

Data evaluation workshop of ICES WKAngHake: Benchmark Workshop on anglerfish (*Lophius budegassa*, *Lophius piscatorius*) and hake (*Merluccius merluccius*). Virtual, 23 – 25 of November 2021.

Estimating biological parameters (Linf, k and M) with Bayesian hierarchical analysis based on life history invariants.

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Abstract

Hake stocks in ICES area can be considered “data poor” stocks in terms of biological information, being this one of the main difficulties to get a good assessment model. Difficulties to estimate growth, as well as the usual problems in estimating M compromise a good quality assessment model. There is a need of increasing stocks assessed and improve the quality of existing assessments. However, there is a lot of biological information in similar species that can help to fill this gap. Life history invariants theory and hierarchical bayesian models can be combined to better understand biological processes needed in most stock assessment models (maturity, growth and natural mortality) providing the required parameters together with their statistical structure (posteriors). As an example of this approach we use the two European hake stocks in the Northeast Atlantic Ocean. The Bayesian hierarchical analysis provides posteriors for the main biological Linf, k and M. In the case of Southern hake, for which sex maturity at length data are available sex separated parameters are also provided. However, these results cannot be used directly in SS and further work is required to implement these in the SS model. Options to do it include fix some of them and allow SS to estimate others, use the posteriors as SS priors or combine these two options.

Warning! An error in the data base of Merluccius information was found and we are now revising these data to guaranty that the selected records accomplish the quality required for this kind of analysis. Results presented here should be considered preliminary although the methodology proposed are the definite one.

Introduction

Biological parameters are one of the weakest areas in current hake ICES assessment models. Growth and M are relatively unknown and were set as constants (Linf=130 and M = 0.4) meanwhile k is estimated by the model based on the length distribution progression through quarters. There is information for maturity at length although this information is not used to fit the model. This information is used to calculate SSB after the model was fit.

The aim of this work is to provide more information regarding biological parameters for the SS hake models that are going to be developed in ICES WKANGHAKE 2022. This information will be based on life history invariants (LHI) theory using hake biological information from literature. LHI theory predicts that the relationship between some life history parameters is relatively constant. Evolutionary life history theory is developed in terms of allocation of resources to the competing ends of growth, reproduction and adult survivorship (Charnov and Barrigan, 1991). The goal of life history theory is to understand the variation in such life history strategies to explain the reproductive success. For instance, higher investment in current reproduction hinders growth and survivorship and reduces future reproduction, while

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investments in growth before maturity will pay off with higher fecundity in the future. Beverton and Holt (1959) and Beverton, (1992) provided empirical evidences that some relationships among parameters are relatively constant like L_m/L_{inf} and M/k in different fish groups. Charnov (1993) developed the theoretical basis for this invariance relationship based on simple maths with VB growth curve, the exponential survivorship and some reproductive traits. Based on this theory, biological parameters might be built based on the expected value of these invariants and their variability estimated from other hake information.

Charnov and Berrigan (1991) present 3 patterns in life history. Charnov (1993) extends the theory explaining the role of these 3 invariants.:

1. M/k tend to be relatively constant in similar taxa (~ 0.6 ; Charnov and Berrigan, 1991)
2. L_m/L_{inf} is relatively constant among similar taxa.
 - 2.1. $L_m/L_{inf} = 1 - \exp(-k \cdot m)$ (where m is age of maturity); if a group of species share the same L_m/L_{inf} value they also share the same $k \cdot m$.
 - 2.2. For species where M/k and L_m/L_{inf} are constant, M is inversely proportional to m , i.e. $M \cdot m$ is constant
3. k and L_{inf} are negatively correlated

Because of the limited information available on these biological parameters and the relationship between them for *Merluccius merluccius*, we use a meta-analysis approach whereby we rely on data from other related species to help estimate these relationships and associated parameters. In order to properly account for the variability between data from *M. merluccius* and the other species within this meta-analysis, a hierarchical modelling approach will be used whereby we estimated the parameters of interest simultaneous at the species level and at the meta-species level. In doing so, hierarchical models allow predicting the parameters for *M. merluccius* for which we have limited data, based on the estimates from all species combined and the similarities/dissimilarity between the individual species.

ICES assessment models for both hakes assume that most biological parameters are constant ($L_{mat} 50\% = 43.85\text{cm}$; $M=0.4 \text{ year}^{-1}$ and $L_{inf}=130 \text{ cm}$) and only k for VonBertalanffy growth are estimated by the model. Length at maturity (L_m) is the unique parameter for which there is available information directly used in the assessment process. Since L_m may be estimated out of the model it may be the basis to develop a link among priors of different biological parameters following Charnov and Berrigan (1991) and Beverton (1992) LHI theory such as:

1. Prior for L_{inf} from ratio L_m/L_{inf} for hakes in literature.
2. Prior for k based on negative correlation between L_{inf} and k from hake literature.
3. Prior for M based on constant relation M/k from hake literature.

Material and methods

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When doing meta-analyses, it is common to use a hierarchical approach (Liermann and Hillborn, 1997; Myers and Mertz, 1998; Myers and Mertz, 1998). Instead of using all the data from the different species combined (thereby placing larger weight on the data from species with more records), hierarchical models still allow to account for the differences between the different species, and at the same time giving higher weight to the data from *M. merluccius* depending on the amount of *M. merluccius* data available.

The analysis will be developed in 3 stages as described in figure 1. In the first stage the maturity information will be described; in the second stage the hake LHI meta-analysis based on hake information from literature will be developed and, in the third stage, the priors for L_{inf} , k and M will be developed sequentially.

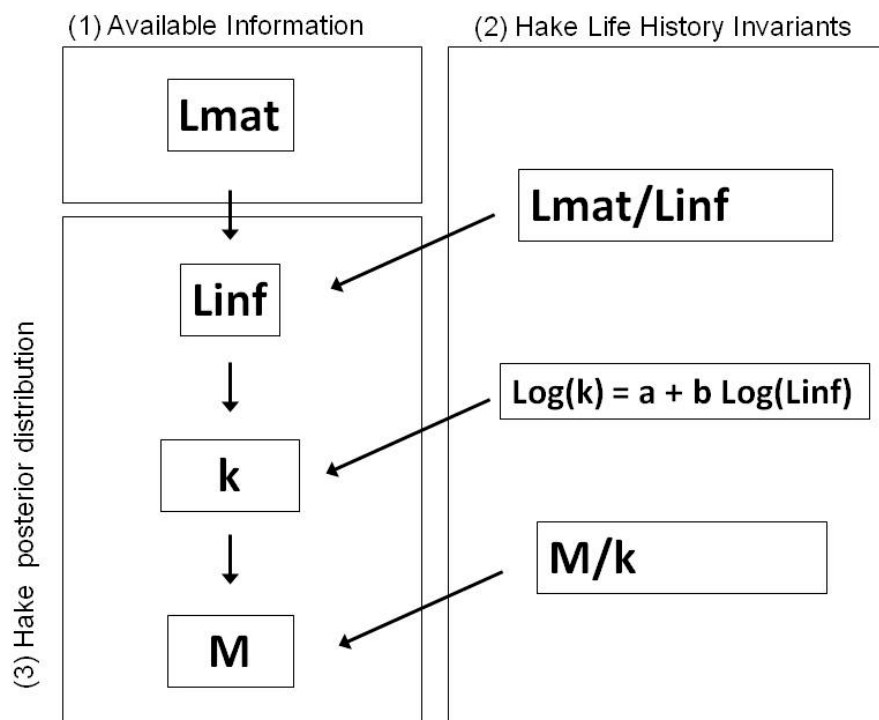


Figure 1. Hake meta-analysis structure

Maturity information

The first stage is having a maturity distribution for Northern and Southern hake. This distribution is built from available information. There are available maturity information from the Northern stock since 1987 (WKROUND, 2010) and from the Southern stocks the maturity ogives were estimated in WKANGHAKE. Length of 50% of maturity for both sexes combined is presented in figure 2. L50 mean and standard deviation for both time series were used to build the normal distributions.

For Southern Hake, there seems to be a trend in the data maturity data. Rather than deriving the distribution for L50 based on all the data whereby the earlier years

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indicate larger values for L50 than the later years, the time series has been split in 3 periods and only the last period has been used to estimate the distribution of L50.

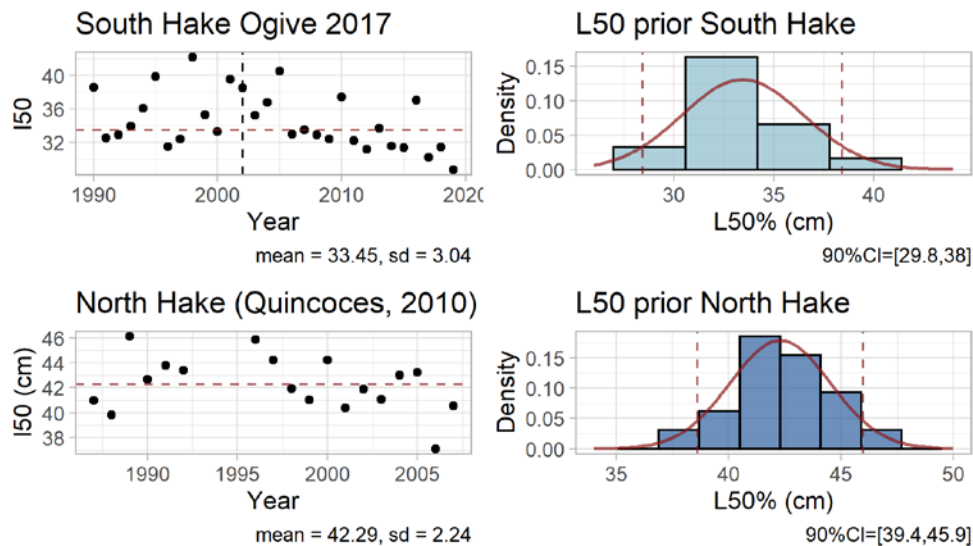


Figure 2. Maturity information from Northern and Southern hake. Time series in the left and L50 distribution with normal fit in the right.

Figure 2 left panel shows the L50 figures for Northern and Southern hake. These figures range from 36 to 46 cm with a mean of 42.29 and s.d. of 2.24 cm (Northern hake) and 29 to 42 cm mean of 33.45 and s.d. of 3.04cm (Southern hake). Right panel shows the resulting female normal priors based on the mean and sd of the L50 figures.

Data review for Life history invariant analysis

The initial idea for hake data review was to use only information from the same specie (*Merluccius merluccius*) to develop priors for Northern hake assessment. However, after the initial review of this information we realized that practically all data are based in a growth model unbelievable. Hake data for the genus *Merluccius* was downloaded from Fishbase (Froese and Pauly, 2013). The total amount of records with life history data in FishBase was 188, although not all of them have all the needed data. A literature review was extended to add new data not already collected in FishBase this review provided 125 new records from the 12 hake species all over the world. The distribution of all the 211 finally accepted records by specie after deleting unrealistic *M. Merluccius*, (Those based in old assumed slow growth) records are presented in next figure 3.

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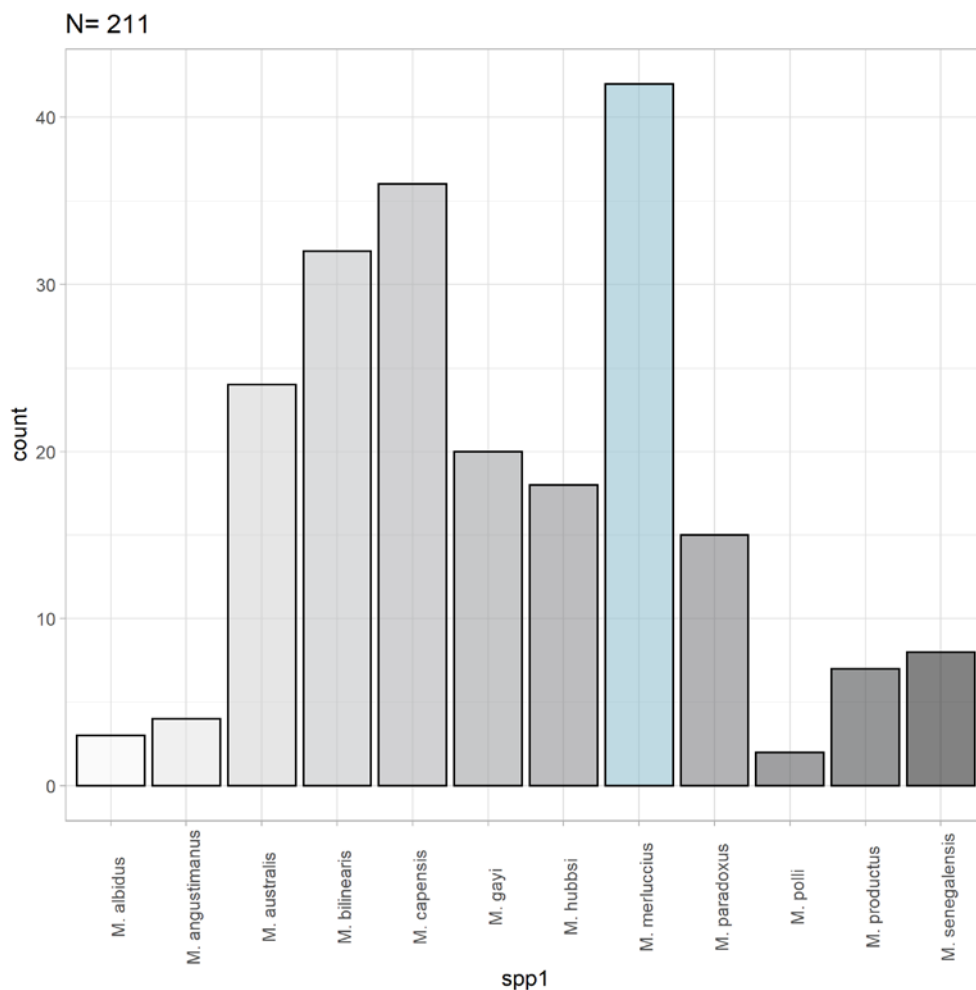


Figure 3. Distribution of records by species after deleting unrealistic records.

Linf from Lmat/Linf invariant.

Lin_f priors were estimated based on the life history invariant for the ratio Lin_f / L_{mat}. The total number of records with Lin_f and L_{mat} data was 29 (Figure 4); 6 belong to *M. australis* and only 3 to *M. merluccius*. The distributions of these ratios by specie are presented in figure 4 (right panel) showing two different groups: those with mean figures above 0.5 and those with figures below. Among the species above 0.5, *M. australis* has 6 records with a mean around 0.75 and a narrow sd. The other 2 species with figures above only has 3 records.

There are certain requirements that need to be met to be able to include data within a Meta-analysis. One of those requirements is that the data from the different species need to be exchangeable, i.e. there should not exist any a priori information that would allow indicate that a particular species would be different from the other ones in the meta-analysis. *M. australis* however matures between 60 and 80 cm and grows until 80- 120 cm depending on the sex, while the other hakes mature between 20 and 50 cm and grow until 40-130 cm. So the knowledge that *M. australis* behaves differently, and thereby violates the assumption of exchangeability within the hierarchical meta-analysis requires us to exclude it from the analysis.

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Exploratory Analysis Lmat/Linf

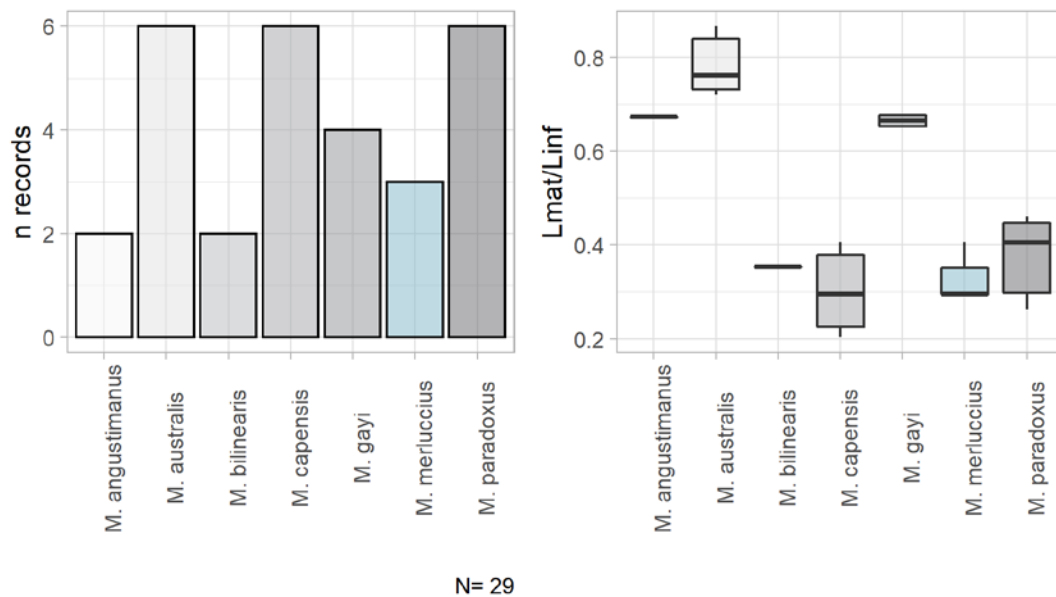


Figure 4. Number of records with Linf and Lmat data (left panel) and their boxplots (left panel)

A hierarchical Bayesian analysis was run to estimate the ratio of Lmat over Linf for *M. merluccius*. The model assumes that the species specific ratios ($Lmat/Linf_{sp}$) are normally distributed as follows;

$$Lmat/Linf_{sp} \sim normal(\mu.sp.Lmat/Linf, var.sp.Lmat/Linf)$$

Whereby $\mu.sp.Lmat/Linf$ is the average ratio of Lmat over Linf for all species combined and $var.sp.Lmat/Linf$ indication of the variance between estimates for the different species. The model predictions of $Lmat/Linf_{sp}$ have been compared against the observations ($Lmat/Linf_{obs}$) using a following normal likelihood function:

$$Lmat/Linf_{obs,i,sp} \sim norm(Lmat/Linf_{sp}, var.Lmat/Linf)$$

To run this analysis, uninformative priors have been placed on $\mu.sp.Lmat/Linf$, $var.sp.Lmat/Linf$ and $var.Lmat/Linf$. The resulting distribution for Lmat/Linf for *M. merluccius* can be seen in Figure 5.

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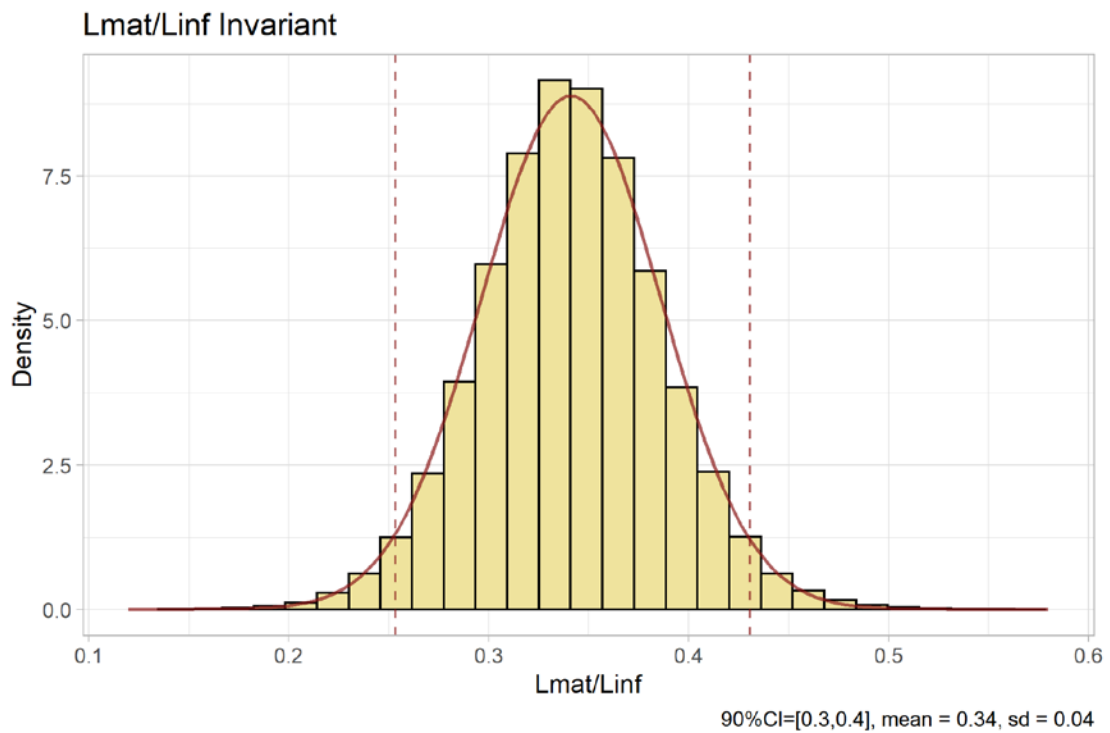


Figure 6. prior distribution for the ratio Lmat/Linf with 90% CI, mean and s.d.

Priors for Linf were developed as the cocient between Lmat distribution (Figure 2) and Lmat/Linf distribution (Figure 6) and are presented in Figure 7.

Linf posteriors

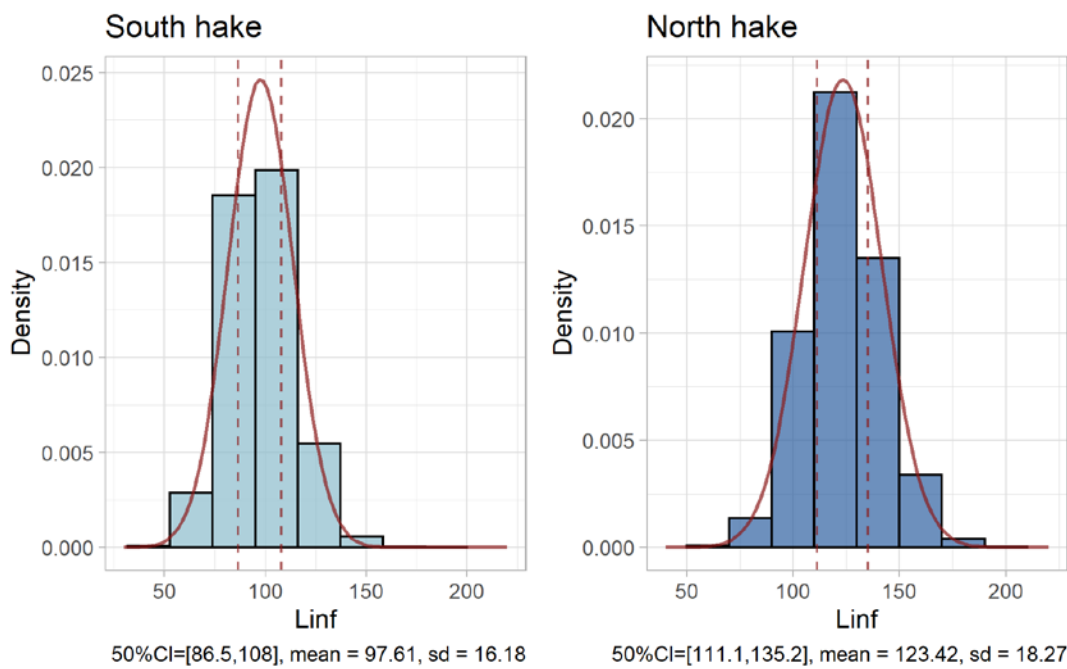


Figure 7. The probability distributions for the ratio Lmat/Linf with 50%CI, mean and s.d. for Norther hake (left panel) and Southern hake (right panel)

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Mean figures and 50% CI for Linf are 97.69 cm [86.5, 108] for Southern hake and 123.42 [111, 135] for Northern hake. These numbers are below the current Linf used within the stock assessment model model (130 cm). Linf=130 is however well within the full probability distributions for Linf. We have to keep in mind that Linf=130 had been based on data from female hake while this analysis was performed for males and females combined.

K from Linf-k invariant

K is modelled in the ICES models (SS3 and GADGET) as a Von Bertalanffy parameter. k prior estimation was based on the high negative correlation among Linf and k. Figure 8 shows the valid records with information on Von Bertalanffy fits providing data for Linf and k. Most *M. merluccius* were excluded since recent tagging studies have showed that k is about two times above those previously estimated (de Puntual *et al.*, 2006; Piñeiro *et al.*, 2007). Figure 8 shows the distribution of valid data for different hake species (left panel) and the plot of k vs Linf for all the data (central plot). This plot shows the negative correlation among both parameters which are linearized through log transformations allowing for a linear model able to predict k from Linf (right plot).

K exploratory analysis

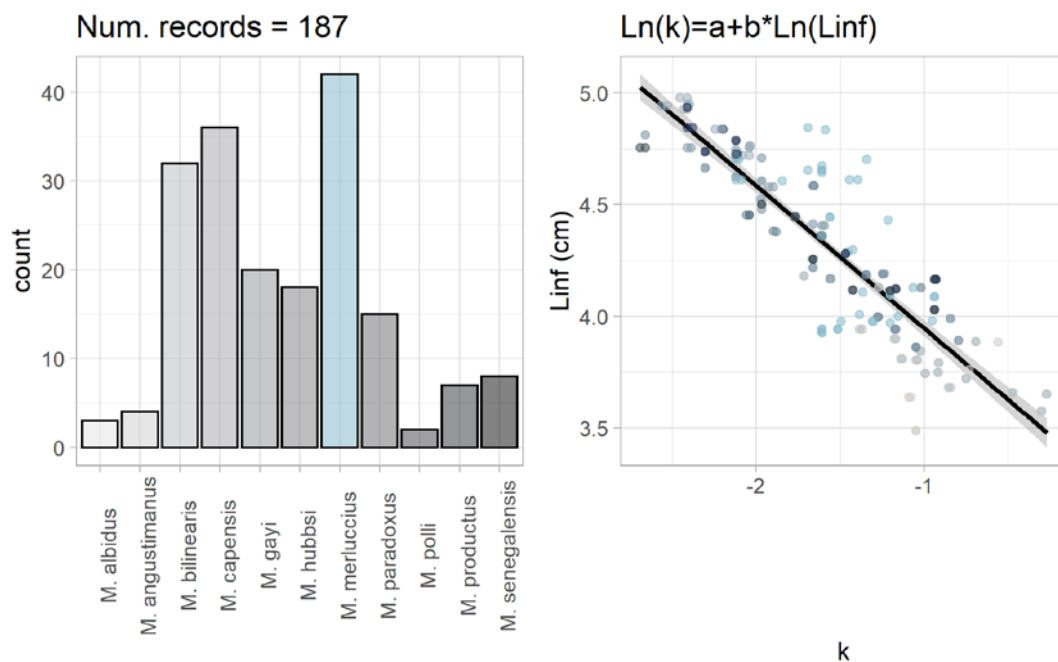


Figure 8. Number of records with information on k and Linf (left panel); Linf vs k log linear model (right panel)

A Bayesian linear regression model was developed to estimate k, with the relationship between k and Linf being expressed by the following equation:

$$\log.k_{i,sp} = a_{sp} + b_{sp} * \log(\text{Linf.obs}_{i,sp})$$

whereby $\text{Linf.obs}_{i,sp}$ are observations of Linf for individual species, a_{sp} and b_{sp} are species specific linear regression parameters. $k_{i,sp}$ are the species specific model

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predicted estimate. These estimates are compared against the observations on the logscale using the following likelihood:

$$\log.k.obs_{i,sp} \sim \text{norm}(\log.k_{i,sp}, \text{var}.k)$$

The stock specific values of the intercept a_{sp} and slope b_{sp} are defined by a mean ($\mu.a$ and $\mu.b$) and variance ($\text{var}.a$ and $\text{var}.b$) across species:

$$\begin{aligned} a_{sp} &\sim \text{norm}(\mu.a, \text{var}.a) \\ b_{sp} &\sim \text{norm}(\mu.b, \text{var}.b) \end{aligned}$$

whereby $\mu.a$, $\mu.b$, $\text{var}.a$ and $\text{var}.b$ have been given uninformative priors, as well as $\text{var}.k$.

The resulting model for *M. merluccius* is used to predict the distribution for k for both Northern and Southern hake by using the a and b parameters for *M. merluccius* in combination with the distributions for $\text{Lin}f$ posterior obtained previously for Northern and Southern hake.

Posteriors K

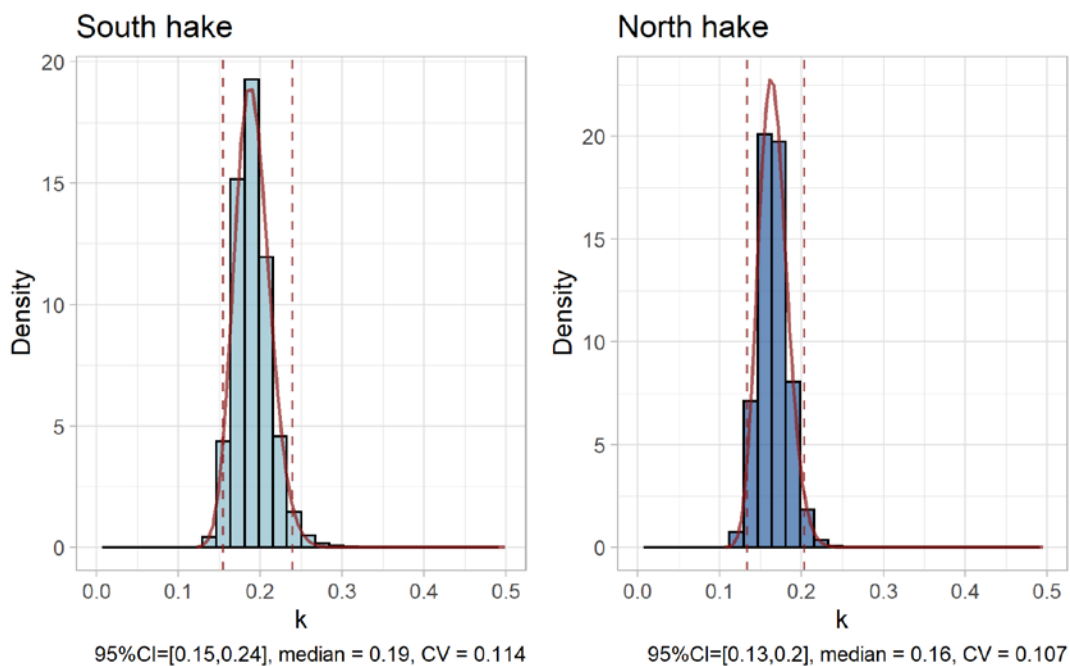


Figure 9. k priors for Northern hake (left panel) and Southern hake (right prior)

K median and 95% CI are 0.16 [0.13, 0.2] for Northern hake and 0.19 [0.15, 0.24] for Southern hake. These figures are similar to those estimated by both ICES models (around 0.17). However we have to take into account that k is the rate at which the population raises $\text{Lin}f$ and in this exercise $\text{Lin}f$ is well below ICES $\text{Lin}f$ (~100 vs. 130 cm).

M from *M/k* invariant

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Natural mortality is set as a constant parameter in time and length in hake ICES models. This estimation is based on the for the assumption that the ratio of M/k is relatively constant among similar taxa.

Figure 10 shows the hake species with records for k and M. As in the previous analysis most *M. merluccius* data were rejected because of wrong k estimation. All *M. australis* records were also eliminated. Many records with a typical 0.2 figure estimation without a justification were also eliminated. Finally only 25 records were used for this analysis. In the central panel of the same figure we can see the distribution of M/k rate for different species. In the left part of this plot we can see the total distribution with a median equal to **2** and **CV=0.41**. Preliminary linear models with this data did not show a good fit and given the relatively low variability around the mean value it was decided to use the mean and s.d. of these figures to develop the informative priors for the M/k ratio.

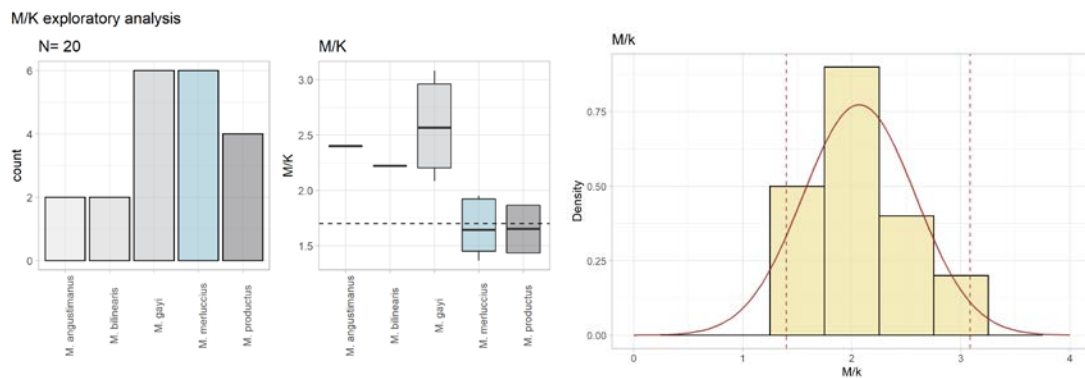


Figure 10. Records with information on M and k (left panel); a boxplot for this ratio M/k in every specie (central panel) and M/k distribution (right panel)

Priors for M were built based on the M/k distribution (Fig 10) and using a Bayesian model very similar to the model used to estimate Lmat/Linf. The model assumes that the species specific ratios are normally distributed as follows;

$$M/k_{sp} \sim \text{normal}(\mu_{sp.M/k}, \text{var}_{sp.M/k})$$

Whereby $\mu_{sp.M/k}$ is the average ratio of M over k for all species combined and $\text{var}_{sp.M/k}$ indicates the variance between estimates for the different species. The model predictions of M/k have been compared against the observations (M/k.obs) using a following normal likelihood function:

$$M/k_{obs,i,sp} \sim \text{norm}(M/k_{sp}, \text{var.M/k})$$

To run this analysis, uninformative priors have been placed on $\mu_{sp.M/k}$, $\text{var}_{sp.M/k}$ and var.M/k . The resulting distribution for M/k has been used in combination with the distributions for k for both Northern and Southern Hake to calculate the distribution of M as seen in Figure 11. The M estimated following Life History Invariants theory represents the expected M after maturity, that has median = 0.23 for Northern hake and 0.28 for Southern hake. In both cases the variability is very high because the

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sequential process from Lmat to M through Linf and k, accumulates the variability of all relationships.

M posterior from M/k invariant

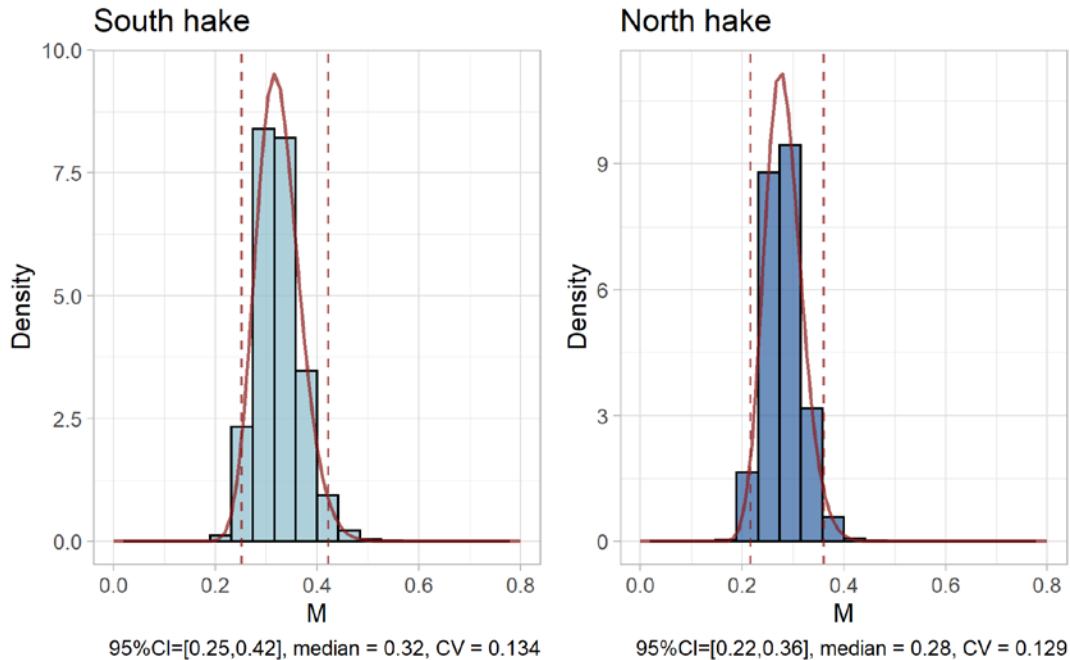


Figure 11. M prior distribution for Northern hake (left panel) and Southern hake (right panel)

Lorenzen (1996) point to the existence of an allometric relationship between natural mortality and body weight, in fish, of the form $M = a + W^b$ where M is natural mortality at weight W , a is mortality at unit weight, and b is the allometric exponent. Based on empirical studies with different populations Lorenzen found out the following parameters: $b = -0.288$ (90% CL[-0.315, -0.261]) and $a = 3.00$ (90% CL[2.70, 3.30]) year⁻¹. More recently Cook (2013) uses this equation in an assessment model for haddock getting the following parameters: $a = 3.69$ and $b = -0.305$ and confirming the Lorenzen assertion that b is relatively constant among different species. Figure 12 shows the M estimated for Southern hake based on Lorenzen figures and hake parameters. The model produces high M at length figures for small hake (e.g. $M = 1.8$ for age 0 and $M = 3.5$ for length 1cm) that decreases until 0.18 at length 130 cm or age 15.

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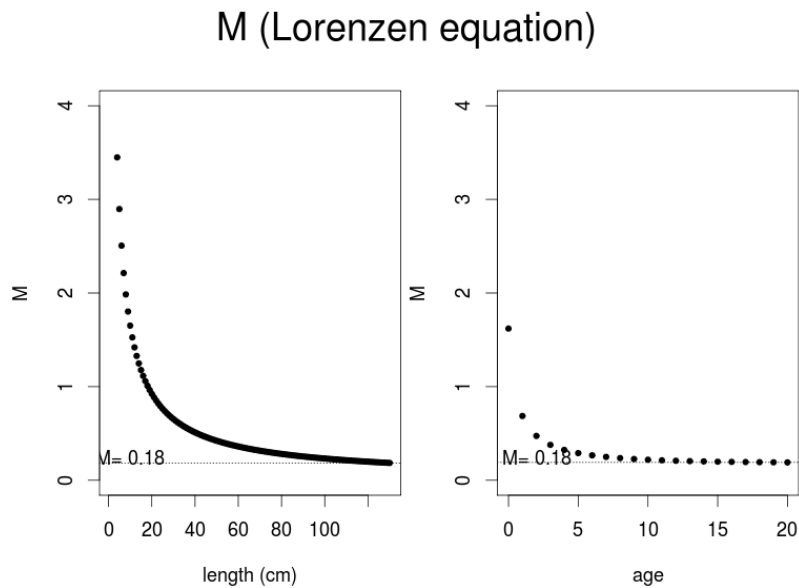


Figure 12. Lorenzen estimates of M at length and M at age.

Table 3. Summary of the developed priors for invariants.

Data	Linf.mean	Linf.sd	k.median	k.CV	M.median	M.CV
North combined	123.416	18.267	0.164	0.107	0.279	0.129
South combined	97.613	16.183	0.189	0.114	0.32	0.134
South female	122.175	17.374	0.165	0.103	0.28	0.127
South male	79.61	12.28	0.212	0.104	0.361	0.126

Discussion

Hake is a sex dimorphic species with different size at maturity and different growth in both sexes. Females mature larger than males and have larger sizes than males. The exercise performed here was done to estimate parameters for a model with sexes combined. So, the initial information for this sequential estimation was Lmat, which is the yearly L50% maturity for both sexes combined. And then, the estimated parameters for growth (k and Linf) and M correspond also to both sexes combined.

Caveats using life history invariants. Temperature as an important additional information in mat-growth-M relationship. Lack of complete records with mat, growth, m and T. Multigroups approach (Pauly and others) vs reduced groups approach (here) => more information with less invariance vs less information with more invariance. Even that t° was not considered, the hierarchical Bayesian approach allows to consider the group (species) contribution together, i.e. each species LHI was analyzed independently and combined afterwards to provide a LHI value for European hake. Since each species has a different optimal temperature range and then different LHI variability the hierarchical approach allows giving more or less weight to species were LHI values are more or less variables. Furthermore, the hierarchical method provides more weight to the information coming from the European hakes

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than to other hakes. These two features of the methods reduce the impact of not considering the T° in the analysis.

An assessment model like those performed for both hakes with SS3 or GADGET with sexes combined always have to make some assumptions. In this case, that L_{inf} is equal to 130 cm and $M=0.4$. With these constant figures k is estimated by the model explaining the observed catches. The L_{inf} estimated here showed figures around 100 cm, well below 130 cm set for ICES models. This is because L_{inf} is estimated from a sex combined L_{mat} . Meanwhile in ICES L_{inf} was mainly based on the higher observed hakes, which are females. Both approaches make different assumptions: (1) the ICES approach assumes that all hakes in the population might reach 130 cm. However we know that approximately half of the population, the males, rarely achieves 75 cm. However, since k (and also recruitment) was estimated to fit the past population productivity, it is expected that the final combination of model parameters for growth and mortality be able also to predict the future productivity. (2) On the other side, the approach presented here based on LHI would assume that all population achieves a L_{inf} around 100 cm. In this case we lost the option of half of the population (females) growing larger and the other half growing shorter (See Cerviño, 2014) for comparisons among hake male and female growth and M parameters). Since fishing selection is mainly based on fish length this assumption might also have an impact on the productivity. Furthermore, there are a lot of catch data with figures well over estimated L_{inf} that will be difficult to implement in the model with a short L_{inf} . Which approach is better? ANY MODEL APPROACH BASED ON SEXES COMBINED WILL LOST AN IMPORTANT PART OF THE REALITY. In any case 130 cm seems to be an extremely large L_{inf} , even for females, where mean historic northern hake L_{mat} is about 48 cm (Dominguez et al, 2008) and the mean L_{inf} based on LHI would be around 114 cm.

To overcome this difficulty we have plan a sex separated model that requires different figures for L_{mat} , L_{inf} , k and M , for males and females. The estimation process is the same than those for the sexes combined. Starting with the length of maturity (for males and females) we use the same invariant posteriors to estimate L_{inf} , k and M for males and females. Figures obtained from this process can be used in the SS model in two different ways: (1) point estimation to fix some parameters or (2) priors to allow the model to estimate some parameters. Combination of fixed and estimated parameters can be explored. Furthermore, the sex ratio data can help to estimate some growth parameters since the observed sex ratio at length can only be seen whether males and females growth in a specific way

The approach also provides information for k and M . k is conditioned to L_{inf} so it cannot be used as a prior if L_{inf} is different. However the prior for the correlation among k and L_{inf} might be used if required.

M/K is required by some data pour assessment methods (Hodryck et al, 2015...)

M presents figures around 0.3. This seems to be below current M (0.4) used in ICES models. The approach used by ICES follows the Hewitt and Hoenig (2005) approach based on longevity and assuming that hake lives around 10 years. This approach provides a mean M for all ages. However we have to consider that LHI approach

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provides M figures only for mature fish (above 40 cm aprox). M for immature fish should be estimated following other methods like Lorenzen's (1996). These approaches might be complementary predicting that immature hake (<40 cm) M should be higher than 0.4 in order to get the mean 0.4 predicted by Hewitt and Hoenig (2005). This is in agreement with other studies based on hake that predict a high M for small hakes because predation, being the main hake predators in this area the cetaceans (Saavedra et al XXX) and hake cannibalism (Jurado-Molina et al., 2006, Smith, 1995). in both cases predating in immature hakes.

An ulterior development of the natural mortality model will aim to the introduction of higher values for small hake based on the high predation mainly caused by cannibalism and dolphins. Literature review and preliminary analysis of Southern hake will provide the information for the M for this small hake. This model will include two parameters plus the usual constant M. At this time only the prior for the constant M was estimated. Lorenzen approach can also help.

In many cases there is not information on length of maturity. However, with some minor corrections, the method can also be developed starting the chain with a proxy for L_{inf} instead of L_{mat} . Information on L_{inf} can be derived from L_{max} (Jensen, 1997; Froese???)

In summary, the ICES models cannot be able to estimate growth and M (apart of other parameters like recruitment, selection, etc), and is required to fix two of these parameters (L_{inf} and M) allowing to estimate k. The approach presented here provide information to explore figures for these parameters that might be directly input in the model (M or L_{inf} means); ranges to explore (e.g. inside a confident interval of 90%) or using the invariants distribution to set one of them once that other have been set.

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