (from ages 1 to 3+)

304 was evaluated. Larger errors were considered unlikely and were not compatible with data.

305 Determination of age 0 was considered fully accurate. In addition, given the low percentage

306 of age 3 in surveys and catches, age 2 errors were considered to occur more often with age 1

307 (in 80% of cases) than with age 3 (only 20%). The tested matrix for age determination error

308 (**E**) is shown in **Table 1**. Given a vector with the observed (assigned) age composition **A**

309 (1*4) of a survey or catches, the corrected estimates of the age composition **C** (1*4) are

310 deduced in matrix notation as:

311 $$\mathbf{C} = \mathbf{A} \cdot \mathbf{E}^{-1}$$ Equation 10

312 Corrections were not allowed to reduce the size of any age class below 20% of its original

313 value (before correction) and *ad hoc* changes were applied to ensure those minimums (by

314 restoring enough numbers from the contiguous age class in proportion to the removals

315 produced on the original amount so as to still allow 20% of the starting amount). As for the

316 catches, corrections were applied to international catches separately over three periods: before

317 surveys (January – mid-May), after surveys (mid-May - June) and in the second half of the

318 year.

319

320 **3. Results**

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

322 The series of Z estimates by survey show a large inter-annual variability (**Figure 1**). Z

323 estimates did not differ statistically between surveys (p>0.95 for Z1+ and p>0.12 for the Z by

324 age, Model A1). During the 2005-2009 closure, Z estimates (proxy of M1+) were markedly

325 lower on average (0.81, CV=13%) than during fishing periods (1.66, CV=9%) (**Figure 2;**

326 **Table 2**). Parallel differences between fishing periods were noticed for the Z by age (**Table 2**)

327 (with p[*Fishing*]<0.002, from Model A.2), and were consistently shown for both surveys

328 (with non-significant interactions of *Fishing* by *Survey*, p>0.6).

329 Natural mortalities deduced from Z estimates by age during the fishing closure period

330 (proxies of M1 and M2+) were slightly affected by the omission of the 2005 and 2006 noisy

331 estimates and turned out to be M1=0.66 (CV=11%) and M2+=1.63 (CV=19%) (**Table 2**).

332 Such big difference in Z by age was consistently shown in both surveys (**Figures 1 & 2 and**

333 **Table 2**) in the time series (Model A.1) and for the two fishing periods (Model A.2) (with

334 P(*Old*)<0.0001 and p(*Old*Survey*)> 0.2 in both models).

335

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

337

338 M estimates (intercepts) did not differ statistically between surveys, neither in the case of Z1+

339 (p[*Survey*]>0.6) nor by ages Z1 and Z2+ (p[*Survey*]> 0.3 and p[*OLD*Survey*]>0.25) for any

340 RC index or subset of data. Therefore the requisite for the joint analysis of the Z from both

341 surveys using this model was verified.

342

343 As regards total mortality (Z1+), the two-slope model on RCSurvey2 (**Figure 3**) resulted in

344 M1+ of 1.05 (CV=19%) (**Table 3**), though the slopes were not significantly different

345 (p=0.283). This estimate was very close to the mean of the individual M1+ estimates from the

346 surveys, which was 1.14 (CV=26%) for the DEPM and 0.953 (CV=26%) for the acoustic

347 (**Table 3**). Forcing a common slope for both surveys on RCSurvey2 made the single slope

348 model significant and resulted in a M1+ of about 1.15 (with a CV of 15%). The RCJoint2

349 estimator results in a M1+ of 0.885 (CV=20%). Removal of the suspicious Z1+ values

350 corresponding to RCSurvey2>0.8 and Year>2011 globally improved the fitting while leading

351 to a reduction of M1+ estimates (**Table 3 and Figure 3**). In summary, if the complete dataset

352 pointed towards an M1+ range of between 0.88 and 1.15, the analysis of the subset of data

353 reduced those values to a range between 0.78-0.92, with RCSurvey2 pointing towards higher

354 M1+ than RCJoint2.

355

356 Analysis of Z by ages (Z1 and Z2+) revealed significant differences in the intercepts (M) by

357 age (P[*Old*]<0.001) for any RC index. In the case of RCSurvey2, the two-slope model

358 (**Figure 4**) pointed to M1=0.94 and M2=1.79, with CVs around 17% and 14%, respectively

359 (**Table 4**). These estimates were close to the mean of individual survey estimates (**Table 4**)

360 but the slopes by survey were not significantly different (p=0.437). The single slopes model

361 became fully significant and resulted in very similar values. Using RCJoint2 (**Table 4** and

362 **Figure 4,** bottom panels) resulted in slightly lower M1 (at 0.82, CV=23%) and rather similar

363 M2 (at 1.73, CV=17%).

364 Working with the subset of data (**Figure 4b** and **Table 4b**) improved the overall fittings and

365 again led to a reduction of M estimates. For the two-slope model on RCSurvey2, the values

366 decreased to 0.78 for M1 (CV= 25%) and to 1.46 for M2+ (CV=20%), and achieved very

367 similar values in the single slope model. For the RCJoint2, the use of the subset of data

368 reduced M1 to 0.58 (CV=35%) and M2 to 1.57 (CV=19%). In summary, the complete dataset

369 resulted in M1 in the range 0.82-0.94 and M2+ around 1.73, whilst analysis restricted to the

370 subset of data reduced those estimates to M1 within the range 0.58-0.78, and M2+ in the

371 range 1.40-1.57, with RCSurvey2 pointing towards higher M1 than RCJoint2.

372

373 C) Natural mortality estimates from integrated assessments

374 Optimization for a single overall natural mortality (M1+, common for all ages) including all

375 input data resulted in M values of around 1.15 and 1 for the WSSQ and LLHR optimizations,

376 respectively (**Table 5a**). In all cases, the response surface was rather flat around the optimum

377 (+/- 0.1), being basically guided by the age-structured survey indexes, followed by the catches

378 at age information and finally, to a lesser extent, by the biomass survey indexes - which in

379 fact favored slightly lower M1+ optimums (around 0.7-1.1) (**Figure 5a**). In all cases, the

380 small contribution of JUVENA favored M1+ values at or above the synthetic optimum. The

381 sensitivity of these results to the omission of the 2012 survey estimates was negligible, with

382 optimums differing by less than 1% (not shown for simplicity).

383

384 Optimization of natural mortality by ages (M1 and M2+) for a Jan-Dec calendar year

385 suggested, for both objective functions, that the lower the M1 the better the fitting achieved,

386 though improvements gradually reduced, being minimal below 0.7 (**Figure 5b**) with optimum

387 M1 around 0.15-0.3 and M2+ around 1.35-1.45 (**Table 5b**). Applying a July-June calendar

388 year provided optimums for both objective functions of around 0.7 for M1 (**Figure 5c** and

389 **Table 5c**) and 1.4-1.5 for M2+ (see joint confidence intervals by models in **Figure 6a&b**).

390 Results are basically guided by the age-structured survey indexes which provide a rather

391 parallel response, whilst all other inputs are non-informative (almost flat) (**Figures 5b & c**).

392 Compared to the assessments assuming a single natural mortality (M1+), the assessments

393 allowing M at age to be estimated (M1/M2+) get a better fitting (higher likelihood - **Figure 6**)

394 and lower Akaike's Information Criterion (**Table 5**). These results were insensitive to the

395 omission of the 2012 survey estimates (not shown).

396 The M at age estimates obtained by the integrated models for the July-June calendar year are

397 consistent with those produced by the direct and linear models previously reported (**Figure 7**).

398

399 D) Sensitivity to Ageing Errors

400

401 Inclusion of 5% ageing errors did not affect the compatibility of Z1+ estimates by survey,

402 neither in the raw data analysis (P=0.97), nor in the log-linear models (P=0.71). This

403 compatibility also applied to the analysis of Z by age where all terms with *Survey* were not

404 significant either. Therefore the joint analysis of both surveys was again statistically

405 supported.

406

407   Consideration of a 5% ageing error raised up the M1+ estimates by about 0.14 in direct and

408   lineal model analyses, resulting for the subset of data all M1+ in the range of 0.94-1.08

409   (**Table 2 and 3**). Incorporation of this ageing error into the integrated models leads to minor

410   increases of the original M1+ estimates (by about 0.04), resulting in poorer fits and larger

411   AICc than for uncorrected data (**Table 5**).

412   By age, consideration of a 5% ageing error meant that paired raw Z1 estimates were still on

413   average below those of Z2+ for both surveys over the whole period (**Table 2b**) (paired t-test

414   p=0.0295), and more intensively during the closure period (p=0.0146).

415   The correction for a 5% ageing error reduces the differences of M between age by increasing

416   M1 estimates by about 0.2 and 0.3-0.4 in the direct and lineal model analysis, respectively,

417   and by reducing M2+ by a lesser extent (by about 0.08- 0.16). Nevertheless, M1 remains

418   invariantly below M2+, even though statistical significance is sometimes lost (**Table 3**). Both

419   integrated models, when considering a 5% ageing error, also obtained a reduction of the

420   differences of M by age by increasing M1 and reducing M2+, but to a larger extent for the

421   January to December calendar year. Nevertheless, M1 remains invariantly below M2+.

422   Certainly, the improvement in fitting achieved by allowing M to change by age is reduced

423   when compared to no ageing errors, but the differences are still significant (even though only

424   at alpha 0.06 for the WSSQ) (**Figure 6**) and the Akaike's Information Criterion improves (is

425   reduced), therefore still endorsing the M by age models over the single M1+ models.

426   Figure 7b shows the general consistency and overlapping of the M at age estimates for the

427   different methods tested before (**Figure 7**).

428

429   **4. Discussion**

430

431 Estimating natural mortality is one of the main challenges in stock assessment (Vetter 1988;

432 Hilborn and Walters 1992; Gislason *et al.* 2010), and in order to do it, availability of research

433 surveys is essential (Sinclair 2001; Sparholt *et al.* 2002; Zhao *et al.* 2003; Francis 2011). The

434 basic assumption of this paper was that the direct monitoring program running since 1987,

435 through two research surveys (23 DEPM and 18 Acoustic surveys) and the closure of the

436 fishery for 5 years should enable the overall level of natural mortality and its pattern by age to

437 be inferred for the Bay of Biscay anchovy. This was supported by the compatibility of the Z

438 estimates from both surveys and because, in spite of the large variability inherent to the data,

439 Z differed significantly between the open and closed fishing periods, being lower during the

440 latter period and therefore indicative of the natural mortality rates. Moreover, mortality at

441 ages two and older ($Z2+$) was significantly higher than at age one ($Z1$) throughout the time

442 series, suggesting an increasing pattern of natural mortality by age.

443

444 The series of Z estimates have a large inter-annual variability which must be linked either to

445 observation errors in the surveys or to variability in natural and fishing mortality, or both.

446 Observation errors in surveys are evidenced by the fluctuations in Z between consecutive

447 surveys (sometimes reaching negative values) and by the occasional strong divergences of

448 survey estimates (as in 2012). Variability of fishing mortality naturally happens for the

449 fisheries, which tend to stabilize catches when exploiting a highly fluctuating population (like

450 anchovy). Some variability of natural mortality has always been presumed and could be

451 linked to changes in the ecological environment (Vetter 1988; Zwolinski and Demer 2013).

452 For these reasons, we have chosen gradually improved estimators of natural mortality,

453 allowing for increasing data input and, in principle, greater noise filtering.

454

455   The direct and linear models provide a natural mortality for all age groups (M1+) of between

456   0.81 and 1.15, which decreases to 0.78-0.92 after filtering the suspected noise. The integrated

457   models indicate M1+ at about 1.15 for WSSQ and 1.00 for LLHR, i.e., at the upper range of

458   the estimates in the former models. Even though these estimates are not statistically different,

459   there can be several reasons explaining this preference for upper M1+ in the integrated

460   models. Firstly, their results include, in addition to the spring surveys, other auxiliary

461   information which partly favors this upper range of M1+ values, mainly by the recruitment

462   index and to a lesser extent the catches by age. Secondly, it should be pointed out that linear

463   models make inferences of M1+ from the decay between age groups 1+ to 2+, whilst

464   integrated models fit simultaneously the three age classes (1/2/3+) with the same M1+, and as

465   such the former estimates may be closer to the weighted mean of M by age (according to their

466   abundance), while the latter is closer to an arithmetic mean (as residuals by age have equal

467   weights). Hence, weighted M1+ to age class abundance should favor the M1+ at the lower

468   range pointed out before, because M1 is lower, and will serve to better describe the average

469   change of the whole population. In any case, this results in a most likely range going from

470   0.78 (RCJoint2) to 1 (log-likelihood assessment), which corresponds with an annual survival

471   of between 46% and 37%. If a single figure is needed, a rough compromise could be in the

472   middle of the ranges, close to 0.9 for M1+ (annual survival rate of 41%).

473   These results point towards a lower M1+ than the currently assumed value of 1.2, which was

474   calculated in the 1990s on the basis of the DEPM survey alone (Uriarte *et al.* 1996; Prouzet *et*

475   *al.* 1999). Moving to an M1+ of 0.9 would imply a reduction of the average historical

476   estimates of SSB by about 30-35%, and an inverse parallel increase of fishing mortality

477   estimates.

478   This average natural mortality for adult anchovy in the Bay of Biscay is just slightly below

479   the values of 1.08 and 1.34 which result from applying Hoening's equation (1983) (for a

480   Tmax of 4) and that of Pauly (1980) (for von Bertalanffy growth parameters Linf, K and t0

481   about 18.05 cm, 0.77 and 0.72, respectively, as fitted to DEPM survey observations and a

482   mean temperature of 16 ºC). Nevertheless, these M1+ estimates are rather similar to, albeit

483   slightly higher than, the ones reported for short-lived species of similar growth, such as sprats,

484   some Sardinops or Engraulidae (Beverton 1963, 1992; MacCall 1973; Methot 1989; Iversen

485   *et al.* 1993; Sinov i 2000), but at a lower level than the ones reported for Peruvian anchovy

486   (Pauly *et al.* 1987), *Anchoa mitchilli* (Newberger and Houde 1995) and other Engraulidae of

487   smaller maximum sizes (Bayliff 1967).

488

489   All the analyses improved by allowing M to change with age: the *Old* factor was retained in

490   the linear models and the likelihood of the integrated models improved significantly when M

491   was estimated by age compared to the single common M1+ modeling (Figure 6). This led to

492   the conclusion that M1 was significantly lower than M2+ (Figure 7): On the one hand, the

493   direct Z estimate and the linear models resulted in a range of M1 from 0.45 to 0.94 when

494   using the full dataset, and a narrower range of about 0.6-0.8 with the most reliable subset of

495   data. This corresponds with an annual survival of about 55%-45% for the 1-year-old group.

496   On the other hand, M2+ was consistently about twice the value of M1: 1.59 to 1.79 for M2+

497   with the full dataset and 1.4-1.65 for the most reliable subset of data. This corresponds with

498   an annual survival rate of about 25%-19% for ages two and older.

499   Furthermore, integrated assessment indicated M at age consistent with the former results, but

500   only for the July-June calendar, whilst the Jan-Dec calendar year suggested a better fit at a

501   lower M1 (Figure 7). For the latter modeling, such discrepancy arises from the pronounced

502   mismatch between the calendar of application of natural mortality by age (January to

503   December) and the calendar between survey observations (from May to May) which have to

504   be fitted. Both integrated assessments from July to June (WSSQ and LLHR) produced almost

505   identical estimates as those from the linear models in RCSurvey2 on the most reliable subset

506   of data. This means that the population modeling context of the integrated assessment,

507   including other auxiliary information, has enabled natural filtering of much of the noise

508   affecting the individual spring survey estimates. In summary, both July-June integrated

509   assessments have captured the pattern of natural mortality at age between survey observations

510   (from May to May) well and are consistent with the former simpler linear models (particularly

511   with those using the reliable subset of data) (Figure 7). Simplifying, they all pointed towards

512   an M1 of around 0.70 and M2+ of around 1.40 (i.e. survivals about 50% and 25%

513   respectively).

514   Our data do not allow saying when this additional mortality at age 2 and older happens during

515   the year; however the sharp decrease of the 2 and 3 year-olds is already noticeable in the

516   fishery after spawning, during the second half of the year (ICES 2005, 2013; Uriarte *et al.*

517   1996). This could have been the result of some permanent emigration of the old (2+) fishes

518   outside of the major fishing grounds, off the Bay of Biscay, but such a possibility has never

519   been proven and it is well known that, every spring, old fishes concentrate again to spawn in

520   the southeast of the Bay of Biscay (Motos *et al.* 1996) where the surveys take place.

521   Therefore, this increasing mortality at age 2 and older is most likely due to either increased

522   vulnerability to predation at older ages or to natural biological mortality, probably reflecting

523   senescence of anchovies at age 2 and older. No major concentration of predators on adults in

524   early summer has been reported. The Bay of Biscay is an area of bottom-up controlling of the

525   upper trophic levels (Lassalle *et al.* 2011), with anchovy being one (and not the main) among

526   several small pelagic and other fishes (such as sardine, sprat, horse mackerel, blue whiting,

527 etc) connecting the plankton communities to piscivorous species (Sanchez and Olaso 2004;

528 Preciado *et al.* 2008). It contributes to the diets of demersal species such as hake, monkfish,

529 megrim and tunnidae but mainly as juveniles (Guichet 1995; Preciado *et al.* 2008; Lezama-

530 Ochoa *et al.* 2010; Goñi *et al.* 2011, 2012; López-López *et al.* 2012), whilst in adult anchovy

531 it seems that some demersal fishes (John dory and hake, etc) and cetaceans prey routinely all

532 year around (Preciado *et al.* 2008; Mahe *et al.* 2007; Lassalle *et al.* 2012; Meynier *et al.*

533 2008). Therefore, by discarding any ecological higher predation on adults, we tend to think

534 that senescence might be occurring at the age of two and older, in accordance with the

535 expectation of observable senescent mortality affecting short-lived cupleoids (Beverton

536 1963).

537

538 We hypothesized that this anchovy population may suffer from "reproductive stress" inducing

539 increased mortality, particularly after its second spawning event. It is known that the large

540 energy cost of reproduction can induce some varying rates of mortality due to "reproductive

541 stress", as shown for cod (Hutchings 2005), or in extreme cases, of semelparous species like

542 Pacific salmon *Oncorhynchus*, which reproduces and dies, whereby dramatic hormonal

543 changes induce starvation that causes intestine deterioration by necrosis and inflammatory

544 processes during spawning migration (McBride *et al.* 1986). Examples of mortality associated

545 to reproductive stress in short-lived species are common, as in invertebrates (squids and

546 shrimps – Caddy *et al.* 1996) and fishes such as *Aphia minuta* (an extremely short-lived goby

547 where apoptosis of enterocytes is related to post spawning mortality – Caputo *et al.* 2002),

548 capelin *Mallotus villosus* (Vilhjálmsson 2002; Gjøsæter 1998) and in the short-lived gadoid

549 Norway pout (Nielsen *et al.* 2012). Anchovy in the Bay of Biscay invests much energy in

550 reproduction having one of the highest spawning frequencies among the Engraulidae, capable

551 of increasing slightly with size and age (Uriarte *et al.* 2012), which results in a very high daily

24

552   fecundity (Santos *et al.* in press). Many of the 1-year-old fishes lay down a spawning check at

553   the end of the spawning season (in early summer) (Petitgas and Grelier 2003; Uriarte *et al.*

554   2002, in press) being probably indicative of the limiting condition of many anchovies after

555   spawning (Pecquerie *et al.* 2009). While they have reached about 88% of their maximum

556   attainable growth (18.3 cm) by the age of 2, spawning starts earlier and probably lasts longer

557   than at age 1, with a likely increase in the number of batch-spawning events during the

558   spawning season (Motos *et al.* 1996; Motos 1996; Pecquerie *et al.* 2009), in accordance with

559   the indications for other Engraulidae (Parrish *et al.* 1986; Claramunt *et al.*2007; Cubillos and

560   Claramunt 2009). On average, 2-year-old anchovies do not resume opaque edge formation in

561   otoliths until mid-June, beyond the mid-point of the spawning season (Uriarte *et al.* 2002, in

562   press), this being also indicative that much of the energy of this age group is invested in

563   reproduction during the first half of the year. This reproductive strategy of anchovy may

564   result in some physiological reproductive stress at the end of the spawning season for the age

565   2+ group, which may explain the increase in natural mortality observed in our analysis. As

566   such, this population of anchovies may have evolved in its fluctuating environment by

567   allowing some non-negligible chances of reproducing over two spawning seasons before

568   senescence. This would enhance the opportunities to overcome single (not repeated)

569   environmentally-induced failures of recruitment. This strategy would place anchovy among

570   capelin, which mostly dies after its first spawning (Vilhjálmsson 2002; Gjøsæter 1998), and

571   sprats, sardines or sandeels which have progressively longer adult life expectation with

572   several annual reproductive cycles (Cook 2004; Nunes *et al.* 2011; Zwolinski and Demer

573   2013); ending up with the herrings, which seem to have up to eight reproductive seasons

574   during their life history before increased mortality by senesce shows up (as for Norwegian

575   spring-spawning herring – Beverton *et al.* 2004). To our knowledge, senescence in

576   Engraulidae had only been suggested previously for Northern anchovy (from age 2 and older

577 – MacCall 1973 – based on analysis of catch ratio from catches and surveys) and for the

578 anchovy in the Yellow Sea (from age 3 and older – Zhao *et al.* 2003 – based on analysis of

579 surveys). We suspect that this pattern of increasing mortality by age may be applicable to

580 other Engraulidae, whereby assessments following the usual constant mortality assumption

581 often results in non-understandable big changes in catchability by age in surveys (Giannoulaki

582 *et al.* 2014).

583 In terms of assessment, the new M estimates would impact the average level of spawning

584 biomass approximately in proportion to the reduction in average M. For instance, for LLHR

585 modeling, moving from the single M1+ hypothesis at 1.2 to its optimum at 1.00 would reduce

586 mean biomass by about 27%, while moving further from the optimum M1+ to its optimal

587 mortality by age would result in a minor reduction of about 5%. So once M1+ is set at its

588 optimum, a further change to the optimum M by age does not imply additional major changes

589 to mean biomass estimates. In spite of this, however, this latter change to M by age will

590 probably have implications in any population and fishery projections which might be required

591 for the provision of advice to managers. For instance, for this anchovy old populations

592 (composed mainly of ages 2+) will decay faster (with M around 1.4) than young ones

593 (composed mainly of age 1) (with an M around 0.7-0.8). Therefore, in terms of management

594 moving to unbiased M estimates should also improve the quality of advice as reported for

595 other species (Lee *et al.* 2011; Zwolinski and Demer 2013). Certainly, the perception of

596 fishing mortality will change inversely to the estimation of biomass levels. Furthermore, as

597 the new M estimates change the perception of cohort dynamics in mass, this will affect the

598 estimation of management-related reference points ($F_{0.1}$, F_{MSY}, etc.).

599

600 These results are partly sensitive to the maximum level of ageing errors put into

601 consideration. Correction of such a 5% ageing error moved the direct and linear model

602 estimates of M1+ and of M1 upwards, while slightly reducing M2+. This was associated with

603 a partial loss of the statistical significance of the difference between M1 and M2+ (Figure 7b).

604 Integrated models were less affected in the M1+ estimates (remaining just slightly above the

605 original optimums), and also showed a reduction of the differences between M1 and M2+

606 (**Table 5**). Nevertheless, integrated assessments show that models allowing M by age

607 estimates achieve better fittings than single M1+ models (with $p < 0.056$ for the WSSQ and

608 $p < 0.000$ for the LLHR) (Figure 6). Therefore, even after consideration of this maximum level

609 of potential ageing errors, the significant increase pattern of natural mortality at age is still

610 supported by integrated assessments. In any case, M estimates will be conditioned by the

611 actual level of ageing errors affecting the observations.

612

613 Certainly, the results depend upon the assumption of the constant catchability of surveys

614 across ages, on which Z estimates rely (an assumption we have proved to be compatible with

615 the data). Sustaining this is not true would be difficult to understand, given the good spatial

616 coverage of the surveys, and would imply that the prevailing null hypothesis should be on the

617 assumption that M is equal across ages. Biologically, this is known not to be true (Vetter

618 1988), even though for simplification this has been the null hypothesis for the assessment of

619 the exploited range of ages of most of the long and short-lived fish resources. Although this

620 has already been questioned and revised for younger ages (Caddy 1991; Abella *et al.* 1997;

621 Gislason *et al.* 2010), it has not been sufficiently revised yet for the inclusion of senescence in

622 the older age classes. And, certainly for short-lived species, senescence should have been

623 presumed to be noticeable not too long after reaching maturity (Beverton 1963). By accepting

624 that the null hypothesis should be that senescence is present, then our analysis shows

625   consistency of the observations with the hypothesis, and we would rely more on the

626   observations of the age structures reported by surveys rather than on doubtful assumptions of

627   constant natural mortality across ages; and finally the assessment can become parsimonious

628   (as in our case with two surveys) in terms of demanding a lesser amount of parameters to

629   infer population size (i.e. lesser amount of catchability at age parameters in comparison to the

630   increased number of natural mortality by age).

631

632   A correct selection of the natural mortality serves to properly scale the assessments around

633   true population abundance values and this becomes particularly relevant in the context of

634   relative indexes of population abundance, and even more for short-lived species. In this paper

635   we have shown that that the overall natural mortality M1+ was somewhat below what had

636   been assumed so far, and furthermore, that natural mortality at ages 2+ is higher than at age 1,

637   in line with expectation of senescence. In achieving this conclusion, the continuous

638   monitoring of the population by two parallel and independent methods for many years,

639   including a period of fishing closure, has been essential, as it has provided sufficient contrast

640   for the analysis. The natural mortality issue should be revisited periodically when additional

641   years of survey observations and improvements in our base knowledge become available.

642   Relevant improvements may come from better understanding of survey catchability, or of the

643   accuracy of age determinations for this anchovy, besides, for instance, from monitoring

644   biological and biochemical markers of aging and reproductive stress or from further studies

645   on eco-trophic interactions.

646

655

656 **REFERENCES:**

657 Abella, A., Caddy, J.F. and Serena, F. 1997. Do natural mortality and availability decline with

658 age? An alternative yield paradigm for juvenile fisheries, illustrated by the hake *Merluccius*

659 *merluccius* fishery in the Mediterranean. Aquat. Living Resour., **10**: 257-269.

660

661 Bayliff, W.H. 1967. Growth, mortality and exploitation of the Engraulidae, with special

662 reference to the anchoveta *Cetengraulis mysticetus*, and the colorado, Anchoa naso, in the

663 eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. **12**: 365-432.

664

665 Beverton, R.J.H. 1963. Maturation, growth, and mortality of clupeid and engraulid stocks in

666 relation to fishing. Rapp. p.-v. réun. - Cons. int. explor. Mer. **154** : 44-67.

667

668 Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost

669 fishes. J. Fish Biol. **41**(Suppl. B): 137–160.

670

671 Beverton, R.J.H., Hylen, A., Østvedt, O.-J., Alvsvaag, J. and Iles, T.C. 2004. Growth,

672 maturation, and longevity of maturation cohorts of Norwegian spring-spawning herring. ICES

673 J. Mar. Sci. **61**: 165–175.

674

675 Boyra G., Martinez, U., Cotano, U., Santos, M., Irigoien, X., and Uriarte, A. 2013: Acoustic

676 surveys for juvenile anchovy in the Bay of Biscay: abundance estimate as an indicator of the

677 next year's recruitment and spatial distribution patterns. ICES J. Mar. Sci. **70**: 1354-1368.

678 doi:10.1093/icesjms/fst096

679

680 Caddy, J.F. 1991. Death rates and time intervals: is there an alternative to the constant natural

681 mortality axiom? Rev. Fish. Biol. Fish. **1**: 109–138.

682

683 Caddy, J.F. 1996. Modelling natural mortality with age in short-lived invertebrate

684 populations: definition of a strategy of gnomonic time division. Aquat. Living Res. **9**: 197-

685 207.

686

687 Caputo, V., Candi, G., Arneri, E., Mesa, M. L., Cinti, C., Provinciali, M., Cerioni, P. N., et al.

688 2002. Short lifespan and apoptosis in *Aphia minuta*. J. Fish Biol. **60**: 775–779.

689

690 Charnov, E.L., Turner, T.F., and Winemiller, K.O. 2001. Reproductive constraints and the

691 evolution of life histories with indeterminate growth. Proc. Natl. Acad. Sci. U.S.A. **98**:9460–

692 9464.

693

694 Charnov, E.L., and Gillooly J.F. 2004. Size and Temperature in the Evolution of Fish life

695 Histories. Integr. Comp. Biol. **44**: 494-497

696

697 Chen S. and Watanabe, S. 1989. Age dependence of Natural Mortality coefficient in Fish

698 Population Dynamics. Nippon Suisan Gakkaishi. **55**(2): 205-208.

699

700 Claramunt, G., Serra, R., Castro, L.R., and Cubillos, L.A. 2007. Is the spawning frequency

701 dependent on female size? Empirical evidence in *Sardinops sagax* and *Engraulis ringens* off

702 northern Chile. Fish. Res. **85**: 248–257.

703

704 Cook R.M. 2004. Estimation of the age-specific rate of natural mortality for Shetland

705 sandeels. ICES J. Mar. Sci. **61**: 159-169.

706

707 Cotter A.J.R., Burst, L., Paxton, C.G.M., Fernandez, C., Buckland S.T., and Pan, J-X. 2004.

708 Are stock assessment methods too complicated? Fish Fish. **5**: 235–254.

709

710 Cubillos, L., and Claramunt, G. 2009. Length-structured analysis of the reproductive sea-son

711 of anchovy and common sardine off central southern Chile. Mar. Biol. **156**:1673–1680.

712

31

713   Francis, R.I.C.C. 2011. Data weighting in statistical fisheries stock assessment models. Can.

714   J. Fish. Aquat. Sci. **68**: 1124–1138.

715

716   Giannoulaki M., Ibaibarriaga L., Antonakakis K., Uriarte A., Machias A., Somarakis S,

717   Sanchez S., and Roel B. 2014. Applying a two-stage Bayesian dynamic model to a short-lived

718   species, the anchovy, in the Aegean Sea (Eastern Mediterranean). Comparison with an

719   Integrated Catch at Age stock assessment model. Medit. Mar. Sci. **15** (2): 350-365

720

721   Gislason H., Daan, N., Rice, J.C., and Pope, J.G. 2010. Size, growth, temperature and the

722   natural mortality of marine fish. Fish Fish. **11**: 149–158.

723

724   Gislason, H., Pope, J.G., Rice, J.C. and Daan, N. 2008. Coexistence in North Sea fish

725   communities: implications for growth and natural mortality. ICES J. Mar. Sci. **65**: 514–530.

726

727   Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in

728   the Barents Sea. Sarsia **83**:453–496.

729

730   Golubev, A. 2009. How could the Gompertz–Makeham law evolve. J. Theor. Biol. **258**: 1–17.

731

732 Goñi N, Logan J, Arrizabalaga H, Jarry M, and Lutcavage M. 2011. Variability of albacore

733 (*Thunnus alalunga*) diet in the Northeast Atlantic and Mediterranean Sea. Mar. Biol. **158**(5):

734 1057-1073

735

736 Goñi N, Peninon V, Arrizabalaga H, and Uriarte A. 2012. Spatial and temporal variation of

737 anchovy predation by albacore and bluefin tuna in the Bay of Biscay ICES CM 2012/I:04

738

739 Gulland J.A. 1983. Fish Stock Assessment: A manual of basic methods. FAO/ Willey series

740 on food and agriculture; v.1. John Willey and Sons, New York.

741

742 Guichet R. 1995. The diet of European hake (*Merluccius merluccious*) in the northern part of

743 the Bay of Biscay. ICES J. Mar. Sci. **52**: 21-31

744

745 Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull.

746 **81**(4):898–903.

747

748 Hewit D. and Hoening J. M. 2004. Comparison of two approaches for estimating natural

749 mortality based on longevity. Fish. Bull. **103**(2): 433-437

750

751 Hilborn, R., and Walters, C.J. 1992. Quantitative Fisheries Stock Assessment: Choice,

752 Dynamics and Uncertainty. Chapman and Hall, New York.

753

754 Hutchings, J.A. 2005. Life history consequences of overexploitation to population recovery in

755 Northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **62**: 824–832.

756

757 Ibaibarriaga, L., Fernandez, C., Uriarte, A and Roel, B.A. 2008. A two-stage biomass

758 dynamic model for the Bay of Biscay anchovy: A Bayesian Approach. ICES J. Mar. Sci. **65**:

759 191 – 205.

760

761 ICES. 2005. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel,

762 Sardine and Anchovy (WGMHSA), 6 - 15 September 2005, Vigo, Spain. ICES C.M.

763 2006/ACFM:08

764

765 ICES. 2013. Report of the Working Group on Southern Horse Mackerel, Anchovy and

766 Sardine (WGHANSA), 21 - 26 June 2013, Bilbao, Spain. ICES CM 2013/ACOM:16.

767

768 Iversen, S.A., Zhu D., Johannessen, A., and Toresen, R. 1993. Stock size, distribution and

769 biology of anchovy in the Yellow Sea and East China. Sea. Fish. Res. **16**: 147-163.

770

771 Jørgensen C., and Holt, R.E., 2013. Natural mortality: Its ecology, how it shapes fish life

772 histories, and why it may be increased by fishing. J. Sea Res. **75**: 8–18

773

774 Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., et

775 al. 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf

776 food web: implications for ecosystem management. Progress in Oceanography. **91**: 61–75.

777

778 Lassalle, G., Gascuel, D., Le Loc'h, F., Lobry, J., Pierce, G. J., Ridoux, V., Santos, M. B.,

779 Spitz, J., and Niquil, N. 2012. An ecosystem approach for the assessment of fisheries impacts

780 on marine top predators: the Bay of Biscay case study. ICES J. Mar. Sci. **69**: 925–938.

781

782 Lezama-Ochoa A., Boyra G., Goñi N., Arrizabalaga H., Bertrand A., 2010. Investigating

783 relationships between albacore (*Thunnus alalunga*) CPUE and prey distribution in the Bay of

784 Biscay. Progress in Oceanography. **86**: 105–114.

785

786 Lee, H.-H., Maunder, M.N., Piner, K.R., Methot R.D., 2011. Estimating natural mortality

787 within a fisheries stock assessment model: an evaluation using simulation analysis based on

788 twelve stock assessments. Fish. Res. **109**: 89–94.

789

790 López- López, L., Preciado, I., Villamor, B., Velasco, F., Iglesias, M., Nogueira, E.,

791 Gutierrez-Zabala, J.L., and Olaso, I. 2012. Is juvenile anchovy a feeding resource for the

792 demersal community in the Bay of Biscay? On the availability of pelagic prey to demersal

793 predators. ICES J. Mar. Sci. **69**: 1394–1402.

794

795   Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile

796   and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish Biol. **49**: 627–647.

797

798   Mahe, K., Amara, R., Bryckaert, T., Kacher, M., and Brylinski, J. M. 2007. Ontogenetic and

799   spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the

800   Celtic Sea. – ICES J. Mar. Sci. **64**: 1210–1219.

801

802   Massé, J. 1996. Acoustic observations in the Bay of Biscay: schooling, vertical distribution,

803   species assemblages and behaviour. Sci. Mar. **60**: 227–234.

804

805   Masse J., Duhamel E., Petitgas P., Doray M., Huret M. Spring Acoustic Surveys: Pelgas

806   survey. *In* Pelagic Surveys series for sardine and anchovy in ICES Areas VIII and IX

807   (WGACEGG) - Towards an ecosystem approach. *Edited by* J. Masse, A. Uriarte, M.M.

808   Angelico, and P. Carrera. ICES CCR (Cooperative Research Report). Copenhagen. Denmark.

809   [In press.]

810

811   MacCall A. 1973. The mortality rate of *Engraulis mordax* in southern California. Calif. Coop.

812   Oceanic Fish. Invest. Rep. Vol **XVII**: 131-135

813

814   McBride, J. R., Fagerlund, U. H. M., Dye, H. M. and Bagshaw, J. 1986. Changes in structure

815   of tissues and in plasma cortisol during the spawning migration of pink salmon,

816   *Oncorhynchus gorbuscha* (Walbaum). J. Fish Biol. **29**: 153–166.

817

818 Method R.D. 1989. Synthetic estimates of historical abundance and mortality for northern

819 anchovy. American Fisheries Society Symposium **6**: 66-82.

820

821 Methot R.D., and Wetzel, C.R. 2013. Stock synthesis: A biological and statistical framework

822 for fish stock assessment and fishery management. Fish. Res. **142**: 86– 99.

823

824 Meynier, L., Pusineri, C., Spitz, J., Santos, M.B., Pierce, G.J., and Ridoux, V. 2008.

825 Intraspecific dietary variation in the short-beaked common dolphin (*Delphinus delphis*) in the

826 Bay of Biscay: importance of fat fish. Mar. Ecol. Pr. Ser. **354**: 277–287.

827

828 Motos, L. 1996. Reproductive biology and fecundity of the Bay of Biscay anchovy population

829 (*Engraulis encrasicolus* L.). Sci. Mar. **60** (Suppl. 2) 195–207.

830

831 Motos, L., Uriarte, A., Valencia, V. 1996. The spawning environment of the Bay of Biscay

832 anchovy (*Engraulis encrasicolus* L.). Sci. Mar. **60** (Suppl. 2), 117–140.

833

834 Motos, L., Uriarte, A., Prouzet, P., Santos, M., Alvarez, P., and Sagarminaga, Y. 2005.

835 Assessing the Bay of Biscay anchovy population by DEPM: a review 1989–2001. *In* Report

836 of the SPACC Meeting on Small Pelagic Fish Spawning Habitat Dynamics and the Daily Egg

837 Production Method (DEPM). *Edited by* L.R. Castro, P. Freón, C. D. van der Lingen and A.

838 Uriarte. GLOBEC Report **22**, xiv, pp. 88-90.

839

840 Nielsen, J.R., Lambert, G., Bastardie, F., Sparholt, H., and Vinther, M. 2012. Do Norway pout

841 (*Trisopterus esmarkii*) die from spawning stress? Mortality of Norway pout in relation to

842 growth, sexual maturity, and density in the North Sea, Skagerrak, and Kattegat. ICES J. Mar.

843 Sci. **69**: 197–207.

844

845 Newberger, T.A., and Houde E.D. 1995 Population biology of bay anchovy *Anchoa mitchilli*

846 in the mid Cheasapeake Bay. Mar. Ecol. Pr. Ser. **116**: 25-37.

847

848 Nunes, C., Silva, A., Marques, V., Ganias, K. 2011. Integrating fish size, condition, and

849 population demography in the estimation of Atlantic sardine annual fecundity. Ciencias

850 Marinas **37**(4B): 565–584

851

852 Parrish, R.H., Mallicoate, D.L. and Klingbeil, R.A. 1986. Age dependent fecundity, number

853 of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis*

854 *mordax*. Fish. Bull. **84**: 503–517.

855

856 Patterson K.R. and Melvin, G.D. 1996. Integrated Catch at age Analysis. Version 1.2. Scottish

857 Fisheries Research Report No. **58**. FRS: Aberdeen.

858

859   Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and

860   mean environmental temperature, in 175 fish stocks. J. Cons. Perm. Int. Explor. Mer **39**: 175-

861   192.

862

863   Pauly, D., Palomares, M.L., Gayanilo, F.C. 1987. VPA estimates of the monthly population

864   length composition, recruitment, mortality, biomass and related statistics of Peruvian

865   anchoveta 1955–1981. *In* The Peruvian Anchoveta and its Upwelling Ecosystem: Three

866   Decades of Change. *Edited by* D. Pauly, and I. Tsukayama. ICLARM Studies and Reviews

867   15, Instituto del Mar del Perú (IMARPE), Callao, Perú; Deutsche Gesellschaft fur Technische

868   Zusammenarbeit (GTZ), Eschborn. Federal Republic of Germany; and International Center

869   for Living Aquatic Resources Management (ICLARM), Manila, Philippines, pp. 142–166.

870

871   Pecquerie L., Petitgas, P., and Kooijman, S.A.L.M. 2009. Modeling fish growth and

872   reproduction in the context of the Dynamic Energy Budget theory to predict environmental

873   impact on anchovy spawning duration. J. Sea Res. **62**: 93–105

874

875   Petitgas, P and Grellier, P. 2003. Size selective processes for anchovy in Biscay, 2000–2002:

876   recruitment, adult survival and spawning. ICES CM2003 /N:07. 11 pp.

877

878   Petitgas, P., Uriarte, A., Nogueira, E., Massé, J., and Cotano, U. 2010. Bay of Biscay

879   anchovy. *In* Life cycle spatial patterns of small pelagic fish in the Northeast Atlantic. *Edited*

880   *by* P. Petitgas. ICES Coop. Res. Rep. **306** (93pp): pp.40-44

881

882   Preciado, I., Velasco, F., and Olaso, I. 2008. The role of pelagic fish as forage for the

883   demersal fish community in the Southern Bay of Biscay. J. Mar. Syst.**72**: 407–417.

884

885   Prouzet, P., Uriarte, A., Villamor, B., Artzruoni, M., Gavrart, O., Albert, E., et Biritxinaga, E.

886   1999: Estimations de la mortalité par pêche (F) et naturelle (M) à partir des méthodes directes

887   d'évaluation de l'abondance chez les petits pélagiques. Précision des estimateurs. Rapport

888   final du contract européen 95/PRO/018.

889

890   Quinn, T.J., and Deriso, R.B. 1999. Quantitative Fish Dynamics. Oxford University Press,

891   New York.

892

893   Reznick, D.N., Ghalambor, C.K., and Nunney, L. 2002. The evolution of senescence in fish.

894   Mech. Age. Dev.**123**: 773–789.

895

896   Reznick, D., Bryant, M., and Holmes, D. 2006. The evolution of senescence and post-

897   reproductive lifespan in guppies (*Poecilia reticulate*). PLoS Biology, **4**(1) e7: 136–143.

898

899   Sanchez, F., and Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem.

900   Ecol. Mod. **172**: 151–174.

901

902   Santos M., Uriarte, A., Boyra G., and Ibaibarriaga L., in press. Anchovy DEPM surveys 2003

903   - 2012 in the Bay of Biscay (subarea VIII) BIOMAN. *In* Pelagic Surveys series for sardine

904   and anchovy in ICES Areas VIII and IX (WGACEGG) - Towards an ecosystem approach.

905   *Edited by* J. Massé, A. Uriarte, M. M. Angelico, P. Carrera. ICES CCR (Cooperative

906   Research Report). Denmark.

907

908   Santos, M., Uriarte, A., Ibaibarriaga, L. 2011. Spawning Stock Biomass estimates of the Bay

909   of Biscay anchovy (*Engraulis encrasicolus*, L.) in 2010 applying the Daily Egg Production

910   Method. Rev. Invest. Mar. **18**(5): 76-90.

911

912   Sinclair, A.F. 2001. Natural mortality of cod (*Gadus morhua*) in the southern Gulf of St.

913   Lawrence. ICES J. Mar. Sci. **58**: 1-10.

914

915   Somarakis, S., Palomera, I., Garcia, A., Quintanilla, L., Koutsikopoulos, C., Uriarte A., and

916   Motos, L. 2004. Daily egg production of anchovy in European waters. ICES J. Mar. Sci. **61**:

917   944-958

918   Sparholt, H., Larsen, L. I., and Nielsen, J. R. 2002. Non-predation natural mortality of

919   Norway pout (*Trisopterus esmarkii*) in the North Sea. ICES J. Mar. Sci. **59**: 1276–1284.

920

921   Tanasichuk, R.W. 2000. Age-specific natural mortality rates of adult Pacific herring (*Clupea*

922   *pallasi*) from southern British Columbia. Can. J. Fish. Aquat. Sci. **57**: 2258–2272

923

924   Terzibasi, E., Valenzano, D.R., and Cellerino, A. 2007. The short-lived fish *Nothobranchius*

925   *furzeri* as a new model system ageing studies. Exp. Gerontol. **42**: 81–89.

926

927   Uriarte, A., Blanco, M., Cendrero, O., Grellier, P., Millán, M., Morais, A., Rico, I. 2002.

928   Report of the Workshop on anchovy otoliths from subarea VIII and division Ixa (Annex to

929   PELASSES report EU study Project -EC DG XIV Contract nº99/010 and Working Document

930   to the ICES Working Group on the assessment of Mackerel, Horse Mackerel, Sardine and

931   Anchovy. Copenhagen, 10-19 September 2002. (ICES Repository, available from

932   http://www.ices.dk/community/Documents/PGCCDBS/) [accessed 16 February 2015]

933

934   Uriarte, A., Prouzet, P., Villamor, B. 1996. Bay of Biscay and Ibero Atlantic anchovy

935   populations and their fisheries. Sci. Mar. **60** (Supl.2): 237-255

936

937   Uriarte A., Alday A., Santos M, and Motos L. 2012. A re-evaluation of the spawning fraction

938   estimation procedures for Bay of Biscay anchovy, a species with short interspawning

939   intervals. Fish. Res. **117–118**: 96-111. doi:10.1016/ j.fishres.2011.03.002

940

941 Uriarte, A., Rico, I., Villamor, B., Duhamel, E., Dueñas, C., Aldanondo, N., and Cotano, U.,

942 in press. Validation of age determination using otoliths of the European anchovy (*Engraulis*

943 *encrasicolus* L.) in the Bay of Biscay. Mar. Freshwater Res.

944

945 Vetter, E.E. 1988. estimation of natural mortality in fish stocks: a review. Fish. Bull. **86**(1):

946 25-43.

947

948 Vilhjálmsson, H. 2002. Capelin (Mallotus villosus) in the Iceland–East Greenland–Jan Mayen

949 ecosystem. – ICES Journal of Marine Science. 59: 870–883.

950

951 Wang Y., Liu, Q., Yu C., and Lian L. 2009. Estimation of instantaneous rate of natural

952 mortality from catch-at-age data and an abundance index based on extended survivors

953 method. Fish. Res. **97**. 127–133.

954

955 Williams, P.D., Day, T., Fletcher Q., and Rowe, L. 2006. The shaping of senescence in the

956 wild. Trends Ecol. Evol. **21** (8): 458-463. doi:10.1016/j.tree.2006.05.008

957

958 Woodhead, A.D. 1998. Aging, the fishy side: an appreciation of Alex Comfort's studies. Exp.

959 Gerontol. **33**: 39–51.

960

961   Zhao, X., Hamre, J., Li, F., Jin, X., and Tang, Q. 2003. Recruitment, sustainable yield and

962   possible ecological consequences of the sharp decline of the anchovy (*Engraulis japonicus*)

963   stock in the Yellow Sea in the 1990s. Fish. Oceanogr. **12**(4/5): 495–501.

964

965   Zwolinski, J. P., and Demer, D. A. 2013. Measurements of natural mortality for Pacific

966   sardine (*Sardinops sagax*). – ICES J. Mar. Sci. **70**: 1408–1415. doi:10.1093/icesjms/fst110.

967

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

4
5
6

7

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%

11
12

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%

17

18 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

19 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

20 columns estimates by surveys, central three columns pooled surveys estimates by RC indicators, and final three columns pooled surveys estimates for

21 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	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:	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	*0.339**	*0.313**	*0.448**
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	*0.412**	*-0.009**	0.634	*0.818**	*-0.474**	0.418	*0.878**
CV	45%	234%	9593%	31%	64%	172%	33%	62%
Additive Slope component			*0.621**			*0.873**		
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	*0.610**	0.684	0.662	0.997	*0.261**	*0.221**	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**

1

	1	2	3	4	5	6	7	8
CV	30%	29%	20%	21%	19%	24%	25%	24%
RC slope coefficient	1.748	0.629*	0.748*	1.535	1.710	0.507*	1.413	1.871
CV	36%	163%	116%	32%	35%	171%	38%	36%
Additive Slope component			0.878*			1.079*		
CV			91%			76%		
Model 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%

22

23

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

26

27
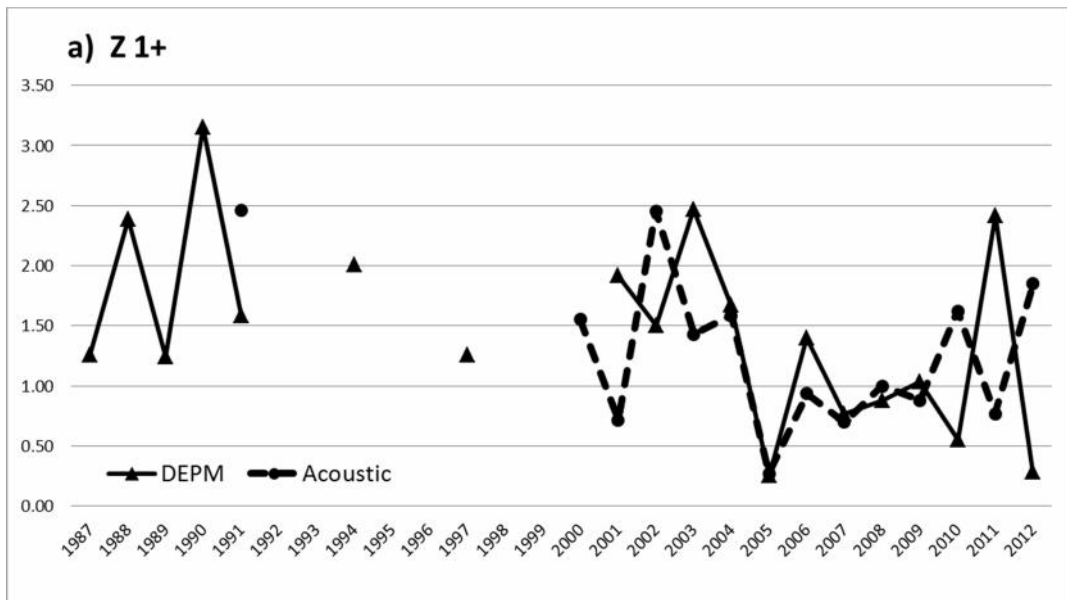
28

29
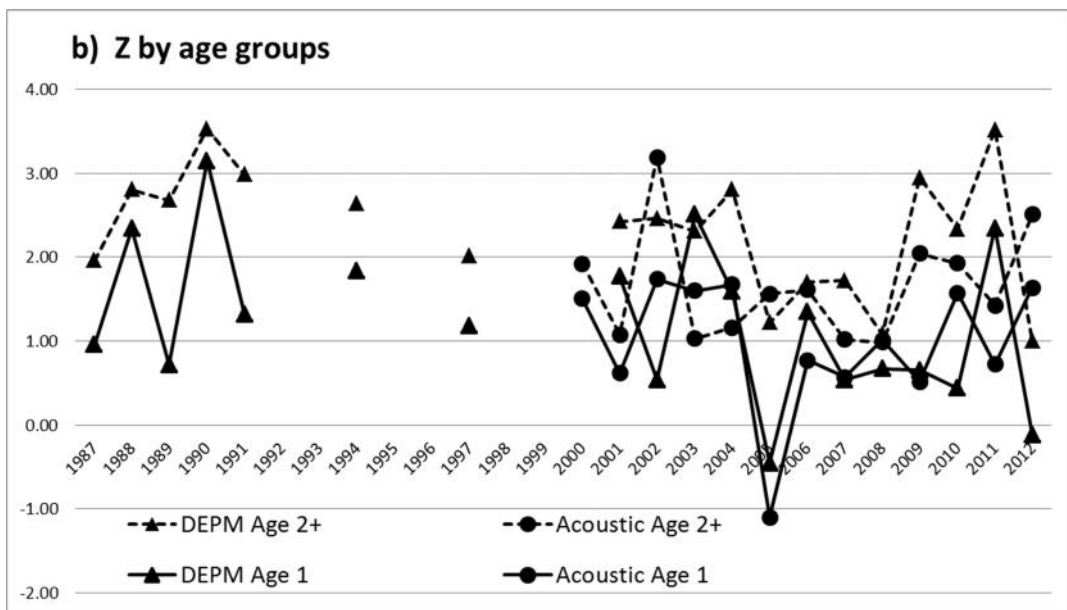
30

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

32 and Z2+).

33

34

35   a) Overall Z (Z1+):   b) Z at age 1 (Z1):   c) Z at age 2 and older (Z2+):
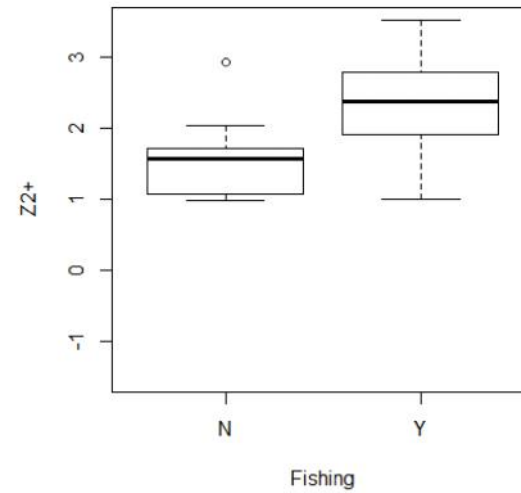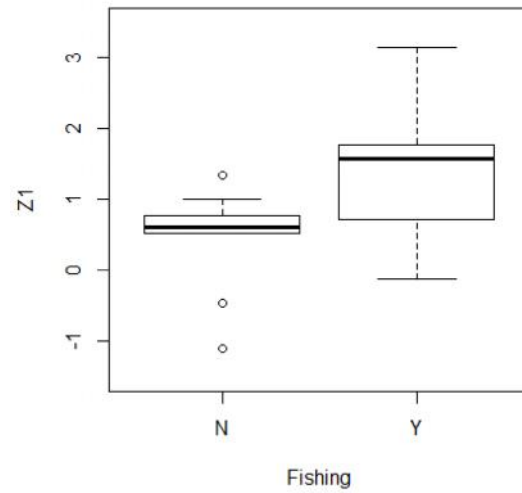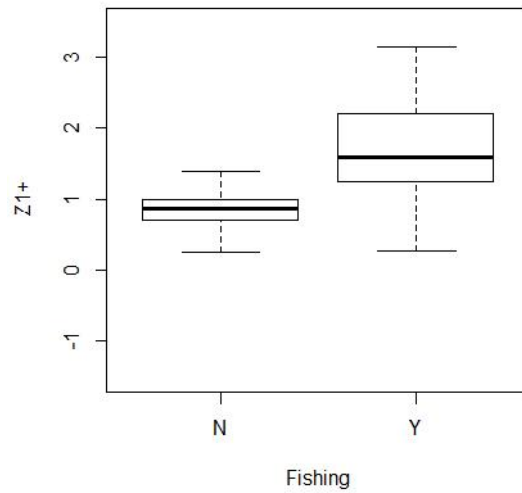
36

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+).

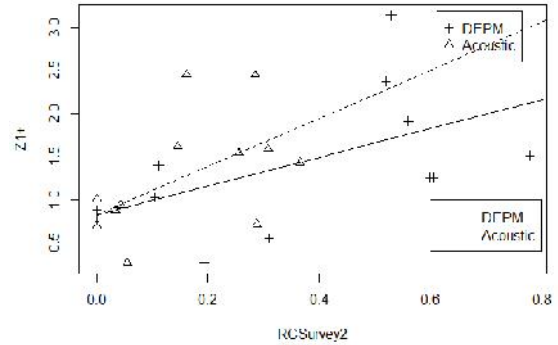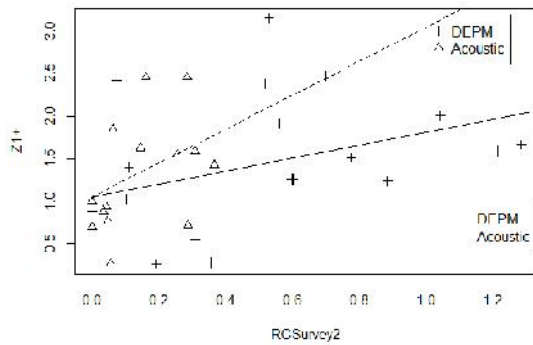Fishing legend: N= No Fishing (Closure period). Y= Fishing period.

39

40   Complete set of data   Subset of data

41

42

43

44
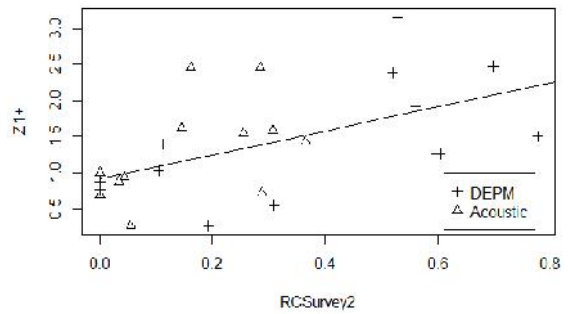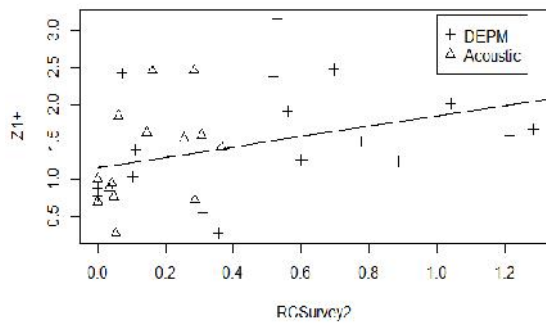
45
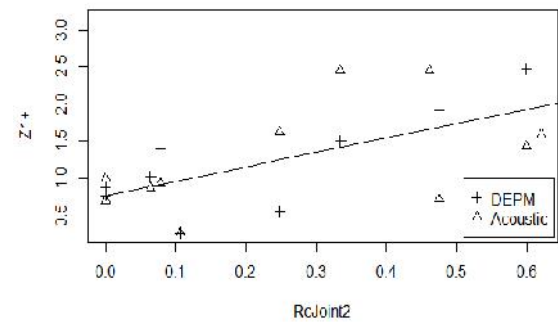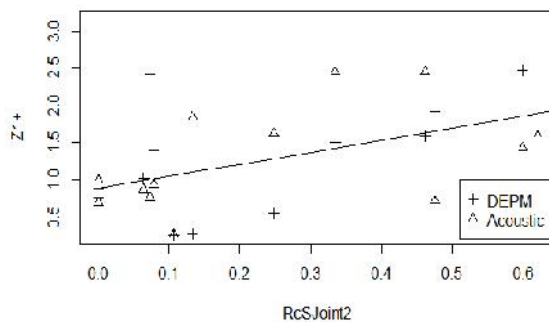
46   Figure 3: Fitted models (Model B1) of total Z estimates (Z1+) as a function of the relative
47   catches between surveys, RCsurvey2 (two and single slope fitting – upper and medium panels)
48   and RCJoint2 (bottom panels), for the complete set of data (left graphs) and for the subset of
49   data (which removes Z values with RC>0.8 and Years>2010) (right graphs).

50   Figure 4

51
52
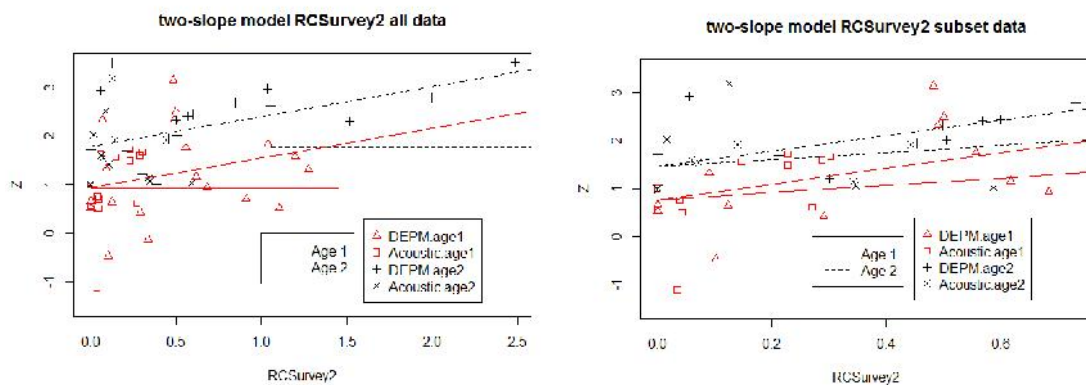
53
54
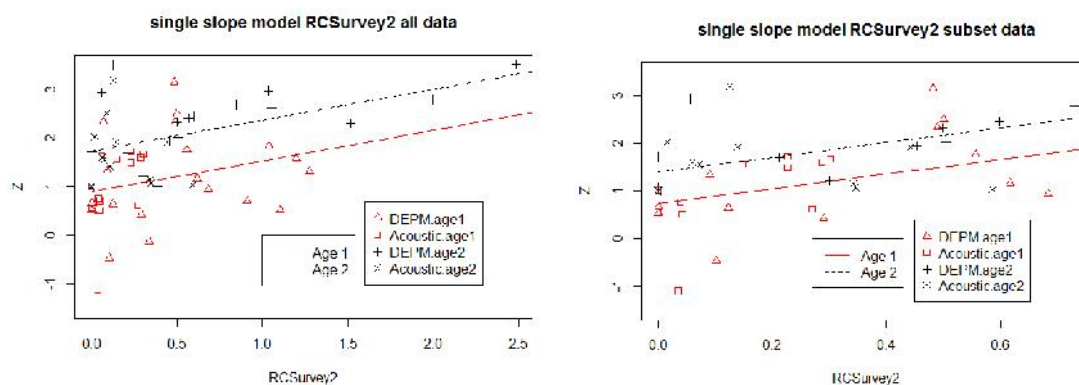
55
56   Figure 4: Fitted models for the Z by age (Z1 and Z2+) as a function of the relative catches
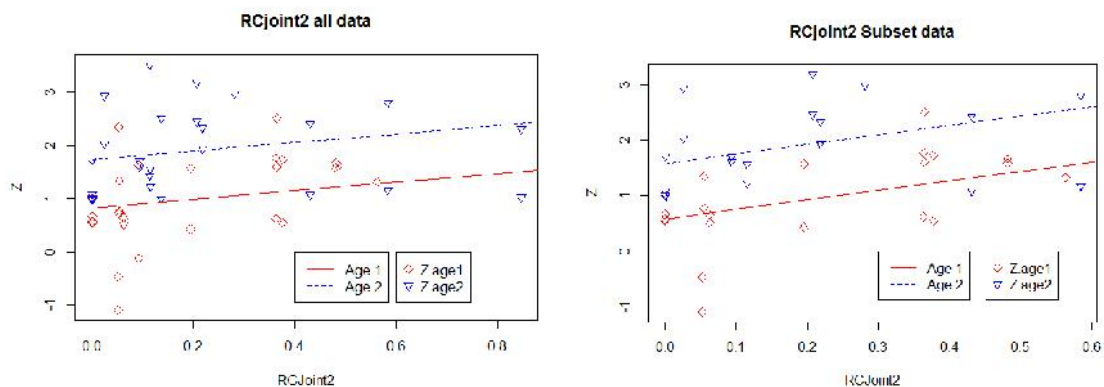
57   between surveys, RCsurvey2 and RCJoint2 for the complete set of data (left graphs) and

58   for the subset of data (which removes Z values with RC>0.8 and Years>2010) (right

59   graphs). In all cases dashed lines correspond with age group 2+ and continuous lines with

60   age 1. For the two slopes model the steeper lines correspond with the fitting of the Z

61   estimates from the DEPM series and the flatter lines refer to the fitting of Z estimates from

62   the acoustic series.

63

64   Figure 5

65   WSSQ minimization   LLHR minimization

66   a)   M1+
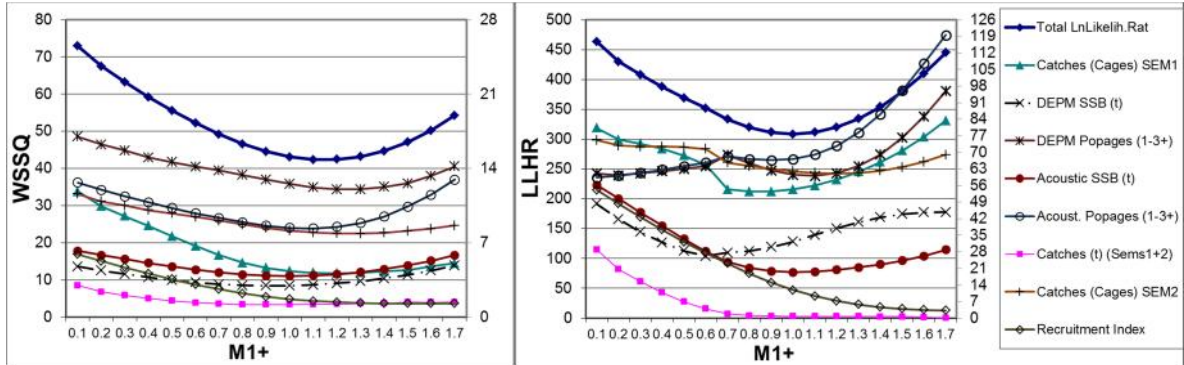
67

68

69   b)   M1 & M2+ (Jan-Dec)

70

71

72   c)   M1 & M2+ (July-June)
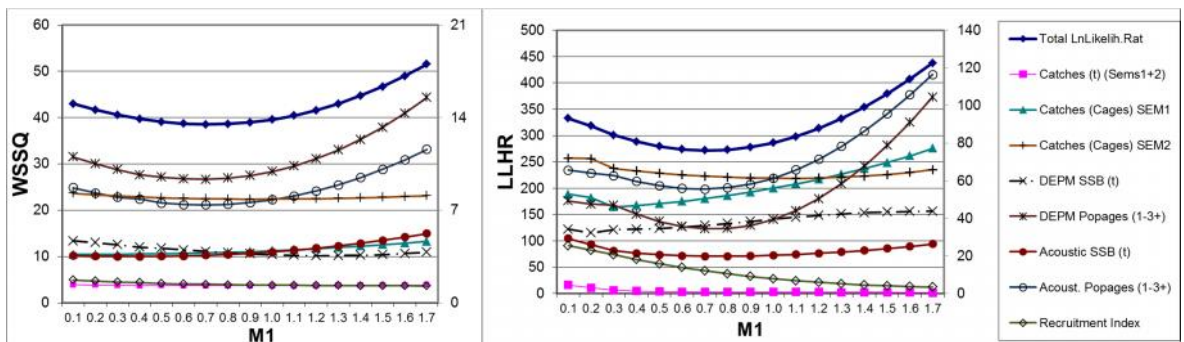
73

74   Figure 5: Response surfaces (total and partial contribution of the different auxiliary

75   information) for the two objective functions, weighted sum of squares (WSSQ, left panels)

76   and Log-Likelihood Ratios (LLHR, right panels) for a) a range of single natural mortality

77 values (M1+), b), for a range of natural mortality at age 1 (M1), optimizing M2+, with a

78 natural calendar year (January to December) and c) by age as before (case b) but with a

79 calendar year from July to June.
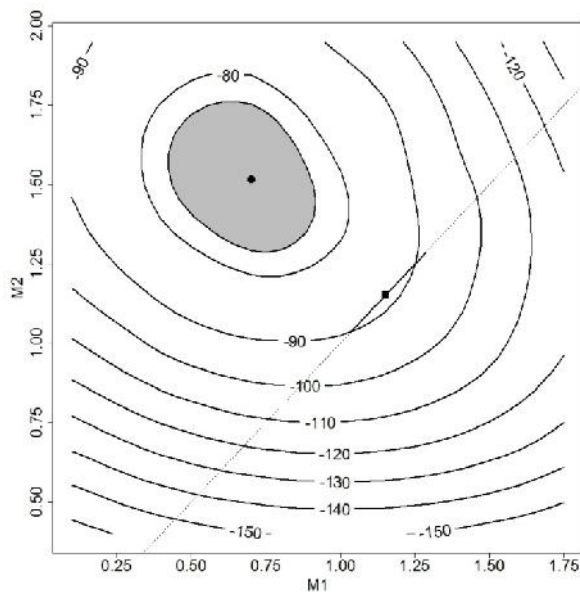
80

81

82   Figure 6
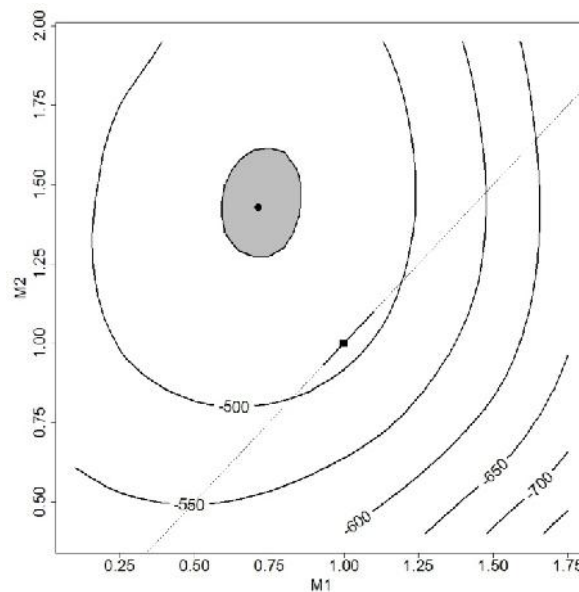
83   a)   No Errors

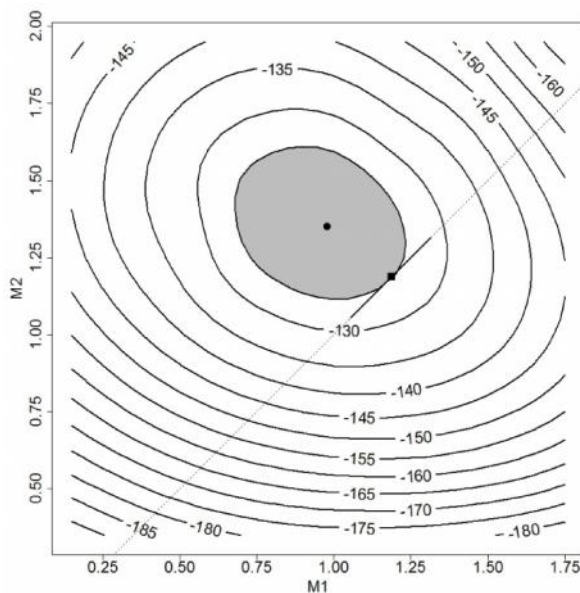84   WSSQ minimization   LLHR minimization
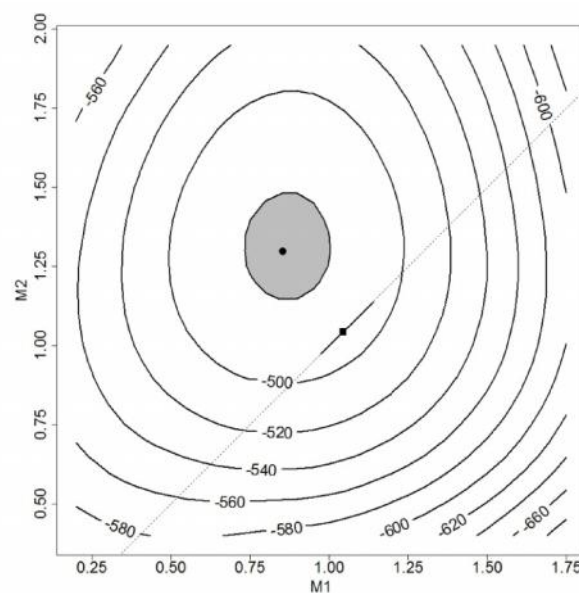

85

86

87   b)   5% Ageing Errors

88   WSSQ minimization   LLHR minimization

89

90   Figure 6: Joint likelihood profile contour plots for natural mortality estimates by age (M1 and

91   M2+), deduced from the two integrated assessments based either on weighted sum of squares

92   (WSSQ, left graphs) or on log-likelihood ratios (LLHR right graphs), both based on a calendar

4

93   year going from July to June, with information about the MLE estimates for M1 and M2+

94   (black dot) with their joint 95% confidence region (grey area) and MLE for a single natural

95   mortality common to all ages (M1+) and its 95% confidence limits (black square point and

96   lines along the 1:1 dotted line) for a) no ageing error default case (upper graphs) and b) for an

97   assumption of 5% ageing errors (see text for details).
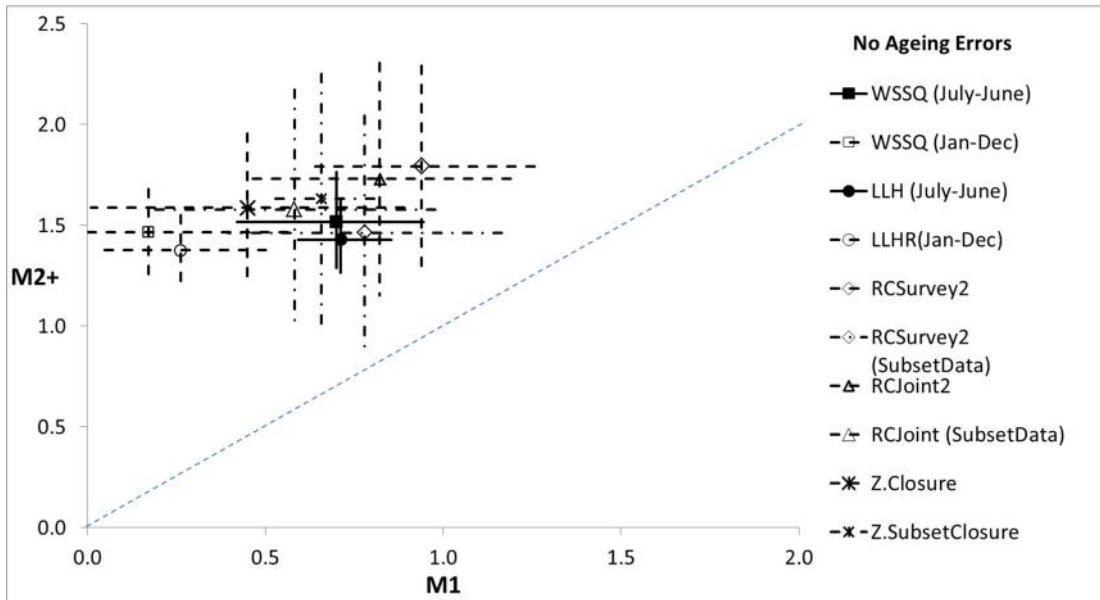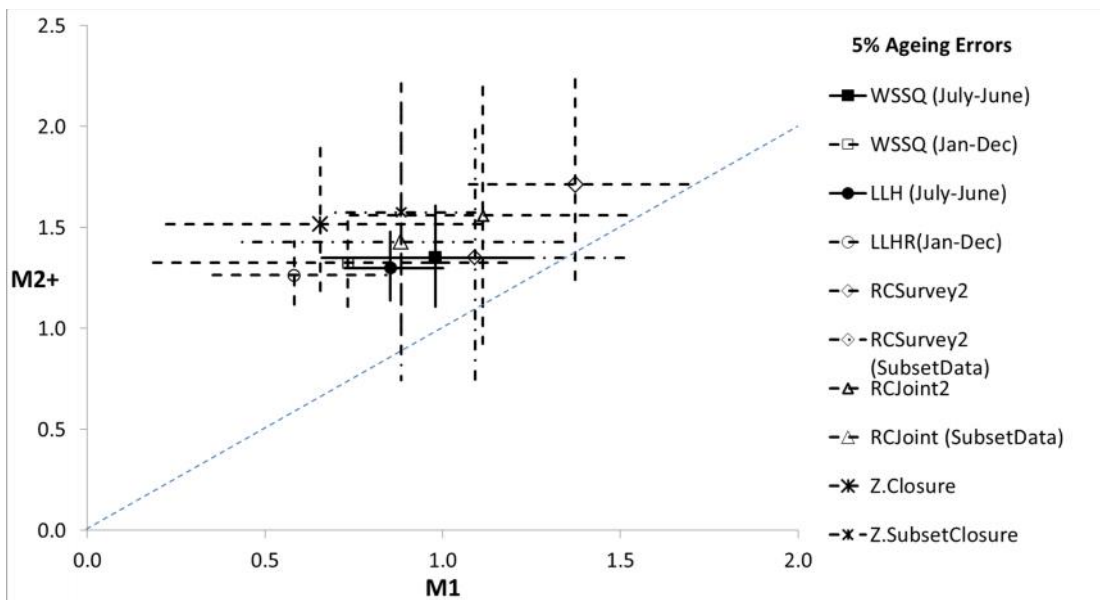
98

99

100

101   Figure 7:

102

103   a) No ageing errors

104

105   b) 5% Ageing Errors

106

107   Figure 7: Comparison of natural mortality estimates by age (M1 and M2+) for the different

108   estimation methods: a) for cases with no ageing errors b) for cases with 5% ageing errors. A

109   1:1 dotted line is included to check compatibility with the typical assumption of a single

110   natural mortality

List of Tables

Table 1: Matrix of age determination errors

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- 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 December 2009.

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).

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).

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

List of Figures:

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

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).

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.

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 year going from July

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