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

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

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 ($M_{2+}$) is markedly higher than at age 1 ($M_1$), which indicates senescent mortality, a possibility suggested a long time ago for this type of short-lived species.

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’œufs (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 appliqués aux séries temporelles de nombres aux âges issues des campagnes, et par des modèles d’évaluations de stock prenant en compte la saison. L’analyse suggère des valeurs de $M$ autour de 0.9 comme mortalité naturelle courante à tous les âges. Cependant, nous avons des éléments forts indicateurs que la mortalité aux âges 2 et plus ($M_{2+}$) est remarquablement plus forte qu’à l’âge 1 ($M_1$) ce qui suppose un signe de mortalité sénéscente, 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
with senescence, such as the mutation accumulation theory or the antagonistic pleiotropy theory (see reviews and discussions in Woodhead 1998; Williams et al. 2006; Golubev 2009).

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

The Bay of Biscay anchovy (Engraulis encrasicolus L.) is a fast growing and short-lived species, fully mature at age 1, and rarely exceeding its third year of life (Uriarte et al. 1996; Petitgas et al. 2010). In this region, anchovy is prey, along with other small pelagic fish, for piscivorous species such as hake, megrim, sea bass, tunnidae or cetaceans, among others (Preciado et al. 2008; Goñi et al. 2011; Lassalle et al. 2011; López-López et al. 2012). The adult anchovy population is monitored yearly by two independent research surveys: an acoustic survey (Massé 1996; Massé et al. in press) and an egg survey applying the Daily Egg Production Method - DEPM (Somarakis et al. 1994; Motos et al. 2005; Santos et al. 2011, in press). Both surveys provide estimates of biomass and population numbers at age, which are included in the assessment of this stock carried out by ICES (International Council for the
Exploration of the Sea). A Bayesian two-stage biomass model (Ibaibarriaga et al. 2008) is used for this assessment. Until 2004, ICA (Integrated Catch at age Analysis, Patterson and Melvin 1996) was used (ICES 2005). Until 2013, natural mortality rate has been assumed to be constant at 1.2 per year for all ages. This value was inferred in the nineties from direct DEPM estimates of the population at age, assuming that they were absolute and unbiased (Uriarte et al. 1996; Prouzet et al. 1999). While the Bayesian model presumes constant catchability across ages and surveys, ICA calculated the catchability at age which was 50% higher for age 2 than for ages 1 or 3 (ICES 2005) in both surveys. This was not regarded as a realistic outcome, taking into account the standard designs of both the DEPM and acoustic surveys, which included non-selective fishing gears for adults (capable of catching sizes well below minimum anchovy sizes in spring), and the sufficient spatial coverage of anchovy distribution (ICES 2013). Certainly, an alternative explanation of the findings could be that natural mortality is not constant over age.

Due to recruitment failures since 2001 and subsequent low biomass estimates (ICES 2013), the anchovy fishery in the Bay of Biscay was closed between 2005 and 2010. However, since scientific surveys were still ongoing during its closure, they provided a unique opportunity to estimate the actual natural mortality rate and possible patterns in natural mortality at age. Likewise, this closure allowed comparisons to be made between total mortality rates during the closed period and those in the former period of exploitation, in order to get natural and fishing mortality estimates under the assumption that no major changes in M occurred between both periods (Gulland 1983; Vetter 1988; Cook 1994; Sinclair 2001).
In this paper, several methods for estimating the natural mortality of the anchovy in the Bay of Biscay were applied. First, a direct analysis of the variance (ANOVA) of total mortality rate (Z) derived from consecutive survey estimates of the population in numbers at age was performed, where Z in the closure period was equivalent to the natural mortality rate (M). Next, M was estimated by regression of Z based on an indicator of fishing mortality (F) derived from the ratio of catches to the survey estimates of abundance. Thus, M is calculated from the intercept of Z at zero fishing mortality, which includes information from surveys at other F rates. Finally, an integrated assessment with a seasonal (half-year) separable fishing mortality model was applied to catch and survey data in order to find natural mortality rates and patterns that would optimize data fit, under the assumption of equal survey catchability at age. This approach provides M estimates that best fit with all historical survey information (including the two spring surveys and an acoustic recruitment index started in 2003 – Boyra et al. 2013) and the historical catches at age. Therefore the successive methods gradually use a larger amount of information. Furthermore, while the first two approaches assume log-normal errors of the population at age estimates from surveys, the integrated assessment will in addition allow for multinomial errors.

2. Materials and Methods

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

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

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

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

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

$$Z_{a,y,s} = \ln \left[ \frac{U_{a,y,s}}{U_{a+1,y+1,s}} \right] = \ln \left[ \frac{N_{a,y}Q_{a,s}\exp(e'_{a,y,s})}{N_{a+1,y+1}Q_{a+1,s}\exp(e'_{a+1,y+1,s})} \right] = Z_{a,y} + \ln \left[ \frac{Q_{a,s}}{Q_{a+1,s}} \right] + e_{a,y,s}$$
We refer to this as a Z estimate. Z estimates are further split into the natural and fishing mortality components:

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

Equation 1

Three Z estimates are derived: Z1+, from ages 1+ to 2+; Z1, from age 1 to 2; and Z2+, from ages 2+ to 3+. Notice that Z1+ will generally be closer to the Z of the most abundant age classes (in this case, age 1). Since surveys are carried out at spawning time in May, Z estimates refer to mortality rates from May to May. These estimates rely on two assumptions: 1) catchability is similar over age, and 2) survey observation errors follow log-normal distribution and are of similar average magnitude in both surveys.

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

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

\[ \hat{Z}_{a,y,s} = Year + Survey + [Old] + \varepsilon \]  

(Model A1, Equation 2)

Old is in brackets because it only applies in the joint analysis of Z1 and Z2+. As the year factor will cover the inter-annual variability in Z due to either natural (ecological) or fishing causes, the former analysis should serve to assess whether or not the Z estimates provided by the two surveys are consistent. This was checked by testing the statistical significance of the Survey factor and, for the analysis by age, of the Survey * Old first order interaction.
Next, we tested the effect of closure on the overall and age-dependent $Z$ values, which during the closure period, will be our direct estimate of the natural mortality rate ($M$):

$$Z_{a,y,s} = \text{Fishing} + \text{Survey}_{y} + \left[\text{Old}\right] + \text{Interactions} + \varepsilon \quad \text{(Model A2, Equation 3)}$$

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

2.2 Natural mortality estimates from linear models

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

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

where the coefficient of proportionality of the Relative Catches over survey estimates ($RC$) to $F$ equals the catchability coefficient of the surveys (assumed constant across ages) ($Q_{s}$). If $RC$ can be estimated then it can be used to calculate $M$ from Equation 1, as the intercept of the linear model. However, the problem with this approach is that the fitted $Z$ will appear in the
independent covariate (RC). In order to avoid this, we considered two alternative formulations of RC and checked the sensitivity to them:

\[
\text{RCSurvey}_2^{a,y} = \frac{C_{a,y}}{(U_{a,y,s} + U_{a+1,y,s})/2}
\]  
\[
\text{RCJoint}_2^{a,y} = \frac{\sum_{s} (U_{a,y,s} + U_{a+1,y,s})/4}{s}
\]

Equation 5

Equation 6

The first RC estimator provides an estimate by survey (RCSurvey2) using as denominator the arithmetic mean of the abundances provided by the survey at the beginning and end of the Z estimate period. The second estimator RCJoint2 provides a single joint indicator of fishing intensity for each year from both surveys together, by taking as denominator the average population provided by both surveys during the same period. In the latter case the analysis will be restricted to the years when both surveys were carried out in parallel, so that the two Zs estimates of the year will be linked by the same RCJoint estimate.

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

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

\[
\hat{Z}_{a,y,s} = M_{a,y,s} + F_{a,y,s} + \varepsilon_{a,y} = M + [\text{Old}_a] + Q_s \cdot \text{RC}_{a,y} + \text{Survey} + \text{Interact} + \varepsilon_{a,y,s}
\]

(Model B, Equation 7)
With $M$ (natural mortality) being the intercept either at age 1 ($M_1$) or for all ages together ($M_1+$) - depending on the subset of data being analyzed - *Old* is now a dummy variable, being 0 for age 1 and 1 for age 2+. This term will indicate the increase of natural mortality in fish of age 2+ relative to $M$ at age 1 ($M_1$), for the joint analysis of $Z_1$ and $Z_{2+}$. $RC$ accounts for the Relative Catches between surveys of the respective age $a$ in year $y$, and coefficient $Q_s$ accounts for proportionality of $RC$ to fishing mortality $F$. *Survey* is a dummy variable, being 0 for DEPM and 1 for acoustics, and this term will reflect any potential effect of the acoustic survey relative to the DEPM on $Z$ estimates. *Interact* are the potential first and second order interactions of the former variables, which were initially checked.

For the joint analysis of $Z$ by age ($Z_1$ and $Z_{2+}$), our assumption about catchability, constant across age and necessary to estimate $Z$, implies that the first or second order interactions referring to the slope changing by age are not significant as the slope coefficient is the catchability of the survey. Secondly, the intercepts reflecting $M$ are population parameters which should be similarly estimated by the surveys. As such, first order interactions of intercepts with surveys should not be significant. Therefore, the only interaction which could be significant is that of the slopes by survey, which would correspond with the common assumptions in most assessments of different catchabilities by survey. We will refer to the two-slope model as the one allowing different slopes on RCSurvey2 by survey (but with constant slopes across ages), while we will refer to the single slope model as the one forcing a common slope for both surveys.

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

### 2.3 Natural mortality estimates from integrated assessments
Finally, an integrated catch at age analysis with a seasonal (half-yearly) separable fishing mortality model was applied to the catch and survey data currently used by ICES for the assessment of this fishery (ICES 2013): Catches in tons and at age on a half-yearly basis, spring surveys; Acoustic and DEPM estimates of total biomass (tons) and populations at age (numbers); and finally, an acoustic survey on juveniles (JUVERA Survey index, started in 2003, which is used to tune the recruitment at age 1 with a power catchability function). The purpose, as before, was to check what levels and patterns of natural mortality at age optimize an integrated assessment, under the assumption of equal catchability at all ages in the surveys. Natural mortality by age was applied either to a calendar year, going from January to December or from July to June (the latter was checked because the main surveys are carried out in May, i.e. closer to July than to January). The model was fitted using two different approaches: the first one assumes, as before, that observations (catches or survey estimates in biomass and by age) are subject to log-normal errors and the objective function is a direct minimization of a weighted sum of squared residuals (WSSQ fitting - like in ICA analysis - Patterson and Melvin 1996); the second approach is similar to the former one except that it assumes that all age disaggregated data (catches and population at age estimates) are subject to multinomial errors and hence are entered as percentages at ages 1, 2 and 3+. In the latter case, model fitting is achieved by maximization of the log-likelihood (using log-likelihood ratios - LLHR fitting). Given the general agreement in both surveys in terms of percentages at age, and the poorer agreement in terms of biomass trends (ICES 2013), it seems that the multinomial approach for indexes at age is probably a suitable way to deal with the type of errors associated with survey observations. Details of the model’s fitted objective functions are given in Appendix A. The two modeling approaches were run in Microsoft Excel, using Solver for objective function optimization. Convergence was verified using different starting parameter values and likelihood of fitted models was calculated (see Appendix). Confidence
intervals for natural mortality estimates were obtained using the profile likelihood method. Based on the likelihood ratio test, the 95% confidence interval around the joint optimum of $\hat{M} 1$ and $\hat{M} 2+$ is defined as the pairs of $M 1$ and $M 2+$ which satisfy the following inequality:

$$\ln(L(\theta, \hat{M} 1, \hat{M} 2+)) - \ln(L(\theta, M 1, M 2+)) \leq \frac{1}{2} \chi^2_2(.95)$$

Equation 8

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

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

$$AICc = -2\ln (\text{likelihood}) + 2*K + (2*K*(K+1))/(n-K-1),$$

Equation 9

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

2.4 Sensitivity analysis

Sensitivity to some observations, that looked noisy at first sight and might have become too influential for the particular methods applied, was tested by including and excluding such data (when excluded we will refer to the subset of data). For raw data direct analysis during the closure period (2005-2010), the 2005 and 2006 survey data resulted in negative $Z$ estimates between them, indicating that either 2005 estimates were too low or 2006 estimates too high.
As for the linear models, years with high RC values (above 0.8) were considered unlikely to be actually happening (due to the difficulty of producing such a fishing impact) which led us to suspect some noisy, excessively low biomass estimates from the surveys during those years. In addition, years 2011 and 2012 were checked for sensitivity as they resulted in extremely different Z estimates by survey due to a large discrepancy in the 2012 biomass estimates (ICES 2013). For the integrated assessment, analyzing sensitivity to the inclusion/exclusion of the 2012 survey biomass estimates was considered sufficient (the year of maximum biomass divergence – ICES 2013).

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

\[ C = A \cdot E^{-1} \]

Equation 10

Corrections were not allowed to reduce the size of any age class below 20% of its original value (before correction) and ad hoc changes were applied to ensure those minimums (by restoring enough numbers from the contiguous age class in proportion to the removals
produced on the original amount so as to still allow 20% of the starting amount). As for the catches, corrections were applied to international catches separately over three periods: before surveys (January – mid-May), after surveys (mid-May - June) and in the second half of the year.

3. Results

a) Direct Z and M estimates (Model A)

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

Natural mortalities deduced from Z estimates by age during the fishing closure period (proxies of M1 and M2+) were slightly affected by the omission of the 2005 and 2006 noisy estimates and turned out to be M1=0.66 (CV=11%) and M2+=1.63 (CV=19%) (Table 2).

Such big difference in Z by age was consistently shown in both surveys (Figures 1 & 2 and Table 2) in the time series (Model A.1) and for the two fishing periods (Model A.2) (with P(Old)<0.0001 and p(Old*Survey)> 0.2 in both models).

b) Natural mortality estimates from linear models (Model B)
M estimates (intercepts) did not differ statistically between surveys, neither in the case of Z1+ (p[Survey]>0.6) nor by ages Z1 and Z2+ (p[Survey]> 0.3 and p[OLD*Survey]>0.25) for any RC index or subset of data. Therefore the requisite for the joint analysis of the Z from both surveys using this model was verified.

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

Analysis of Z by ages (Z1 and Z2+) revealed significant differences in the intercepts (M) by age (P[Old]<0.001) for any RC index. In the case of RCSurvey2, the two-slope model (Figure 4) pointed to M1=0.94 and M2=1.79, with CVs around 17% and 14%, respectively (Table 4). These estimates were close to the mean of individual survey estimates (Table 4) but the slopes by survey were not significantly different (p=0.437). The single slopes model
became fully significant and resulted in very similar values. Using RCJoint2 (Table 4 and Figure 4, bottom panels) resulted in slightly lower M1 (at 0.82, CV=23%) and rather similar M2 (at 1.73, CV=17%).

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

C) Natural mortality estimates from integrated assessments

Optimization for a single overall natural mortality (M1+, common for all ages) including all input data resulted in M values of around 1.15 and 1 for the WSSQ and LLHR optimizations, respectively (Table 5a). In all cases, the response surface was rather flat around the optimum (+/- 0.1), being basically guided by the age-structured survey indexes, followed by the catches at age information and finally, to a lesser extent, by the biomass survey indexes - which in fact favored slightly lower M1+ optimums (around 0.7-1.1) (Figure 5a). In all cases, the small contribution of JUVENA favored M1+ values at or above the synthetic optimum. The sensitivity of these results to the omission of the 2012 survey estimates was negligible, with optima differing by less than 1% (not shown for simplicity).
Optimization of natural mortality by ages (M1 and M2+) for a Jan-Dec calendar year suggested, for both objective functions, that the lower the M1 the better the fitting achieved, though improvements gradually reduced, being minimal below 0.7 (Figure 5b) with optimum M1 around 0.15-0.3 and M2+ around 1.35-1.45 (Table 5b). Applying a July-June calendar year provided optimums for both objective functions of around 0.7 for M1 (Figure 5c and Table 5c) and 1.4-1.5 for M2+ (see joint confidence intervals by models in Figure 6a&b). Results are basically guided by the age-structured survey indexes which provide a rather parallel response, whilst all other inputs are non-informative (almost flat) (Figures 5b & c). Compared to the assessments assuming a single natural mortality (M1+), the assessments allowing M at age to be estimated (M1/M2+) get a better fitting (higher likelihood - Figure 6) and lower Akaike’s Information Criterion (Table 5). These results were insensitive to the omission of the 2012 survey estimates (not shown).

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

D) Sensitivity to Ageing Errors

Inclusion of 5% ageing errors did not affect the compatibility of Z1+ estimates by survey, neither in the raw data analysis (P=0.97), nor in the log-linear models (P=0.71). This compatibility also applied to the analysis of Z by age where all terms with Survey were not significant either. Therefore the joint analysis of both surveys was again statistically supported.
Consideration of a 5% ageing error raised up the M1+ estimates by about 0.14 in direct and lineal model analyses, resulting for the subset of data all M1+ in the range of 0.94-1.08 (Table 2 and 3). Incorporation of this ageing error into the integrated models leads to minor increases of the original M1+ estimates (by about 0.04), resulting in poorer fits and larger AICc than for uncorrected data (Table 5).

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

The correction for a 5% ageing error reduces the differences of M between age by increasing M1 estimates by about 0.2 and 0.3-0.4 in the direct and lineal model analysis, respectively, and by reducing M2+ by a lesser extent (by about 0.08- 0.16). Nevertheless, M1 remains invariantly below M2+, even though statistical significance is sometimes lost (Table 3). Both integrated models, when considering a 5% ageing error, also obtained a reduction of the differences of M by age by increasing M1 and reducing M2+, but to a larger extent for the January to December calendar year. Nevertheless, M1 remains invariantly below M2+.

Certainly, the improvement in fitting achieved by allowing M to change by age is reduced when compared to no ageing errors, but the differences are still significant (even though only at alpha 0.06 for the WSSQ) (Figure 6) and the Akaike’s Information Criterion improves (is reduced), therefore still endorsing the M by age models over the single M1+ models.

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

4. Discussion
Estimating natural mortality is one of the main challenges in stock assessment (Vetter 1988; Hilborn and Walters 1992; Gislason et al. 2010), and in order to do it, availability of research surveys is essential (Sinclair 2001; Sparholt et al. 2002; Zhao et al. 2003; Francis 2011). The basic assumption of this paper was that the direct monitoring program running since 1987, through two research surveys (23 DEPM and 18 Acoustic surveys) and the closure of the fishery for 5 years should enable the overall level of natural mortality and its pattern by age to be inferred for the Bay of Biscay anchovy. This was supported by the compatibility of the $Z$ estimates from both surveys and because, in spite of the large variability inherent to the data, $Z$ differed significantly between the open and closed fishing periods, being lower during the latter period and therefore indicative of the natural mortality rates. Moreover, mortality at ages two and older ($Z_{2+}$) was significantly higher than at age one ($Z_1$) throughout the time series, suggesting an increasing pattern of natural mortality by age.

The series of $Z$ estimates have a large inter-annual variability which must be linked either to observation errors in the surveys or to variability in natural and fishing mortality, or both. Observation errors in surveys are evidenced by the fluctuations in $Z$ between consecutive surveys (sometimes reaching negative values) and by the occasional strong divergences of survey estimates (as in 2012). Variability of fishing mortality naturally happens for the fisheries, which tend to stabilize catches when exploiting a highly fluctuating population (like anchovy). Some variability of natural mortality has always been presumed and could be linked to changes in the ecological environment (Vetter 1988; Zwolinski and Demer 2013). For these reasons, we have chosen gradually improved estimators of natural mortality, allowing for increasing data input and, in principle, greater noise filtering.
The direct and linear models provide a natural mortality for all age groups (M1+) of between 0.81 and 1.15, which decreases to 0.78-0.92 after filtering the suspected noise. The integrated models indicate M1+ at about 1.15 for WSSQ and 1.00 for LLHR, i.e., at the upper range of the estimates in the former models. Even though these estimates are not statistically different, there can be several reasons explaining this preference for upper M1+ in the integrated models. Firstly, their results include, in addition to the spring surveys, other auxiliary information which partly favors this upper range of M1+ values, mainly by the recruitment index and to a lesser extent the catches by age. Secondly, it should be pointed out that linear models make inferences of M1+ from the decay between age groups 1+ to 2+, whilst integrated models fit simultaneously the three age classes (1/2/3+) with the same M1+, and as such the former estimates may be closer to the weighted mean of M by age (according to their abundance), while the latter is closer to an arithmetic mean (as residuals by age have equal weights). Hence, weighted M1+ to age class abundance should favor the M1+ at the lower range pointed out before, because M1 is lower, and will serve to better describe the average change of the whole population. In any case, this results in a most likely range going from 0.78 (RCJoint2) to 1 (log-likelihood assessment), which corresponds with an annual survival of between 46% and 37%. If a single figure is needed, a rough compromise could be in the middle of the ranges, close to 0.9 for M1+ (annual survival rate of 41%).

These results point towards a lower M1+ than the currently assumed value of 1.2, which was calculated in the 1990s on the basis of the DEPM survey alone (Uriarte et al. 1996; Prouzet et al. 1999). Moving to an M1+ of 0.9 would imply a reduction of the average historical estimates of SSB by about 30-35%, and an inverse parallel increase of fishing mortality estimates.
This average natural mortality for adult anchovy in the Bay of Biscay is just slightly below the values of 1.08 and 1.34 which result from applying Hoening’s equation (1983) (for a Tmax of 4) and that of Pauly (1980) (for von Bertalanffy growth parameters Linf, K and t0 about 18.05 cm, 0.77 and 0.72, respectively, as fitted to DEPM survey observations and a mean temperature of 16 ºC). Nevertheless, these M1+ estimates are rather similar to, albeit slightly higher than, the ones reported for short-lived species of similar growth, such as sprats, some Sardinops or Engraulidae (Beverton 1963, 1992; MacCall 1973; Methot 1989; Iversen et al. 1993; Sinovčić 2000), but at a lower level than the ones reported for Peruvian anchovy (Pauly et al. 1987), Anchoa mitchilli (Newberger and Houde 1995) and other Engraulidae of smaller maximum sizes (Bayliff 1967).

All the analyses improved by allowing M to change with age: the Old factor was retained in the linear models and the likelihood of the integrated models improved significantly when M was estimated by age compared to the single common M1+ modeling (Figure 6). This led to the conclusion that M1 was significantly lower than M2+ (Figure 7): On the one hand, the direct Z estimate and the linear models resulted in a range of M1 from 0.45 to 0.94 when using the full dataset, and a narrower range of about 0.6-0.8 with the most reliable subset of data. This corresponds with an annual survival of about 55%-45% for the 1-year-old group. On the other hand, M2+ was consistently about twice the value of M1: 1.59 to 1.79 for M2+ with the full dataset and 1.4-1.65 for the most reliable subset of data. This corresponds with an annual survival rate of about 25%-19% for ages two and older.

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

Our data do not allow saying when this additional mortality at age 2 and older happens during the year; however the sharp decrease of the 2 and 3 year-olds is already noticeable in the fishery after spawning, during the second half of the year (ICES 2005, 2013; Uriarte et al. 1996). This could have been the result of some permanent emigration of the old (2+) fishes outside of the major fishing grounds, off the Bay of Biscay, but such a possibility has never been proven and it is well known that, every spring, old fishes concentrate again to spawn in the southeast of the Bay of Biscay (Motos et al. 1996) where the surveys take place. Therefore, this increasing mortality at age 2 and older is most likely due to either increased vulnerability to predation at older ages or to natural biological mortality, probably reflecting senescence of anchovies at age 2 and older. No major concentration of predators on adults in early summer has been reported. The Bay of Biscay is an area of bottom-up controlling of the upper trophic levels (Lassalle et al. 2011), with anchovy being one (and not the main) among several small pelagic and other fishes (such as sardine, sprat, horse mackerel, blue whiting, ...
connecting the plankton communities to piscivorous species (Sanchez and Olaso 2004; Preciado et al. 2008). It contributes to the diets of demersal species such as hake, monkfish, megrim and tunnidae but mainly as juveniles (Guichet 1995; Preciado et al. 2008; Lezama-Ochoa et al. 2010; Goñi et al. 2011, 2012; López-López et al. 2012), whilst in adult anchovy it seems that some demersal fishes (John dory and hake, etc) and cetaceans prey routinely all year around (Preciado et al. 2008; Mahe et al. 2007; Lassalle et al. 2012; Meynier et al. 2008). Therefore, by discarding any ecological higher predation on adults, we tend to think that senescence might be occurring at the age of two and older, in accordance with the expectation of observable senescent mortality affecting short-lived cupleoids (Beverton 1963).

We hypothesized that this anchovy population may suffer from “reproductive stress” inducing increased mortality, particularly after its second spawning event. It is known that the large energy cost of reproduction can induce some varying rates of mortality due to “reproductive stress”, as shown for cod (Hutchings 2005), or in extreme cases, of semelparous species like Pacific salmon Oncorhynchus, which reproduces and dies, whereby dramatic hormonal changes induce starvation that causes intestine deterioration by necrosis and inflammatory processes during spawning migration (McBride et al. 1986). Examples of mortality associated to reproductive stress in short-lived species are common, as in invertebrates (squids and shrimps – Caddy et al. 1996) and fishes such as Aphia minuta (an extremely short-lived goby where apoptosis of enterocytes is related to post spawning mortality – Caputo et al. 2002), capelin Mallotus villosus (Vilhjálmsson 2002; Gjøsæter 1998) and in the short-lived gadoid Norway pout (Nielsen et al. 2012). Anchovy in the Bay of Biscay invests much energy in reproduction having one of the highest spawning frequencies among the Engraulidae, capable of increasing slightly with size and age (Uriarte et al. 2012), which results in a very high daily
fecundity (Santos et al. in press). Many of the 1-year-old fishes lay down a spawning check at
the end of the spawning season (in early summer) (Petitgas and Grelier 2003; Uriarte et al.
2002, in press) being probably indicative of the limiting condition of many anchovies after
spawning (Pecquerie et al. 2009). While they have reached about 88% of their maximum
attainable growth (18.3 cm) by the age of 2, spawning starts earlier and probably lasts longer
than at age 1, with a likely increase in the number of batch-spawning events during the
spawning season (Motos et al. 1996; Motos 1996; Pecquerie et al. 2009), in accordance with
the indications for other Engraulidae (Parrish et al. 1986; Claramunt et al. 2007; Cubillos and
Claramunt 2009). On average, 2-year-old anchovies do not resume opaque edge formation in
otoliths until mid-June, beyond the mid-point of the spawning season (Uriarte et al. 2002, in
press), this being also indicative that much of the energy of this age group is invested in
reproduction during the first half of the year. This reproductive strategy of anchovy may
result in some physiological reproductive stress at the end of the spawning season for the age
2+ group, which may explain the increase in natural mortality observed in our analysis. As
such, this population of anchovies may have evolved in its fluctuating environment by
allowing some non-negligible chances of reproducing over two spawning seasons before
senescence. This would enhance the opportunities to overcome single (not repeated)
environmentally-induced failures of recruitment. This strategy would place anchovy among
capelin, which mostly dies after its first spawning (Vilhjálmsson 2002; Gjøsæter 1998), and
sprats, sardines or sandeels which have progressively longer adult life expectation with
several annual reproductive cycles (Cook 2004; Nunes et al. 2011; Zwolinski and Demer
2013); ending up with the herrings, which seem to have up to eight reproductive seasons
during their life history before increased mortality by senesce shows up (as for Norwegian
spring-spawning herring – Beverton et al. 2004). To our knowledge, senescence in
Engraulidae had only been suggested previously for Northern anchovy (from age 2 and older
– MacCall 1973 – based on analysis of catch ratio from catches and surveys) and for the anchovy in the Yellow Sea (from age 3 and older – Zhao et al. 2003 – based on analysis of surveys). We suspect that this pattern of increasing mortality by age may be applicable to other Engraulidae, whereby assessments following the usual constant mortality assumption often results in non-understandable big changes in catchability by age in surveys (Giannoulaki et al. 2014).

In terms of assessment, the new M estimates would impact the average level of spawning biomass approximately in proportion to the reduction in average M. For instance, for LLHR modeling, moving from the single M1+ hypothesis at 1.2 to its optimum at 1.00 would reduce mean biomass by about 27%, while moving further from the optimum M1+ to its optimal mortality by age would result in a minor reduction of about 5%. So once M1+ is set at its optimum, a further change to the optimum M by age does not imply additional major changes to mean biomass estimates. In spite of this, however, this latter change to M by age will probably have implications in any population and fishery projections which might be required for the provision of advice to managers. For instance, for this anchovy old populations (composed mainly of ages 2+) will decay faster (with M around 1.4) than young ones (composed mainly of age 1) (with an M around 0.7-0.8). Therefore, in terms of management moving to unbiased M estimates should also improve the quality of advice as reported for other species (Lee et al. 2011; Zwolinski and Demer 2013). Certainly, the perception of fishing mortality will change inversely to the estimation of biomass levels. Furthermore, as the new M estimates change the perception of cohort dynamics in mass, this will affect the estimation of management-related reference points (F_{0.1}, F_{MSY}, etc.).
These results are partly sensitive to the maximum level of ageing errors put into consideration. Correction of such a 5% ageing error moved the direct and linear model estimates of M1+ and of M1 upwards, while slightly reducing M2+. This was associated with a partial loss of the statistical significance of the difference between M1 and M2+ (Figure 7b). Integrated models were less affected in the M1+ estimates (remaining just slightly above the original optimums), and also showed a reduction of the differences between M1 and M2+ (Table 5). Nevertheless, integrated assessments show that models allowing M by age estimates achieve better fittings than single M1+ models (with p<0.056 for the WSSQ and p<0.000 for the LLHR) (Figure 6). Therefore, even after consideration of this maximum level of potential ageing errors, the significant increase pattern of natural mortality at age is still supported by integrated assessments. In any case, M estimates will be conditioned by the actual level of ageing errors affecting the observations.

Certainly, the results depend upon the assumption of the constant catchability of surveys across ages, on which Z estimates rely (an assumption we have proved to be compatible with the data). Sustaining this is not true would be difficult to understand, given the good spatial coverage of the surveys, and would imply that the prevailing null hypothesis should be on the assumption that M is equal across ages. Biologically, this is known not to be true (Vetter 1988), even though for simplification this has been the null hypothesis for the assessment of the exploited range of ages of most of the long and short-lived fish resources. Although this has already been questioned and revised for younger ages (Caddy 1991; Abella et al. 1997; Gislason et al. 2010), it has not been sufficiently revised yet for the inclusion of senescence in the older age classes. And, certainly for short-lived species, senescence should have been presumed to be noticeable not too long after reaching maturity (Beverton 1963). By accepting that the null hypothesis should be that senescence is present, then our analysis shows
consistency of the observations with the hypothesis, and we would rely more on the
observations of the age structures reported by surveys rather than on doubtful assumptions of
constant natural mortality across ages; and finally the assessment can become parsimonious
(as in our case with two surveys) in terms of demanding a lesser amount of parameters to
infer population size (i.e. lesser amount of catchability at age parameters in comparison to the
increased number of natural mortality by age).

A correct selection of the natural mortality serves to properly scale the assessments around
true population abundance values and this becomes particularly relevant in the context of
relative indexes of population abundance, and even more for short-lived species. In this paper
we have shown that that the overall natural mortality M1+ was somewhat below what had
been assumed so far, and furthermore, that natural mortality at ages 2+ is higher than at age 1,
in line with expectation of senescence. In achieving this conclusion, the continuous
monitoring of the population by two parallel and independent methods for many years,
including a period of fishing closure, has been essential, as it has provided sufficient contrast
for the analysis. The natural mortality issue should be revisited periodically when additional
years of survey observations and improvements in our base knowledge become available.
Relevant improvements may come from better understanding of survey catchability, or of the
accuracy of age determinations for this anchovy, besides, for instance, from monitoring
biological and biochemical markers of aging and reproductive stress or from further studies
on eco-trophic interactions.

Acknowledgements: The surveys for the monitoring of the anchovy fishery have been
supported by national funds from France and Spain (including the autonomous government of
the Basque Country) and by the EU Data Collection Regulation (through national programs).

Pablo Abaunza, Unai Cotano, Eneko Bachiller, Nicolás Goñi, Maite Louzao, Francisco Velasco and Izaskun Preciado are thanked for comments and discussion on some parts of the paper. Finally we wish to thank two anonymous referees for their valuable suggestions and comments which largely improved the paper. This paper is contribution nº 741 from AZTI (Marine Research).

REFERENCES:


Jørgensen C., and Holt, R.E., 2013. Natural mortality: Its ecology, how it shapes fish life histories, and why it may be increased by fishing. J. Sea Res. 75: 8–18


Table 1: Matrix of age determination errors

<table>
<thead>
<tr>
<th>True Age</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3+</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>1</td>
<td>0.00</td>
<td>0.95</td>
<td>0.05</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>2</td>
<td>0.00</td>
<td>0.04</td>
<td>0.95</td>
<td>0.01</td>
<td>1.00</td>
</tr>
<tr>
<td>3+</td>
<td>0.00</td>
<td>0.00</td>
<td>0.05</td>
<td>0.95</td>
<td>1.00</td>
</tr>
</tbody>
</table>
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.

### a) No Ageing Errors

<table>
<thead>
<tr>
<th>Data Sources</th>
<th>DEPM Surveys</th>
<th>ACOUSTIC Surveys</th>
<th>Pooled Surveys</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Z Means by periods</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Z1+</td>
<td>Z1</td>
<td>Z2+</td>
</tr>
<tr>
<td>N (complete data)</td>
<td>19</td>
<td>19</td>
<td>19</td>
</tr>
<tr>
<td>Complete Series</td>
<td>1.48</td>
<td>1.22</td>
<td>2.32</td>
</tr>
<tr>
<td>(1987-2012) CV</td>
<td>13%</td>
<td>19%</td>
<td>8%</td>
</tr>
<tr>
<td>Fishing Period</td>
<td>1.69</td>
<td>1.47</td>
<td>2.53</td>
</tr>
<tr>
<td>(1987-2004 &amp; 2010-12) CV</td>
<td>12%</td>
<td>17%</td>
<td>7%</td>
</tr>
<tr>
<td>Closure Period</td>
<td>0.87</td>
<td>0.55</td>
<td>1.73</td>
</tr>
<tr>
<td>(2005-2009) CV</td>
<td>21%</td>
<td>53%</td>
<td>19%</td>
</tr>
<tr>
<td>Subset Closure Period</td>
<td>0.89</td>
<td>0.62</td>
<td>1.92</td>
</tr>
<tr>
<td>(2007-2009) CV</td>
<td>9%</td>
<td>7%</td>
<td>29%</td>
</tr>
</tbody>
</table>

### b) 5% Ageing Errors

<table>
<thead>
<tr>
<th>Data Sources</th>
<th>DEPM Surveys</th>
<th>ACOUSTIC Surveys</th>
<th>Pooled Surveys</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Z Means by periods</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Z1+</td>
<td>Z1</td>
<td>Z2+</td>
</tr>
<tr>
<td>N (complete data)</td>
<td>19</td>
<td>19</td>
<td>19</td>
</tr>
<tr>
<td>Complete Series</td>
<td>1.79</td>
<td>1.64</td>
<td>2.17</td>
</tr>
<tr>
<td>(1987-2012) CV</td>
<td>12%</td>
<td>15%</td>
<td>8%</td>
</tr>
<tr>
<td>Fishing Period</td>
<td>2.06</td>
<td>1.95</td>
<td>2.36</td>
</tr>
<tr>
<td>(1987-2004 &amp; 2010-12) CV</td>
<td>10%</td>
<td>13%</td>
<td>7%</td>
</tr>
<tr>
<td>Closure Period</td>
<td>1.03</td>
<td>0.78</td>
<td>1.66</td>
</tr>
<tr>
<td>(2005-2009) CV</td>
<td>18%</td>
<td>35%</td>
<td>20%</td>
</tr>
<tr>
<td>Subset Closure Period</td>
<td>1.05</td>
<td>0.85</td>
<td>1.88</td>
</tr>
<tr>
<td>(2007-2009) CV</td>
<td>18%</td>
<td>18%</td>
<td>30%</td>
</tr>
</tbody>
</table>
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>
<thead>
<tr>
<th>CASE Z1+</th>
<th>Estimates by Surveys</th>
<th>Pooled Estimates</th>
<th>Pooled Estimates &amp; 5% Ageing Errors</th>
</tr>
</thead>
<tbody>
<tr>
<td>RC estimator</td>
<td>RCsurvey2 RCsurvey2</td>
<td>RCsurvey2 RCsurvey2</td>
<td>RCJoint2 RCJoint2</td>
</tr>
<tr>
<td>Linear model with</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) Complete set of Data \ N:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept (= M1+)</td>
<td>1.136 0.954</td>
<td>1.052 1.152 0.885</td>
<td>1.137 1.301 1.001</td>
</tr>
<tr>
<td>CV</td>
<td>26% 26%</td>
<td>19% 15% 20%</td>
<td>20% 15% 23%</td>
</tr>
<tr>
<td>RC slope coefficient</td>
<td>0.656* 2.380*</td>
<td>1.991* 0.694 1.633</td>
<td>3.107 1.048 2.188</td>
</tr>
<tr>
<td>CV</td>
<td>69% 55%</td>
<td>62% 49% 33%</td>
<td>44% 36% 32%</td>
</tr>
<tr>
<td>Additive Slope component</td>
<td>-0.915*</td>
<td>-1.951*</td>
<td></td>
</tr>
<tr>
<td>CV</td>
<td>81%</td>
<td>65%</td>
<td></td>
</tr>
<tr>
<td>Model P-Value</td>
<td>0.1636 0.095</td>
<td>0.0837 0.0496 0.0064</td>
<td>0.0119 0.0099 0.0043</td>
</tr>
<tr>
<td>R-Squared</td>
<td>11% 21%</td>
<td>15% 12% 27%</td>
<td>26% 20% 29%</td>
</tr>
<tr>
<td>b) Subset of Data \ N:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept (= M1+)</td>
<td>0.762 0.884</td>
<td>0.826 0.920 0.781</td>
<td>0.936 1.078 0.941</td>
</tr>
<tr>
<td>CV</td>
<td>45% 32%</td>
<td>26% 22% 22%</td>
<td>29% 23% 27%</td>
</tr>
<tr>
<td>RC slope coefficient</td>
<td>1.787 2.583*</td>
<td>2.804 1.651 1.831</td>
<td>3.829 2.103 2.309</td>
</tr>
<tr>
<td>CV</td>
<td>41% 54%</td>
<td>44% 33% 27%</td>
<td>38% 34% 31%</td>
</tr>
<tr>
<td>Additive Slope component</td>
<td>-1.130*</td>
<td>-1.731*</td>
<td></td>
</tr>
<tr>
<td>CV</td>
<td>96%</td>
<td>75%</td>
<td></td>
</tr>
<tr>
<td>Model P-Value</td>
<td>0.0333 0.0927</td>
<td>0.015 0.006 0.0013</td>
<td>0.014 0.0079 0.0039</td>
</tr>
<tr>
<td>R-Squared</td>
<td>35% 26%</td>
<td>32% 25% 41%</td>
<td>34% 28% 35%</td>
</tr>
</tbody>
</table>
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>
<thead>
<tr>
<th>CASE Z by ages</th>
<th>Estimates by Surveys</th>
<th>Pooled Estimates</th>
<th>Pooled Estimates &amp; 5% Ageing Errors</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RC estimator</td>
<td>RC survey2</td>
<td>RC survey2</td>
</tr>
<tr>
<td>SURVEY Series</td>
<td></td>
<td>DEPM</td>
<td>POOLED</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Acoustic</td>
<td>Single</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Single-Slope</td>
<td>Single</td>
</tr>
<tr>
<td>Linear model with</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) Complete set of Data \ N:</td>
<td>38</td>
<td>26</td>
<td>64</td>
</tr>
<tr>
<td>Intercept1 (= M1)</td>
<td>0.951</td>
<td>0.933</td>
<td>0.940</td>
</tr>
<tr>
<td>CV</td>
<td>23%</td>
<td>26%</td>
<td>17%</td>
</tr>
<tr>
<td>OLD (addition for M2+)</td>
<td>0.999</td>
<td>0.644</td>
<td>0.854</td>
</tr>
<tr>
<td>CV</td>
<td>26%</td>
<td>46%</td>
<td>23%</td>
</tr>
<tr>
<td>Intercept2 (= M2+)</td>
<td>1.951</td>
<td>1.577</td>
<td>1.794</td>
</tr>
<tr>
<td>CV</td>
<td>18%</td>
<td>24%</td>
<td>14%</td>
</tr>
<tr>
<td>RC slope coefficient</td>
<td>0.527</td>
<td>0.412*</td>
<td>-0.009*</td>
</tr>
<tr>
<td>CV</td>
<td>45%</td>
<td>234%</td>
<td>9593%</td>
</tr>
<tr>
<td>Additive Slope component</td>
<td>0.621*</td>
<td>0.873*</td>
<td>90%</td>
</tr>
<tr>
<td>Model P-Value</td>
<td>0.0002</td>
<td>0.0875</td>
<td>0.1942</td>
</tr>
<tr>
<td>R-Squared</td>
<td>39%</td>
<td>19%</td>
<td>15%</td>
</tr>
<tr>
<td>b) Subset of Data \ N:</td>
<td>23</td>
<td>22</td>
<td>45</td>
</tr>
<tr>
<td>Intercept1 (= M1)</td>
<td>0.682</td>
<td>0.861</td>
<td>0.780</td>
</tr>
<tr>
<td>CV</td>
<td>44%</td>
<td>32%</td>
<td>25%</td>
</tr>
<tr>
<td>OLD (addition for M2+)</td>
<td>0.754</td>
<td>0.610*</td>
<td>0.684</td>
</tr>
<tr>
<td>CV</td>
<td>41%</td>
<td>54%</td>
<td>32%</td>
</tr>
<tr>
<td>Intercept2 (= M2+)</td>
<td>1.436</td>
<td>1.471</td>
<td>1.464</td>
</tr>
<tr>
<td></td>
<td>30%</td>
<td>29%</td>
<td>20%</td>
</tr>
<tr>
<td>------------------</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>RC slope coefficient</td>
<td>1.748</td>
<td>0.629*</td>
<td>0.748*</td>
</tr>
<tr>
<td>CV</td>
<td>36%</td>
<td>163%</td>
<td>116%</td>
</tr>
<tr>
<td>Additive Slope component</td>
<td></td>
<td>0.878*</td>
<td>1.079*</td>
</tr>
<tr>
<td>CV</td>
<td></td>
<td>91%</td>
<td></td>
</tr>
<tr>
<td>Model P-Value</td>
<td>0.0044</td>
<td>0.1474</td>
<td>0.1474</td>
</tr>
<tr>
<td>R-Squared</td>
<td>42%</td>
<td>18%</td>
<td>18%</td>
</tr>
</tbody>
</table>
Table 5: Summary results of the integrated assessments for a) No ageing errors and b) 5% ageing errors.

<table>
<thead>
<tr>
<th></th>
<th>a) No ageing errors</th>
<th>b) 5% ageing errors</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>WSSQ</td>
<td>LLHR</td>
</tr>
<tr>
<td>Mean M1</td>
<td>1.148</td>
<td>1.000</td>
</tr>
<tr>
<td>CV (aprox)</td>
<td>5.4%</td>
<td>4.3%</td>
</tr>
<tr>
<td>Objective Function</td>
<td>42.3093</td>
<td>308.5502</td>
</tr>
<tr>
<td>Total LogLikelihood</td>
<td>-88.1095</td>
<td>-490.0735</td>
</tr>
<tr>
<td>AIC</td>
<td>362.2191</td>
<td>1166.1470</td>
</tr>
<tr>
<td>AICc</td>
<td>419.3563</td>
<td>1223.2842</td>
</tr>
<tr>
<td></td>
<td>M. (January to December)</td>
<td>M. (January to December)</td>
</tr>
<tr>
<td>Mean M1</td>
<td>0.172</td>
<td>0.262</td>
</tr>
<tr>
<td>CV (aprox)</td>
<td>88%</td>
<td>44%</td>
</tr>
<tr>
<td>Mean M2+</td>
<td>1.467</td>
<td>1.376</td>
</tr>
<tr>
<td>CV (aprox)</td>
<td>7.5%</td>
<td>6.1%</td>
</tr>
<tr>
<td>Objective Function</td>
<td>38.1907</td>
<td>270.0725</td>
</tr>
<tr>
<td>Total LogLikelihood</td>
<td>-73.1320</td>
<td>-451.5218</td>
</tr>
<tr>
<td>AIC</td>
<td>334.2641</td>
<td>1091.0436</td>
</tr>
<tr>
<td>AICc</td>
<td>392.8215</td>
<td>1149.6009</td>
</tr>
<tr>
<td>LogLikelihood ratio vs single M</td>
<td>14.9775</td>
<td>38.5517</td>
</tr>
<tr>
<td>Probability of the Ratio</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td></td>
<td>M. (July to June)</td>
<td>M. (July to June)</td>
</tr>
<tr>
<td>Mean M1</td>
<td>0.700</td>
<td>0.712</td>
</tr>
<tr>
<td>CV (aprox)</td>
<td>19%</td>
<td>9%</td>
</tr>
<tr>
<td>Mean M2+</td>
<td>1.518</td>
<td>1.429</td>
</tr>
<tr>
<td>CV (aprox)</td>
<td>8.0%</td>
<td>6.4%</td>
</tr>
<tr>
<td>Objective Function</td>
<td>38.5194</td>
<td>271.5586</td>
</tr>
<tr>
<td>Total LogLikelihood</td>
<td>-74.6555</td>
<td>-452.8735</td>
</tr>
<tr>
<td>AIC</td>
<td>337.3109</td>
<td>1093.7471</td>
</tr>
<tr>
<td>AICc</td>
<td>395.8683</td>
<td>1152.3045</td>
</tr>
<tr>
<td>LogLikelihood ratio vs single M</td>
<td>13.4541</td>
<td>37.1999</td>
</tr>
<tr>
<td>Probability of the Ratio</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
</tbody>
</table>
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.
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