

1 **Estimating growth from sex ratio-at-length data in species with sexual size**  
2 **dimorphism.**

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6 **Abstract**

7 Individual growth is one of main processes which drive the population dynamic and  
8 stock productivity. Many fish have differential individual growth by sex. Growth is  
9 affected by sexual development, which is frequently reached at different sizes in males  
10 and females. Differences in growth per sex after maturity produce different patterns in  
11 sex proportions-at-length in the population. If these patterns are the consequence of  
12 changes in life history parameters, sex ratio-at-length data can be expected to contain  
13 significant information on the population life history. In this paper I first explore how  
14 post-maturity changes in life history may shape these patterns in sex ratio-at-length;  
15 secondly I explore how these data may be used to estimate growth parameters and  
16 finally I discuss how this information may be useful for stock assessment purposes. I  
17 use European hake data and life history parameters to model expected sex ratios. The  
18 results suggest that reproductive energy allocation leads to a lower growth rate in male  
19 hakes than in females. Moreover the sex ratio-at-length may provide useful information  
20 for estimating growth parameters in dimorphic species if additional information from  
21 other sources is available. Finally, these data can easily be factored into stock  
22 assessment models to help provide a better estimation of growth parameters and  
23 mortality rates. This valuable, accurate and cheap biological information (sex ratio-at-

24 length) may play an important role in population dynamic models and stock assessment  
25 for species with sexual size dimorphism.

26 Keywords: individual growth; sex ratio; sexual dimorphism; stock assessment models;  
27 hake.

## 28 **1. Introduction**

29 Individual growth is one of main processes which drive productivity and population  
30 dynamics. Biological knowledge about individual growth is essential to perform fish  
31 stock assessments and to be able to give scientific advice for management decision-  
32 making. Stock assessment models deal with the individual growth in many different  
33 ways. In age-based models such as VPA (Megrey, 1989; Shepherd, 1999), individual  
34 growth is frequently factored into the model by assigning weights to age groups based  
35 on hard structures such as otoliths, scales, etc. When this is not possible due to  
36 difficulties in interpreting hard structures, as in the case of European hake (de Pontual et  
37 al., 2006; Piñeiro et al., 2007), there are two options: if information is scarce a biomass  
38 dynamic model (Punt and Hilborn, 1996) can be drawn up. In such models individual  
39 growth is not estimated directly; instead a population growth rate that considers  
40 individual growth, natural mortality and recruitment all together is estimated. If stock  
41 information is good enough, different variants of length-based models can be drawn up.  
42 Platforms able to develop this kind of model include GADGET (Taylor, et al., 2007)  
43 and SS3 (Methot and Wetzel, 2013). Examples of these two implementations have been  
44 used for European hake (ICES 2010). In these statistical models individual growth  
45 parameters such as von Bertalanffy model parameters (von Bertalanffy, 1957) may be  
46 estimated within the model using the data available, which mainly comprise length-  
47 frequency in catches or surveys, although other sources of growth information such as

48 tagging-recapture data may also be used (Maunder and Punt, 2013). The growth  
49 parameters are estimated in such a way that the observed length frequency in each time  
50 step can be explained by the population dynamic model. A common problem is that the  
51 same information (length distributions) is also used to estimate other model parameters  
52 such as recruitment, selectivity and fishing mortality. This might create problems of  
53 over-parameterisation, correlation between parameters and the usual difficulties in  
54 estimating too many parameters with a limited amount of information. For this reason,  
55 the aforementioned models for European hake (ICES, 2010) have set  $L_{\infty}$  and only  
56 estimate  $k$  with the length frequency data.

57 This lack of data can be overcome with additional biological information. Kuparinen et  
58 al. (2012a) review ways of increasing biological realism in stock assessment models and  
59 conclude that scientists must go beyond the traditional assessment process and explore  
60 other information sources from other fields such as ecology, life history theory and  
61 evolutionary biology. Informative data are crucial in providing scientific advice. In  
62 fishery stock assessment “informative data” means those that lead to accurate estimates  
63 of abundance and reference points (Magnusson and Hilborn, 2007). Individual growth is  
64 a key datum in estimating population abundance and reference points; however, apart  
65 from age-length keys and tag-recapture data there is little additional information that  
66 could improve their estimation through length-based assessment models (Maunder and  
67 Punt, 2013).

68 Two important points not frequently addressed in stock assessment models are  
69 significant when individual growth data are sought. One is the impact of sexual  
70 development on growth and other life history traits, and the other (related to the first), is  
71 sexual dimorphism. Many fish species have indeterminate growth, which means that

72 they keep growing asymptotically after reaching adulthood. Indeterminate growth  
73 results from allocating less and less energy to growth and more to reproduction. Length  
74 at maturity affects the shape of the growth curve as a result of trade-offs between  
75 reproduction and growth (Czarnowleski and Kozłowski, 1998). The von Bertalanffy  
76 growth equation is an approximation of this growth process; however, its use has been  
77 criticised because it implies that the change in energy allocation after maturity does not  
78 influence the growth rate. Day and Taylor (1997) hold that growth models for  
79 indeterminate growth species should be specified by two different equations: a pre-  
80 maturity equation in which no energy is allocated to reproduction and a post-maturity  
81 equation where at least some energy is devoted to reproduction. Growth models of this  
82 kind are known as biphasic growth models (Quince et al., 2008), and they have been  
83 applied to explain the individual growth of numerous species (Alós et al., 2010a; Alós  
84 et al., 2010b; Porch et al., 2002).

85 Sexual size dimorphism (SSD) refers to different body sizes in adult sexes. SSD is very  
86 frequent in many fish species including plaice and most flatfish (Rijnsdorp et al., 2010)  
87 or Spanish mackerel, where females mature at a larger body size, grow at a slower rate  
88 and attain larger body sizes than males (Juan-Jordá et al., 2012). Hake is another species  
89 in which adult females have larger body sizes than adult males (Murua, 2010). If length-  
90 at-maturity is different in males and females, so might other traits be, such as growth  
91 and natural mortality. The differentiation of male and female reproductive strategies is  
92 expected to produce sex-specific optima for traits that affect longevity and ageing, often  
93 favouring a faster life strategy in males than in females (Bonduriansky et al., 2008).  
94 Fecundity selection favours larger females because fish fecundity increases  
95 isometrically with body weight (Stearns, 1992).

96 SSD species with different growth and mortality rates may produce a sex ratio-at-length  
97 that differs by 50%, with variable proportions depending on size (Marshall et al., 2006;  
98 Murua, 2010). Changes in growth after maturity and growth differences between males  
99 and females are the processes that shape the sex ratio-at-length. How these two  
100 processes interplay and produce different patterns in sex ratio-at-length is not well  
101 known and I have found no significant information on this issue in my review of the  
102 relevant literature. If sex ratios-at-length patterns result from different life history traits,  
103 the data can also be expected to contain information on growth and mortality. In  
104 European hake (*Merluccius merluccius*), males mature at a smaller sizes than females  
105 and also have smaller adult sizes than females (Murua, 2010). These different traits  
106 produce specific patterns in European hake sex ratio-at-length (Cerviño et al., 2013).  
107 This pattern could be useful for stock assessment models if a quantitative link between  
108 life history and sex ratios can be found. In this paper I explore this link, first developing  
109 a model to help understand how post-maturity changes in growth and mortality may  
110 shape the sex ratio-at-length; secondly developing a likelihood function that compares  
111 the observed and modelled sex ratio-at-length so as to enable growth parameters to be  
112 estimated; and finally discussing how this information may be factored into stock  
113 assessment models so that better scientific advice can be offered.

## 114 **2. Material and methods**

115 I use two sources of information in this analysis: (1) sex ratio-at-length data from  
116 European hake; and (2) a length-based model that takes into account sexual differences  
117 in growth and mortality after maturity.

118 The sex ratio-at-length is presented in Figure 1. The left-hand panel shows the historic  
119 figures from 1982 to 2008, and the right-hand panel shows the mean for 3 years (2006-

120 08), which is used later as a reference for examining the sex ratios produced by the  
121 model. These data come from Spanish sampling (IEO and AZTI) in the Bay of Biscay  
122 area (ICES Division VIIIa, b, c, d) including commercial fishing (trawl gillnet and long  
123 liners) and surveys. Sex data on hake north of the Bay of Biscay are not available  
124 because the fleets that operate in those areas land the fish un-gutted. The sex ratios  
125 shown in Figure 1 begin with figures of around 0.5 for fishes at 20 cm. Length classes  
126 below 20 cm are more difficult to sex accurately and were not sexed in the sampling  
127 process. From 25-30 cm the proportion of females starts to decrease, and reaches its  
128 minimum at around 40 cm, where the female ratio may be as low as 0.1. From 40 cm to  
129 60-70 cm the proportion of females rises progressively. Above 70 cm females account  
130 for 100% of the fish sampled. A similar pattern has been observed in recent years,  
131 although these extremely low historic proportions of females are never reached: the  
132 minimum ratio of females stands at slightly below 0.4.

133 *Length-based model.*

134 A length-based model is developed to reproduce hake dynamics. The model is sexed  
135 separately with a view to simulating the expected sex ratios under different life  
136 histories, considering different lengths at maturity,  $M$  and growth. These parameters  
137 may be different for pre-mature and post-mature fish, and also for post-mature males  
138 and females. The population is projected forward with constant recruitment, equal for  
139 males and females, until equilibrium is reached.

140 The different simulations are performed under different biological parameters that  
141 consider the current biological knowledge for males and females.

142 1. Pre-mature parameters (ICES 2010):

- 143           a.  $k=0.165$ ;
- 144           b.  $L_{\infty}=130$ ;
- 145           c.  $t_0=0$ ;
- 146           d.  $M=0.4$ .
- 147       2. Length at maturity (Murua, 2010; Dominguez-Petit et al., 2008):
- 148           a. Males ~32 cm
- 149           b. Females ~45 cm
- 150       3. Post-maturity:  $M$ ,  $L_{\infty}$  and  $k$  may take different values in males and females.
- 151           Given the reproduction cost these values are constrained by the pre-maturity
- 152           figures ( $k<0.165$ ;  $L_{\infty}<130$ ;  $M>0.4$ ).

153   The population model follows a length based dynamic similar to that described by

154   Taylor et al. (2007). The model works on a quarterly basis. The lengths range from 1 to

155   130 cm. To compute the equilibrium population based on the equation below a fish

156   population is started with a single recruit per year (0.5 males and 0.5 females) and

157   simulated throughout its lifetime, applying the dynamics described in following

158   equations, for a fixed level of fishing mortality, until the single initial individual is

159   virtually extinguished due to mortality (i.e. when abundance is reduced to  $1e-10$ ). In

160   each quarter the sequential dynamic comprises 3 processes: recruitment, mortality and

161   finally growth. The dynamic continues in the next quarter with the new recruitment.

162   Recruitment is apportioned equally on the first of May and the first of June, at the end

163   of quarters 1 and 2, which are the main recruitment season (Mehault et al., 2010;

164   Murua, 2010). Every year the recruitment abundance vectors for the four quarters are 0,

165   0.5, 0.5 and 0. The recruitment length distribution has the following mean:  $L_{\infty} * (1 -$

166    $\exp(-k * 0.25))$  and a standard deviation of 2 truncated to lengths 1.5 to 19.5 cm.

167 The number of individuals in the population after mortality (N1) is given by:

168 (1) 
$$N1_{t,l} = Rec_{t,l} * \exp(- (F_{t,l}+M_l) * 0.25)$$

169 where  $N1_{t,l}$  denotes the population numbers at length at the start of a quarter  $t$ .  $M$   
170 is the natural mortality and 0.25 is a the time step (quarter). Fishing mortality ( $F$ )  
171 is determined by a vector  $F_{t,l}$ , where  $F_{t,l} = f_t * S_l$ ; with  $S_l = 1 / (1 + \exp(-a*(l -$   
172  $L_{50})))$ ; where  $L_{50}=27$ ;  $a=0.2$ . Subindex  $t$  stands for time (always quarters in this  
173 model) and  $l$  stands for length.  $N$  is the population abundance.

174 Expected growth follows a von Bertalanffy model with parameters  $L_{\infty}$  and  $k$  with beta-  
175 binomial variability. The underlying idea is that an individual of length  $l$  grows  
176 according to the random variable:

177 (2) 
$$Growth_l \sim \text{Binomial}(g_{\max}, p_l), \text{ where } p_l \sim \text{Beta}(\beta \alpha_l, \beta),$$

178 (3) with  $\alpha_l$  chosen such that  $E[Growth_l] = g_{\max} * \alpha_l / (\alpha_l + 1) = (L_{\infty} - l) * (1 - \exp(-k_l$   
179  $* 0.25))$ .

180 where  $\beta$  controls the amount of variability in growth, with larger values of  $\beta$   
181 corresponding to lower variance in  $Growth(l)$ . The proportion of individuals in  $N1_{t,l}$   
182 that grow to length  $l'$ , denoted as  $g_{l,l'}$ , is given by the probability of the variable  
183  $Growth(l)$  taking the value  $l' - l$  and can be explicitly written as a function of  $g_{\max}, L_{\infty},$   
184  $k$  and  $\beta$ ; where  $g_{\max}=15$  and  $\beta=4$  in all simulations and  $L_{\infty}$  and  $k$  varies in different  
185 simulations.

186 The number of individuals of length  $l$  in the population after growth (N2) is given by

187 (4) 
$$N2_{t,l} = \sum_{l' \leq l} (N1_{t,l'} g_{l,l'})$$



188 All population numbers after a new recruitment (N) is incorporated to the population are  
189 given by:

$$190 \quad (5) \quad N_{t,l} = N2_{t,l} + \text{Rec}_{t,l}$$

191 where Rec is the recruitment in the quarter with figures 0, 0.5, 0.5 and 0 over the four  
192 quarters. And the model loops continue in equation 1 until the population is virtually  
193 extinguished. N1, N2 and N refer to the 3 sequential processes in each quarter.

194 Equilibrium catch numbers (C) at length are given by the equation:

$$195 \quad (6) \quad C_{t,l} = N_{t,l} * (1 - \exp(- F_{t,l} * 0.25))$$

196 Notice that this catch equation, like the dynamic model equations, does not follow the  
197 cohorts. It is not the same as the classic Baranov equation. This F can not be interpreted  
198 in the same way: for instance it does not have the same additive properties, although it  
199 is a close approximation to the Baranov equation when the time step is reduced.

200 The model works with the sexes separated. Sex subindices (m and f) are not presented  
201 in previous equations for simplicity. The equations for estimating sex-related results are  
202 the following:

203 The female sex ratio-at-length (SexRat) is calculated by:

$$204 \quad (7) \quad \text{SexRat}_{l,f} = N_{l,f} / (N_{l,m} + N_{l,f})$$

205 A Least Square fit is developed to minimise differences between observed (Obs) and  
206 modelled (Exp) sex ratios to explore the options for estimating growth parameters from  
207 sex ratio-at-length. The Least Square score (LS) is:

208 (8)  $LS = \text{sum}[(\text{Obs}(\text{SexRat}_{l,f}) - \text{Exp}(\text{SexRat}_{l,f}))^2]$ .

209 Operational sex ratios (OSR) refer to the ratio of individuals which are sexually active  
210 at a given time. The operational sex ratio in the population is estimated as follows:

211 (9)  $OSR = \text{sum}[N_{l,f} * \text{Mat}_{l,f}] / (\text{sum}[N_{l,f} * \text{Mat}_{l,f}] + \text{sum}[N_{l,m} * \text{Mat}_{l,m}])$

212 Finally, as a support for the growth estimations, some figures for sex  $L_\infty$  are required.  
213 These are estimated following the Charnov (1993) life history invariants for the ratio of  
214 length at maturity ( $L_{mat}$ ) to asymptotic length ( $L_\infty$ ). Charnov (1993) says that the ratio of  
215  $L_{inf}$  to  $L_{mat}$  is relatively constant among similar species. To estimate male and female  
216  $L_{inf}$  the aforementioned figures for length at maturity were used, along with the ratio  
217  $L_\infty / L_{mat}$  taken from different hakes all over the world as presented in FishBase  
218 ([www.fishbase.org](http://www.fishbase.org)). The 19 records available provide a mean value for this ratio of 2.49  
219 and an s.e. of 0.20.

### 220 3. Results and discussion

#### 221 3.1. How do growth and mortality affect sex ratio-at-length?

222 This section explores how different changes in life history parameters ( $k$ ,  $L_\infty$  and  $M$ )  
223 after maturity may shape the sex ratio-at-length. In the absence of post-maturity changes  
224 in life histories the female ratio should remain at 0.5 for all lengths.

225 Figure 2 shows the impact of a change in  $L_\infty$ ,  $k$  or  $M$  after maturity when males and  
226 females experience the same post-maturity figures. Males mature at 32 cm and females  
227 mature at 45 cm. This means that males change their life history figures before females.  
228 Reduction of  $L_\infty$  after maturity produces a decrease in the ratio of females (Figure 2.  
229 Left-hand panel). This decrease begins at 32 cm and is higher when the reduction of  $L_\infty$

230 is also higher. After reaching its minimum (0.3 with  $L_{\infty}$  reduction from 130 cm to 50  
231 cm), the female ratio increases to its maximum at around 50 cm. This increase is also  
232 higher and steeper when  $L_{\infty}$  reductions are more noticeable. After reaching the  
233 maximum, the female ratio stabilises up to maximum length (130 cm). Reducing  $k$  after  
234 maturity produces patterns similar to those found when reducing  $L_{\infty}$ . In both cases the  
235 modelled sex ratio is similar to the observed patterns (Figure 1). However, to reach  
236 similar figures, with 100% females for fish of 70 cm and longer, the growth reduction  
237 ( $L_{\infty}$  or  $k$ ) would have to be incredibly high. For instance, with a reduction of  $L_{\infty}$  from  
238 130 cm to 50 cm for mature males and females, the maximum ratio is never reached. 50  
239 cm is an unrealistic  $L_{\infty}$  for European hake, where females more than 100 cm long and  
240 males of around 60-70 cm are frequently found in commercial landings.

241 Figure 2 (right-hand panel) shows the impact of an equal (male and female) post-  
242 maturity  $M$  increase. In this case the pattern is totally different from the one described  
243 above for growth. When the male  $M$  increases (at 32 cm) the female sex ratio increases  
244 up to a size of 45 cm. At this size the female  $M$  also increases and becomes the same as  
245 the male  $M$ . Subsequently the female sex ratio stabilises with figures above 0.5. The  
246 higher the  $M$  increase, the higher the female sex ratio for larger fish is. However,  
247 although post maturity changes in  $M$  may shape the sex ratio-at-length, the  $M$  cannot by  
248 itself explain the sex ratios observed in Figure 1, because it never produces female  
249 figures below 0.5 after male maturity (32 cm).

250 Figure 3 presents the results of a simulation similar to those presented in Figure 2.  
251 However, by contrast with the previous simulation, in this case the changes in post-  
252 maturity parameters are different in males and females. Post maturity reductions in  $L_{\infty}$   
253 produce the female sex ratios presented in the left-hand plot. If the reduction in females

254 (from 130 to 90) is greater than the reduction in males (from 130 to 110 cm) the sex  
255 ratio decreases after male maturity, then increases until female maturity and then  
256 decreases again sharply (solid line). The pattern changes if the reduction in males is  
257 greater than that in females. In this case (dashed lines) the female sex ratio decreases  
258 after male maturity, then increases to 100% females. The size at which 100% females is  
259 achieved depends on the differences in  $L_{\infty}$  reduction between males and females. The  
260 greater the differences, the smaller the size at which a ratio of 100% females is  
261 achieved. If growth reduction is simulated with changes in  $k$  (middle plot) the results  
262 are quite similar to those for the  $L_{\infty}$  reduction. However, in this case a small proportion  
263 of males remains until the largest size is reached (130 cm). The sex ratio patterns are  
264 completely different if the post-maturity changes take effect at  $M$ . The reduction  
265 observed in the ratio of females after male maturity never happens. If the  $M$  increase is  
266 greater for females, then the female sex ratio tends towards zero for greater lengths. If  
267 the  $M$  increase is greater for males then the female sex ratio for large fish goes to 1.

268 This preliminary analysis shows some important features that reveal how changes in life  
269 histories after maturity may help to explain the sex ratios-at-length observed. First of all  
270 a post-maturity growth reduction is needed for a sex ratio pattern similar to those  
271 observed to be obtained. Furthermore, it is important for this reduction in growth to be  
272 more pronounced in males than in females. Changes in  $M$  may also alter the sex ratio-  
273 at-length, but they cannot by themselves explain the sex ratios observed.

### 274 3.2. *Optimisation analysis.*

275 An optimisation model is implemented to explore the usefulness of sex ratio-at-length  
276 data for estimating growth parameters. All the parameters that have an impact on the  
277 sex ratio at length must be considered, i.e.  $M$ ,  $L_{\infty}$  and  $k$  before and after maturity for

278 both sexes, making a total of 12 parameters. To avoid over-parametrisation problems,  
279 some additional information is needed to perform these simulations.  $L_{\infty}$  and  $k$  for pre-  
280 mature individuals are set equal in male and females as in the ICES (2010) model  
281 ( $L_{\infty}=130\text{cm}$ ;  $k=0.165$  and  $M=0.4$ ). Given the reproduction cost, these figures also act as  
282 a limit for the estimation of post-maturity parameters, with  $L_{\infty}=130$  and  $k=0.165$  being  
283 the upper limit for post maturity growth and with  $M=0.4$  being the lower limit for post-  
284 maturity natural mortality. This approach enables the options for estimating growth with  
285 sex ratio-at-length data to be explored. However, some limitations are observed and an  
286 alternative approach is also proposed. This consists of reducing the number of  
287 parameters estimated and setting  $L_{\infty}$  according to the ratio of maturity length to  $L_{\infty}$   
288 (Charnov, 1993). This ratio is calculated from additional data taken from different hake  
289 species in the FISHBASE database ([www.fishbase.org](http://www.fishbase.org)). The estimated mean ratio is  
290 2.5. Considering that males mature at 32 cm and females at 45 cm, this ratio makes  $L_{\infty}$   
291 80 cm for males and 112 cm for females.

292 Figure 4 shows the least square fit for two options: with free  $L_{\infty}$  and two different  
293 scenarios (left-hand panel) and with fixed  $L_{\infty}$  and 3 different scenarios (right-hand  
294 panel). Table 1 shows the parameters for each of these 5 scenarios (Sce. 1 and 2 for free  
295  $L_{\infty}$  and Sce. 3, 4 and 5 for fixed  $L_{\infty}$ ) with the corresponding least squares scores. The  
296 symbol “\*” in Table 1 indicates which parameters are estimated in each scenario.

297 The left-hand plot (Figure 4) shows the model fit for the four post-maturity growth  
298 parameters, i.e.  $L_{\infty}$  and  $k$  for males and females (solid line). Female  $L_{\infty}$  and  $k$  and male  $k$   
299 remain the same as in the pre-maturity levels. Male  $L_{\infty}$  is reduced from 130 cm to 66.5  
300 cm with an LS score of 0.150. If male  $M$  and  $L_{\text{mat}}$  (length at maturity) are also

301 estimated, these values increase from 0.4 to 0.44 (M) and from 32 cm to 33.2 cm  
302 (Lmat). The corresponding LS score is reduced from 0.15 to 0.129.

303 The right-hand plot (Figure 4. Solid line) shows that the post-maturity  $L_{\infty}$  reduction  
304 (from 130 cm to 112 in females and from 130 to 80 cm in males) approaches the  
305 observed values with  $LS=0.50$  (Table 1. Sce. 3). In this case no parameters are  
306 estimated. This fit may be improved if the values of  $k$  for males and females are also  
307 estimated (dashed line). In this case female  $k$  does not change and male  $k$  is reduced  
308 from 0.17 year<sup>-1</sup> to 0.11 year<sup>-1</sup> (Table 1. Sce. 4). This male post-maturity  $k$  reduction  
309 brings the LS score down from 0.50 to 0.189. This fit may also be improved if male  $M$   
310 and male Lmat (length at maturity) are also estimated (dashed line). In this case the LS  
311 score is reduced from 0.189 to 0.161 (Table 1. Sce 5). The corresponding  $M$  and Lmat  
312 figures are 0.45 and 33.1 cm. The best fit is obtained with a greater reduction in growth  
313 among males and a greater increase in  $M$  compared with the figures for females. These  
314 results are consistent with a higher cost of reproduction for males than females.

315 The system presented here to estimate growth based on the sex ratio-at-length has  
316 certain limitations. Firstly, the sex ratio-at-length is influenced by many different  
317 parameters ( $L_{mat}$ ,  $M$ ,  $k$  and  $L_{\infty}$ ), and those parameters differ for males and females.  
318 Different combinations of them may provide similar fits, making it hard to estimate  
319 growth. However, once these limitations are taken into consideration, the exercise  
320 performed is still useful in helping to understand how the cost of reproduction may  
321 affect the growth of males and females differently. In most scenarios the female  
322 parameters are constrained at the limit of the range, while the male parameters are  
323 estimated to get the best fit. This indicates the value of these data in relative terms, i.e.  
324 different combinations of the same parameter, such as  $L_{\infty}$  for both sexes, may result in

325 similar fits. To solve this situation additional information may be useful. Here the model  
326 fit is explored setting  $L_{\infty}$  for both sexes based on life history invariants ( $L_{\infty}/L_{mat}$  ratio).  
327 This constraint provides more realistic results and also provides a better estimation of  
328 other parameters. The fit without this constraint is female  $L_{\infty}=130$  and male  $L_{\infty}=66.5$   
329 cm, with these differences between males and females being much bigger than  
330 expected. Moreover, in this case  $k$  does not change since the cost of reproduction in  
331 terms of growth is only charged to  $L_{\infty}$  by the model. With post-maturity  $L_{\infty}$  based on life  
332 history invariants, the model charges the cost of reproduction in terms of growth to both  
333 parameters ( $L_{\infty}$  and  $k$ ). In both cases the increase in post-maturity  $M$  is also a cost of  
334 reproduction. Differences in natural mortality for the different sexes have also been  
335 observed in other hake species where males have a higher  $M$  than females (Gatica and  
336 Cubillos, 2004) and in summer flounder (Maunder and Wong, 2011).

337 The importance of the survival cost of reproduction has received little attention in  
338 fishery assessment models. This cost arises from the energy allocated to reproduction,  
339 e.g. gonad development and egg production, and to reproductive behaviour, e.g.  
340 increased risk of being caught or a loss of efficiency in foraging (Kuparinen et al.,  
341 2012b). The simulations performed here show that there is information in sex ratio-at-  
342 length data that enables post-maturity  $M$  to be estimated. This estimation is more  
343 accurate if additional information on other parameters and constraints on those  
344 parameters can be set according to ecological knowledge. The models drawn up also  
345 show that males, which have a relatively higher survival cost than females, help to  
346 explain the sex ratio observed. The lack of knowledge of the reproductive behaviour of  
347 hake makes difficult to figure out why males have a higher reproductive cost than  
348 females. However, it has been observed that hake caught by gillnetters and long-liners  
349 in the reproductive areas and seasons are mainly females. The presence of hydrated eggs

350 in these females is evidence that males are also present. Gillnets catch fish that are  
351 moving and long-lines catch fish that are eating. Male reproductive behaviour involving  
352 reduced movement and reduced food intake might explain the higher reproductive cost  
353 of males.

354 The negative correlation between  $k$  and  $L_{inf}$  is also a known life history invariant  
355 (Charnov and Berrigan, 1993). Estimating a value for this parameter based on similar  
356 populations or species might also help to reduce the over-parameterisation problem and  
357 help to better estimate growth parameters.

### 358 *3.3. Impact of fishing on sex ratios*

359 Finally, some simulations with different fishing mortality ( $F$ ) values are presented in  
360 figure 5 to explore the impact of  $F$  on sex ratios. The biological parameters for this  
361 exercise are those of Sce. 5 in Table 1. The model is an equilibrium model implemented  
362 on a “per-recruit” basis. This means that the population is projected forward with  
363 constant recruitment (1 individual) until equilibrium is reached.  $F_{max}$  is the level of  $F$   
364 that produces the maximum catch in equilibrium. The model is run with 3 different  $F$   
365 levels:  $F=0$  means that there is no fishing;  $F_{max}$  means that  $F$  is at the level that  
366 produces the maximum catch; and  $2 \cdot F_{max}$  means that  $F$  is twice the level that produces  
367 the maximum catch. This last level may be considered as overexploitation. In all  
368 previous simulations the  $F$  level was set as  $2 \cdot F_{max}$ , which is in consonance with the  
369 actual exploitation levels in 2006-08.

370 Figure 5 (upper plot) shows how the modelled sex ratio-at-length changes under  
371 different fishing intensities. With no fishing (continuous line) the presence of females is  
372 relatively lower between 32 and 80 cm. with a minimum around 0.3 at 37 cm and a



373 maximum at 80 cm. When the fishing mortality increases, the minimum shifts from 0.3  
374 ( $F=0$ ) to 0.36 at  $2 \cdot F_{max}$ , and the maximum is reached at a lower size: 70 cm ( $2 \cdot F_{max}$ ),  
375 compared to 80 cm ( $F=0$ ). The middle plot shows how the increase in  $F$  changes the  
376 population structure by truncating the larger size classes. In the absence of fishing  
377 ( $F=0$ ), fish larger than 70 cm are relatively abundant. Since most of these large fish are  
378 females, when  $F$  increases and truncates the population to a lower size the number of  
379 large females may be expected to decrease. So although  $F$  is not sex selective in the  
380 model, it has an impact on the sex ratio and also on the reproductive success of the  
381 population. To better illustrate this idea, the lower plot in Figure 5 shows how the  
382 increase in  $F$  alters the operating sex ratios (OSR). OSR refers to the ratio between the  
383 number of mature females and total mature fish (males and females). In the absence of  
384 fishing the OSR in the population is 0.44. This is because males mature at a smaller size  
385 (32 vs. 45 cm) and because the higher post-maturity male  $M$  (0.45 vs. 0.4) is not enough  
386 to counteract the smaller maturity size. Differences in growth do not affect OSR but the  
387 different sizes of mature males and females. As explained above, when  $F$  increases the  
388 proportion of males also increases because of the truncation of the large size population.  
389 Thus, at  $F_{max}$  OSR decreases to 0.35 and under overexploitation ( $2 \cdot F_{max}$ ) the female  
390 sex ratio is 0.28. This strong decrease in OSR may have an important impact on the  
391 reproductive success of the population. Models that not consider sexual size  
392 dimorphism may ignore the risk associated with the loss of large females.

393 The simulations performed here show that sex ratio-at-length patterns are also affected  
394 by fishing mortality. This means that changes over time in sex ratios might help to  
395 understand changes in  $F$ , making these data valuable for assessment purposes. The  
396 consideration of time series of sex ratio data in fishery stock assessment models is  
397 simple in the Integrated Analysis framework (Maunder and Punt, 2013).

398 It has been determined that the proportion of females in the mature population decreases  
399 when fishing increases. This is true under the assumption that fishing mortality is only  
400 size dependent. If fishing mortality is also sex dependent the results might change  
401 depending on which sex has higher catchability. If the assumption is correct this may  
402 have implications for fishery management in terms of defining biomass reference points  
403 or diagnosing stock status. Fishing mortality truncates larger length classes. As females  
404 are larger than males, females are especially truncated, thus decreasing the reproductive  
405 potential of the population and its resilience in a changing environment (Hidalgo et al.,  
406 2012). This effect may be exacerbated if female fecundity per weight increases with size  
407 as is the case in hake (Mehault et al., 2010; Cerviño et al., 2013)

#### 408 **4. Conclusions**

409 Changes in growth after maturity explain the shape of the sex ratio–at-length curve.  
410 Males mature smaller than females. The reduction on post-maturity growth among  
411 males increases the proportion of males at post-maturity sizes. This proportion is  
412 balanced at larger sizes due to the relative growth reduction in males. Then females  
413 mature and their growth are also reduced. If growth reduction among females is the  
414 same as among males then the sex ratio for sizes larger than the length of females at  
415 maturity stabilises with a higher proportion of females, although a figure of 100%  
416 females is never reached. For this to happen the growth reduction must be greater in  
417 males than in females. Changes in post-maturity mortality also result in the sex ratio  
418 shifting away from 50%, but those changes cannot by themselves explain the sex ratios  
419 observed. Sex differences in growth are the main factor that explains the shape of the  
420 sex ratio-at-length.

421 European hake is an important commercial species with unknown growth, which makes  
422 it more difficult to provide scientific advice on its management. The use of sex ratio-at-  
423 length data is a novel approach that helps provide a better understanding of hake  
424 growth, where trade-offs between reproduction and growth are explained, which  
425 contributes to a better implementation of the ecosystem approach to fisheries. The  
426 exercise presented here shows the utility of sex ratio-at-length for estimating growth in  
427 SSD species. Other factors such as length at maturity and mortality may also help to  
428 explain patterns in sex ratio-at-length. Since not all the parameters that explain the sex  
429 ratio data can be estimated at the same time, the method presented here may be useful  
430 for estimating growth parameters if additional information is available. That additional  
431 information could be the figures for one or more known parameters such as length at  
432 maturity or life history theory, which may help to keep the relationships between  
433 parameters within credible boundaries (Beverton, 1992; Charnov, 1993).

434 The most promising application of sex ratio-at-length is in integrated stock assessment  
435 models (Maunder and Punt, 2013). These data can easily be factored into models  
436 separated by sex merely by adding a new likelihood function that compares observed  
437 and modelled sex ratios-at-length. This novel source of information may help to  
438 estimate F, M and growth parameters throughout the time series of such models. Sex  
439 ratio-at-length is cheap information and long time series data are available for most fish  
440 stocks. In SSD species where there are differences in growth and reproduction, this  
441 information enables the assessment process to be improved so that better parameter  
442 estimation is obtained.

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Table 1. Optimization scenarios with different estimated parameters. Sce 1 and 2 represent optimization scenarios where Linf is also estimated. Sce3, 4 and 5 represent optimization scenarios where Linf is set based in hake correlation among length at maturity and Linf. The symbol \* indicates which parameters were estimated. M, Linf and k are the parameters before maturity (equal for males and females); Lm is the length at maturity; M2, Linf2 and k2 are the post maturity parameters, different in males and females. LS is the Least Square value for every optimization scenario.

	Sce1		Sce2		Sce3		Sce4		Sce5	
	fem1	mal1	fem2	mal2	fem3	mal3	fem4	mal4	fem5	mal5
<b>M</b>	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4
<b>Linf</b>	130	130	130	130	130	130	130	130	130	130
<b>k</b>	0.165	0.165	0.165	0.165	0.165	0.165	0.165	0.165	0.165	0.165
<b>Lm</b>	45	32	45	33.2 *	45	32	45	32	45	33.1 *
<b>M2</b>	0.4	0.4	0.4	0.44 *	0.4	0.4	0.4	0.4	0.4	0.45 *
<b>Linf2</b>	130 *	66.5 *	130	66.5	112	80	112	80	112	80
<b>k2</b>	0.165 *	0.165 *	0.165	0.165	0.165	0.165	0.165 *	0.11 *	0.165	0.11
<b>LS</b>	0.15		0.129		0.500		0.189		0.161	

Figure 1. Female proportion-at-length for a time series from 1984 to 2008 (left panel) and mean of recent years, from 2006 to 2008 (right panel) in the Gulf of Biscay.

Figure 2. Impact of post-maturity change in life histories ( $L_{inf}$ ,  $k$  and  $M$ ) on modelled sex ratio-at-length. The three plots show the same post-maturity changes in males and females. Vertical dashed lines represent the length-at-maturity for males (32 cm) and females (45 cm). Left panel shows the impact of reduced  $L_{inf}$  after maturation; middle panel shows the impact of reduced  $k$  after maturation; right panel shows impact of increased  $M$ . Pre-maturity figures ( $M=0.4$ ;  $L_{inf}=130$  and  $k=0.165$ ) have been modified after maturity following the plot labels.

Figure 3. Impact of post-maturity change in life histories ( $L_{inf}$ ,  $k$  and  $M$ ) on modelled sex ratio-at-length. The three plots show different post-maturity changes in males and females. Vertical dashed lines represent the length at maturity for males (32 cm) and females (45 cm). Left panel shows the impact of reduced  $L_{inf}$  after maturation; middle panel shows the impact of reduced  $k$  after maturation; right panel shows impact of increased  $M$ . Pre-maturity figures ( $M=0.4$ ;  $L_{inf}=130$  and  $k=0.165$ ) have been modified after maturity following the plot labels, that show first the new male value, and second the new female value.

Figure 4. Least square fit for two different approaches. The left plot shows the model fit estimating post-maturity  $L_{inf}$  plus  $k$  in males and females (continuous line) and two more parameters, i.e. male  $M$  and male  $L_{mat}$  (dotted line). The right plot shows the model fit for three different scenarios with fixed  $L_{inf}$  for females (112 cm) and males (80 cm). The continuous line shows the modelled results where  $L_{inf}$  was set (112 cm and 80 cm). Dashed line shows the fit where  $k$  (males and females) are also estimated. Dashed line shows the fit based in the previous plot fit plus two more parameters (male length at maturity and male  $M$ ) which are also estimated.

Figure 5. Impact of different fishing levels ( $F=0$ ;  $F=F_{max}$  and  $F=2 \cdot F_{max}$ ) on the sex ratio. Upper plot shows the impact on sex ratio-at-length. The middle plot shows the impact on equilibrium sex distribution. Lower plot shows the impact on operational sex ratios. X axis values are the three aforementioned  $F$  values.

Figure 1:

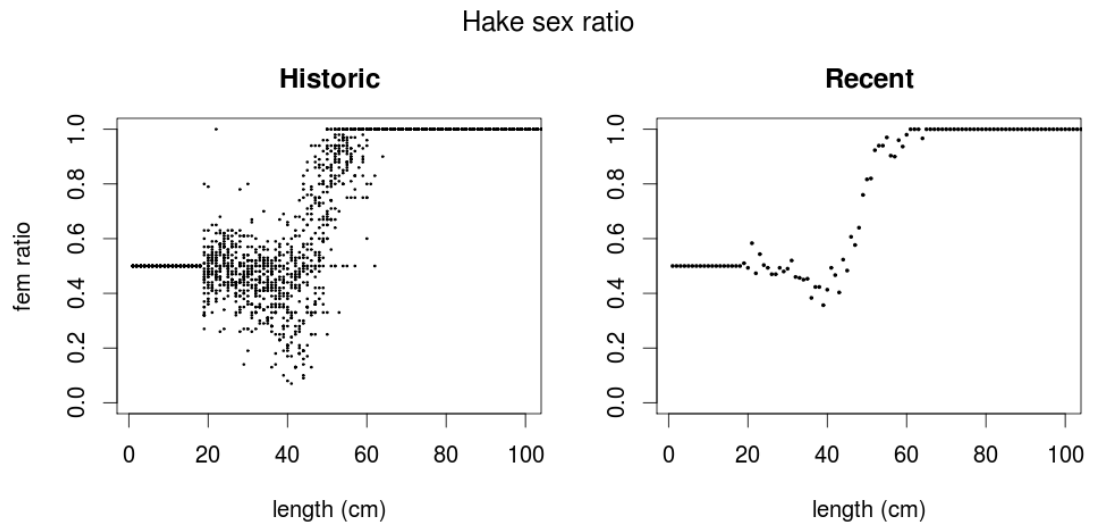


Figure 2:

Equal change in males and females after maturity

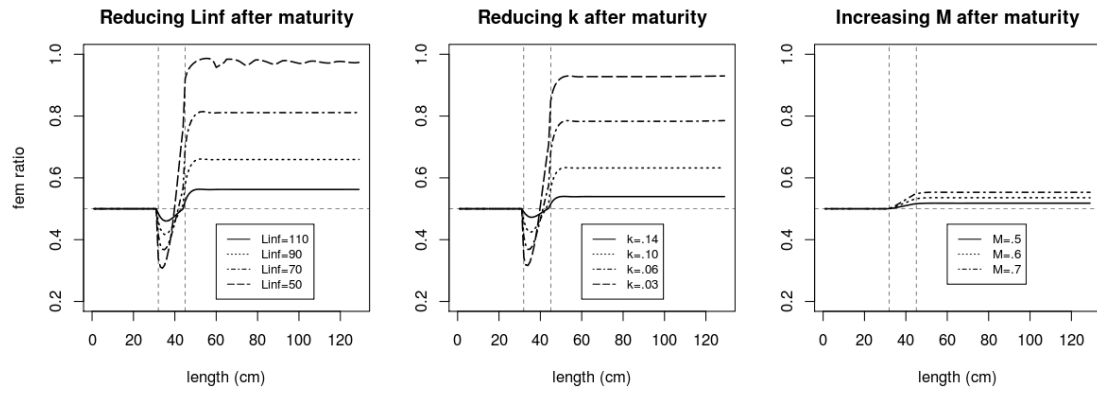


Figure 3.

Different change in males and females after maturity

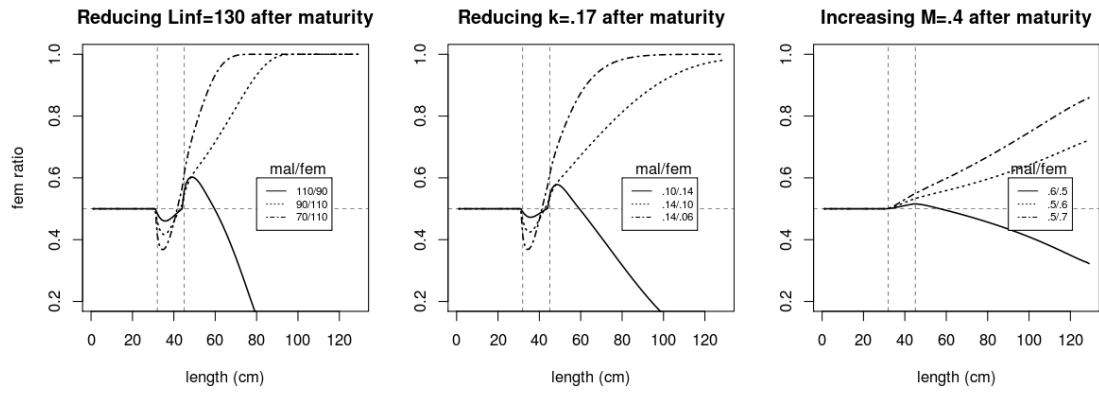


Figure 4.

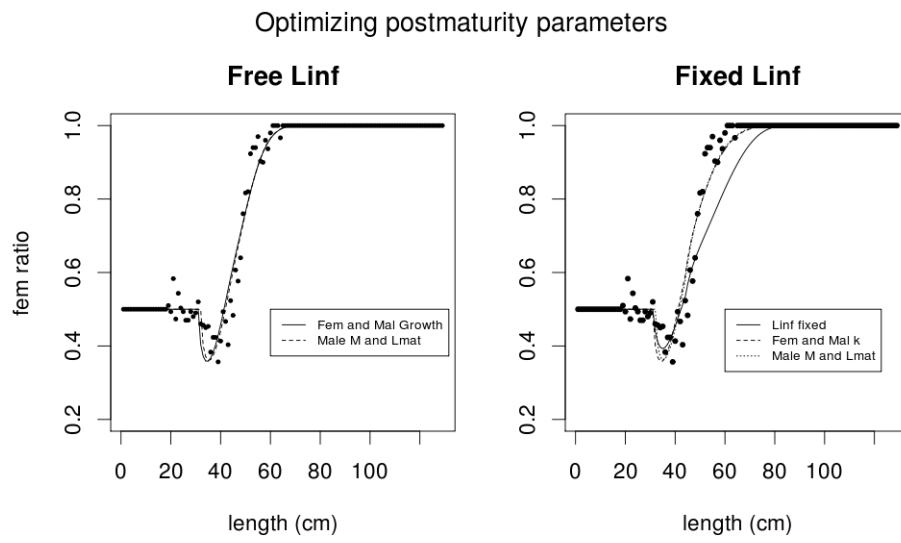


Figure 5.

impact of F on sex ratio

