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A length-structured spatially explicit model for estimating hake growth and migration rates

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Abstract:

Despite an abundant literature, hake growth and migration remain poorly understood. A recent tagging campaign and an analysis of the growth increments on juvenile hake otoliths demonstrate that the growth rate has probably been largely underestimated. Migration rates have been studied through qualitative analysis of catch rate, but have not been confirmed by a more-quantitative analysis. Those biological uncertainties affect stock assessments and predictions by the uncertainty they bring to age-length keys and by hindering our ability to assess the impact of spatial management measures. Here, a spatially explicit length-structured model is developed to improve the biological knowledge of European hake (*Merluccius merluccius*), in terms specifically of migration and growth. The model belongs to the state-space class of models and is fitted by maximum likelihood on commercial landings, survey abundance indices, and tagging data. The estimated growth curve is close to estimates from tagging data, lending weight to the assumption of the species being fast-growing. Few migrations are long in distance, and there are none between the Bay of Biscay and the Celtic Sea. The model also demonstrates a high level of heterogeneity in the spatial distribution of spawning-stock biomass, with concentrations on the margins of the continental shelf.

Keywords: growth, length-structured model, *Merluccius merluccius*, migration, spatial model

1. Introduction

European hake (*Merluccius merluccius*) is a demersal species widely distributed in the Northern East Atlantic, from Norway to Mauritania (Casey et Pereiro, 1995). Hake has supported valuable commercial fisheries, especially in Spain, France and in the United Kingdom. The International Council for the Exploration of the Sea (ICES) has defined northern and southern hake stocks since the 70's, separated by the Cap Breton Canyon which is supposed to constitute a geographical barrier limiting exchanges between them, though there is no genetic proof that these are distinct populations (Castillo *et al.*, 2004 ; Cimmaruta *et al.*, 2005 ; Roldan *et al.*, 1998). The Northern stock extends from the Southern Bay of Biscay to Norway (ICES division IIIa, sub-areas IV, VI, VII and divisions VIIIa, b and d). Presently, Spain accounts for the largest part of the landings (59% of the total in 2007), followed by France (27%) and the United-Kingdom (7%) (ICES, 2008). Northern hake is targeted by several gear types in mixed fisheries (trawls, gillnet, longline) throughout its distribution area (Commission of the European Communities, 2001b). The landings rapidly declined during the 60's from about 100,000 t to about 60,000t, remaining relatively stable until the 1990's when landings declined again to about 40,000 t and have remained stable since (Casey et Pereiro, 1995). A high fishing mortality and a succession of poor recruitment events at the beginning of the millennium (Commission of the European Communities, 2001b) prompted management to introduce new technical measures and to the implementation of a recovery plan (Commission of the European Communities, 2001a ; Commission of the European Communities, 2002 ; Commission of the European Communities, 2004). Presently, the stock seems to be responding to these actions and the explicit management objectives stated in the recovery plan have been achieved (ICES, 2008).

Despite numerous studies on hake, some of its biological characteristics, especially growth and migrations, are poorly known. Based on otolith age determination, hake was assumed to be a slow growing species (Martin, 1991); however, a recent tagging campaign in the Bay of Biscay suggests that the current interpretation of otolith rings is not valid (de Pontual *et al.*, 2003 ; de Pontual *et al.*, 2006). These studies on adult hake growth and analysis of juveniles' otolith daily growth increments (Kacher et Amara, 2005) show that growth rate is probably much higher than previously thought. Migration has been studied mainly through catch per unit of effort analysis (Belloc, 1935 ; Casey et Pereiro, 1995 ; Hickling, 1935 ; Poulard, 2001). Mature hakes aggregate along the slope of the continental shelf from Portugal to Scotland (Alvarez *et al.*, 2004) during the spawning season (Casey et Pereiro, 1995 ; Poulard, 2001) and seem to disperse the rest of the year, whereas juveniles are concentrated on the two main nursery areas: on the "Grande Vasière" in the Bay of Biscay and on the continental shelf of the Celtic Sea (Alvarez *et al.*, 2004 ; Alvarez *et al.*, 2001 ; Kacher et Amara, 2005). Spawning and nursery areas are rather distant and migrations flows between those zones are poorly known. Moreover, exchanges between the Celtic Sea and the Bay of Biscay are not quantified at all.

Those biological uncertainties have an impact on both stock assessment and predictions. Hake stock assessment is conducted annually using the eXtended Survivors Analysis

(XSA) assessment model (Shepherd, 1999). This model has proved to be useful to detect trends and estimate stock abundance. However, it requires input data based on age while data are collected on the basis of length. Age-length keys are thus constructed annually and these are expensive and carry with them the uncertainty in otolith implied age. Moreover, XSA assumes when fitting abundance indices that population and fishing activity are spatially uniformly distributed though this assumption is likely to be violated and may lead to unreliable assessment (Horbowy, 2005 ; Kraak *et al.*, 2009 ; Pelletier et Parma, 1994).

Concerning predictions, lack of knowledge of hake migration hinders our ability to implement effective spatial management measures, which are recognised as some of the best tools to protect particular population stages and/or to preserve habitat and food webs (Botsford *et al.*, 1997 ; Holland, 2000). Currently, in the Bay of Biscay and Celtic Sea, management areas requiring larger trawl mesh size have been enforced to protect juvenile hake. Unfortunately, our uncertainty in hake growth rate and residence time in these areas prevents us from knowing their efficacy and refining the management measures accordingly (Bertignac et de Pontual, 2007).

Length-structured models have proved to be especially relevant for species whose growth is poorly known and/or ageing is difficult. Length structured models have been used for various objectives: (i) stock assessment (Breen *et al.*, 2003 ; Fournier *et al.*, 1998 ; Froysa *et al.*, 2002 ; Hampton et Fournier, 2001 ; Kristensen *et al.*, 2006 ; Maunder et Watters, 2003 ; Sullivan *et al.*, 1990), (ii) estimate unknown parameters (DeLong *et al.*, 2001 ; Fu et Quin II, 2000 ; Zhang *et al.*, 2004), especially growth parameters (Banks *et al.*, 1991 ; DeLong *et al.*, 2001 ; Drouineau *et al.*, 2008) and (iii) assessing the impact of management measures (Kvamme et Froysa, 2004 ; Mahévas et Pelletier, 2004 ; Pelletier *et al.*, 2009 ; Pelletier *et al.*, 2001 ; Pet *et al.*, 1996). Spatially explicit models are required to estimate migration rates and to assess the impact of spatial management measures.

In this context, we developed a length-structured spatially explicit population model for the Northern stock of European hake aiming at improving the biological knowledge of the stock by estimating unknown parameters, especially growth and migration. The model belongs to the family of the state space model (Figure 1): a spatially explicit and deterministic state model describes the population dynamics and fishing activity, and an observation model describes the uncertainties on the observation processes of the states. First, we present the data used, then we describe the state model, the observation model and the method used to estimate unknown parameters. Finally, growth and migration rates estimates are presented and discussed.

2. Methods

2.1. Data

Available data are aggregated at the level of ICES fishery units (ICES, 1991). Fishery units are characterised by a fishing gear, a fishing zone and target species.

Fishery units 2 (long-line in shallow water – sub-area VII) and 6 (beam trawling in shallow water – sub-area VII) were not incorporated in the analysis because they capture few hakes. Fishery unit 16 (all gears in subareas IIIa, IV, V & VI) was not considered because it fishes in a zone not studied in the model. Fishery unit 15 (miscellaneous) was also removed because of the lack of data on that unit. The 10 considered fishery units are subdivided into 18 national sub-units (Table 1). An estimation of total landings by sub-unit and quarter is provided by the declarative flow (Table 1). Sampling programs in auction markets provide length-composition of landings per sub-unit on variable time scales (either quarter or year) (Table 1).

A length-proportion of discards relationship is available for fishery unit 09 which generates most of the discards (ICES, 2008). This proportion was estimated by onboard observations (Système d'Informations Halieutiques: <http://www.ifremer.fr/sih>).

Three survey indices are available, namely FR-EVHOE, FR-RESSGASCS and UK-WCGFS. FR-RESSGASCS was conducted in the Bay of Biscay from 1978 to 2002 operating a bottom trawl similar to commercial fisheries. This survey was carried out twice a year in May and November since 1997 (also in August 1997) but indices are considered to be poorly reliable in 2002. From 1997, the FR-EVHOES survey is conducted in autumn and covers both the Bay of Biscay and the Celtic Sea using a random stratified sampling design and a GOV 36/47 trawl. UK-WCGFS started in 1988 in the Celtic Sea and ended 2004. As it was conducted in March, the survey did not catch hake of age 0.

One hundred and twenty tagged and recaptured fishes (de Pontual *et al.*, 2003 ; de Pontual *et al.*, 2006) are also used to fit the model; only fishes with at least a quarter of liberty after their release (i.e. at least the time step of the model) were selected.

A maturity-at-length relationship (Piñeiro et Sainza, 2003) is used to compute $p_{\text{mat}}(c)$ the proportion of mature fishes in a length class c . Piñeiro et Sainza (2003) also provide a length-weight relationship used to compute w_c the weight of an individual in a length class c .

Natural mortality M is assumed to be known and constant equals to 0.2 year^{-1} (ICES, 2008).

2.2. State model: population dynamics and fishing activity

A formulation of a discrete time and length-structured population model is given by the four following equations:

$$(1) \quad N(t + \tau_1, z, c) = \sum_{i=1}^L g_{i,c} \cdot N(t, z, i)$$

with $N(t, z, c)$ abundance in zone z and length class c at time t , $g_{i,c}$ the probability to grow from class i to class c in a time step t and L the number of length classes.

$$(2) \quad N(t + \tau_2, z, c) = R(t, z, c) + N(t + \tau_1, z, c)$$

with $R(t, z, c)$ recruitment in zone z and length class c at time t .

$$(3) \quad N(t + \tau_3, z, c) = \sum_{i=1}^Z (1 - p_{\text{mat}}(c)) mi_{\text{imm}}(t, i, z) \cdot N(t + \tau_2, i, c) \\ + \sum_{i=1}^Z p_{\text{mat}}(c) mi_{\text{mat}}(t, i, z) \cdot N(t + \tau_2, i, c)$$

with $p_{\text{mat}}(c)$ the proportion of matures in class c , $mi_{\text{imm}}(t, i, z)$ (respectively $mi_{\text{mat}}(t, i, z)$) the proportion of immature (respectively mature) fishes migrating from zone i to zone z during time step t and Z the number of zones.

$$(4) \quad N(t+1, z, c) = Sr(t, z, c) \cdot N(t + \tau_3, z, c)$$

with $Sr(t, z, c)$ the survival probability of a fish of class c in zone z during time step t .

The three processes, namely growth (equation 1), recruitment (equation 2) and migrations (equation 3) are assumed to occur in an insignificant time (respectively τ_1 , τ_2 and τ_3) at the beginning of the time step.

The model has a quarterly time step which is consistent with a preliminary sensitivity analysis (Drouineau *et al.*, 2008). For computation time reasons, length classes were set to 2 cm width (from 3 to 109 cm, lower bound), instead of 1 cm as recommended by Drouineau *et al.* (2008). Space is divided into 4 zones (Figure 2) in which the population and the fishing activity are assumed to be uniformly distributed. Zones 1 and 3 cover respectively the spawning zone of the Celtic Sea and of the Bay of Biscay, whereas the nursery areas of the Celtic Sea and of the Bay of Biscay are located respectively in zones 2 and 4.

2.3. Growth

Growth increments are assumed to follow a gamma distribution (DeLong *et al.*, 2001), whose mean is given by a von Bertalanffy growth equation and whose variance is proportional to its mean:

$$(5) \quad \begin{cases} E(\Delta l / l) = (L_{\infty} - l) \cdot (1 - e^{-K \cdot \Delta t}) \\ V(\Delta l / l) = C \cdot E(\Delta l / l) \end{cases}$$

We assume that individuals in a length class are all of equal length (equal to the midpoint length of the class). Consequently, the probability $g_{i,j}$ of transition from class i to class j is given by:

$$(6) \quad g_{i,j} = \int_{(m_j - \Delta l / 2) - m_i}^{(m_j + \Delta l / 2) - m_i} \left(\frac{1}{C^{\alpha_{\Delta l / l}} \cdot \Gamma(\alpha_{\Delta l / l})} x^{\alpha_{\Delta l / l} - 1} e^{-\frac{x}{C}} \right) dx$$

with $E(\Delta l / l) = \alpha_{\Delta l / l} \cdot C$ and $V(\Delta l / l) = \alpha_{\Delta l / l} \cdot C^2$

with Δl the width of the length classes (2cm) and m_i the midpoint size of the departure class i .

Following de Pontual *et al.* (2006), we assume that L_∞ is known equal to 110cm. Growth rate K and constant C (equation 5) should be estimated. Spatial or seasonal heterogeneities in growth are not taken into account.

A complete description of the growth model may be found in Drouineau *et al.* (2008).

2.4. Recruitment

Hake recruitment occurs in two main nursery areas: one located in the continental shelf of the Bay of Biscay (zone 4 Figure 2), the other located on the continental shelf of the Celtic Sea (zone 2 Figure 2) (Casey et Pereiro, 1995 ; Kacher et Amara, 2005). Recruitment in the Bay of Biscay starts during the second quarter of the year, while it occurs during the third quarter in the Celtic Sea. No clear relationship has been established between the two nursery areas, therefore we assume recruitment in the two areas are independent. Length at recruitment is assumed to follow normal distribution of mean L_0 and standard deviation σ_0 . Consequently, if p_c denotes the proportion of recruits in length class l , the recruitment is given for each quarter by the following equations:

$$(7) \quad \begin{aligned} R(t, z, c) &= p_c \cdot R_{BB}(y) \quad \text{quarter 2, zone } z = 4 \text{ (nursery Bay of Biscay)} \\ R(t, z, c) &= p_c \cdot R_{CS}(y) \quad \text{quarter 3, zone } z = 2 \text{ (nursery Celtic Sea)} \\ R(t, z, c) &= 0 \quad \text{else} \end{aligned}$$

$$(8) \quad p_c = \int_{(m_c - \Delta l / 2)}^{(m_c + \Delta l / 2)} \frac{1}{\sigma_0 \sqrt{2 \cdot \pi}} \exp \left[\frac{-1}{2} \cdot \left(\frac{x - L_0}{\sigma_0} \right)^2 \right] dx$$

with $R_{BB}(y)$ the recruitment in the Bay of Biscay (zone 4) in year y (corresponding to time step t) and $R_{CS}(y)$ the recruitment in the Celtic Sea (zone 2) in year y .

Migrations

As mentioned in the introduction, hake migration patterns are poorly known. Migrations are assumed to be related to reproduction and juvenile and adult hake are clearly spatially segregated at certain times of year. Accordingly, we model

migration of matures and immatures differently. Migrations are supposed to be seasonal and are described by a proportion of matures moving from one zone to another during a quarter.

We set some of the migration proportions $mi_{imm}(t)$ and $mi_{mat}(t,i,z)$ using biological life cycle and existing literature (Table 2). Consequently, only 23 coefficients are unknown. However, given that the $\sum_{i=1}^Z mi_{imm}(t,z,i)=1$ and $\sum_{i=1}^Z mi_{mat}(t,z,i)=1$, only 12 parameters should be estimated.

2.5. Survival

Survival is the result of both natural and fishing mortality. Survival is computed by the following equation.

$$(9) \quad Sr(t, z, c) = e^{-\Delta t \cdot (M + F_{tot}(t, z, c))}$$

with $F_{tot}(t, z, c)$ the total fishing mortality applied during time step t on class c in zone z .

2.6. Estimation of fishing mortality and catches

Fishing activity is based on *metiers*, subdivided in national *sub-metiers*. According to the Data Collection Regulation (ICES, 2004), a *metier* is characterised by a fishing zone, a fishing gear and target species. This definition matches ICES fishery units therefore, we use ICES fishery units *fu* as a *metier*, and sub-units *su* as national *sub-metiers*. Each sub-unit in a fishery unit are assumed to share a same gear and same target species, and consequently to have a same selection pattern $s_{fu}(c)$, and to fish in a same *metierzone*_{*fu*} which covers one or several population zones (Figure 2). The area of *metierzone*_{*fu*} is noted S_{fu} .

Assuming a constant selection pattern between sub-units of a fishery unit is consistent with the assumption made by the ICES working group WGHMM (ICES, 2008) which often uses the length composition of landings of a country to estimate the length composition of another country within the same fishery unit. Moreover, by looking at the observed data, we do not see any major inconsistencies between length composition of landings of sub-units within a fishery unit.

Fishing mortality generated by a sub-unit *su* is equal to the product of the sub-unit catchability q_{su} , of the fishery unit *fu* selection pattern $s_{fu}(c)$ and of fishing effort E_{su} :

$$(10) \quad F_{su}(t, z, c) = q_{su} \cdot s_{fu}(c) E_{su}(t) \frac{Surface(z)}{S_{fu}} \quad \text{if } z \in \text{metierzone}_{fu}$$

The ratio $Surface(z)/S_{fu}$ aims at distributing the total fishing effort among the different model zones of the metier zone.

The selection pattern is modelled either by a sigmoid (for example (Froysa *et al.*, 2002)) to mimic selection increasing pattern (fishery units using trawl) or by a gamma function (Deriso *et al.*, 1985) (longlines or gillnets).

Total fishing mortality is the sum of the fishing mortalities generated by the different sub-units:

$$(11) \quad F_{tot}(t, z, c) = \sum_{su} F_{su}(t, z, c)$$

Catches are then computed using the traditional Baranov equation and reallocated to each sub unit. Discards are not taken into account except for the metier corresponding to Fishery unit 09, i.e. catches and landings are assumed to be equivalent for all sub-units except fishery unit 09 where a fraction is discarded.

Total landings $Y_{su}(t)$ (in weight) by sub-unit and time step is then computed:

$$(12) \quad Y_{su}(t) = \sum_{z \in metierzone} \sum_{c=1}^C w_c \cdot (1 - dis_{su}(c)) \cdot C_{su}(t, z, c)$$

with $C_{su}(t, z, c)$ number of fishes of length class c caught by sub-unit su in zone z during time step t , and $dis_{su}(c)$ proportion of fishes of length class c discarded by sub-unit su . $dis_{su}(c) = 0$ for all sub-units but fishery-unit 09 for which a discard ogive was previously estimated from onboard observations.

Length composition of the landings is also computed over a *periode* $f_{su}(periode, c)$:

$$(13) \quad f_{su}(periode, c) = \frac{\sum_{t \in periode} \sum_{z \in metierzone} C_{su}(t, z, c)}{\sum_{t \in periode} \sum_{z \in metierzone} \sum_{c=1} C_{su}(t, z, c)}$$

2.6.1. Survey abundance indices

Abundance indices per survey and zone are summarized in table 3. The number of individuals $C_{surv}(t, z, c)$ of class c caught by a survey $surv$ during time step t in zone z is given by the product of a catchability q_{surv} , a sampling effort (time fishing) $E_{surv}(t, z)$, of the number of individuals in the zone $N(t + \tau_3, z, c)$ and of a selection pattern $s_{surv}(c)$. A ratio of surface is also used to make indices comparable between zone ($SurfaceMin$ stands for the surface of the smallest zone sampled by the survey; this choice is rather arbitrary).

$$(14) \quad C_{surv}(t, z, c) = q_{surv} \cdot s_{surv}(c) \cdot E_{surv}(t, z) \cdot N(t + \tau_3, z, c) \cdot \frac{SurfaceMin}{Surface(z)}$$

We assume that the selection pattern of FR-EVHOE and UK-WCGFS is constant equal to 1. FR-RESSGASCS using a professional trawl, we model the selection pattern by a sigmoid function.

We then compute total abundance estimates $IA_{surv}(t,z)$ and length compositions $f_{surv}(t,z,c)$:

$$(15) \quad IA_{surv}(t,z) = \sum_c C_{surv}(t,z,c)$$

$$(16) \quad f_{surv}(t,z,c) = \frac{C_{surv}(t,z,c)}{IA_{surv}(t,z)}$$

2.6.2. Initial numbers by class and zone

Theoretically, initial numbers by class and zone should be estimated. It would imply the estimation of 216 parameters. Therefore, we assume that the population at the beginning of the simulation period is at the equilibrium with the fishing mortality and the recruitment of first year. Consequently we ran a pre-simulation over 10 years previously to the simulation in which:

initial numbers are zero

population is submitted to fishing mortality and recruitment of first year during the 10 years of pre-simulation

The final numbers in each class and zone after the pre-simulation period are used as initial numbers for the simulation

2.7. Observation model and likelihood function

The likelihood function (equation 17) is equal to the sum of four components: (i) total landings in weight per sub-unit and per time step (equation 18, $\log LY_{obs_{su}}(\theta)$), (ii) total survey abundance estimates (equation 19, $\log LIA_{surv}(\theta)$), (iii) length composition of the landings per sub-unit and of the survey abundance estimates (equation 20, $\log LP_s(\theta)$) and (v) tagging data (equation 22, $\log L_{tag}(\theta)$):

$$(17) \quad \log L(\theta) = \sum_{su} \log LY_{obs_{su}}(\theta) + \sum_{surv} \log LIA_{surv}(\theta) + \sum_s \log LP_s(\theta) + \sum_{tag} \log L_{tag}(\theta)$$

2.7.1. Contribution of total landings $Y_{su}(t)$ and total survey abundance estimates

Observed total catches of a survey per zone and total landings of sub-units are assumed to follow gamma distributions (Froysa *et al.*, 2002) with a constant coefficient of variation. The loglikelihood of observed total landings for a sub-unit is therefore:

$$(18) \quad \log LY_{obs_{su}}(\theta) = \lambda \sum_t \left[\log \left(\frac{Y_{obs,su}(t)}{Y_{su}(t)} \right) - \frac{Y_{obs,su}(t)}{Y_{su}(t)} \right]$$

and the loglikelihood of total survey abundance estimates is:

$$(19) \quad \log LIA_{surv}(\theta) = \lambda \sum_t \sum_z \left[\log \left(\frac{IA_{obs,surv}(t,z)}{IA_{surv}(t,z)} \right) - \frac{IA_{obs,surv}(t,z)}{IA_{surv}(t,z)} \right]$$

λ is a constant proportional to the inverse of the coefficient of variation. We fix $\lambda=100$ which corresponds to a CV of 10%. This value is rather high but we choose to give a small weight in absence of more information.

2.7.2. Contribution of length-composition of landings and survey abundance estimates

We use a robust likelihood proposed by Fournier *et al.* (1990) to account for length composition of the landings. The loglikelihood of a sample s of landings from sub-unit su collected during a period $period$ is then:

$$(20) \quad \log P_s(\theta) = \sum_c -\frac{1}{2} \cdot \log(v_s(c)) + \log \left(e^{-\frac{1}{2} \frac{(f_{su}(period,c) - f_{obs,su}(c))^2}{v_s(c)} + 10^{-6}} \right)$$

$$\text{with } v_s(c) = \left(\frac{1 - f_{su}(period,c)}{f_{su}(period,c)} + \frac{0.1}{C} \right) \cdot \frac{1}{n_s}$$

with n_s the number of fishes samples. To limit the influence of large samples, n_s is bounded to 500. The same assumption is used for the length composition of survey abundance estimates.

2.7.3. Contribution of tagging data

Initial length l_0 , time of liberty after release ΔT and growth increments ΔL of tagged fishes were available for this study. Considering length at release, we assumed that all released fishes are fully recruited to commercial gears (mainly fishery unit 09) since size at release is large enough (27.5cm). The increments were first extrapolated to get an increment ΔL_q corresponding to a quarter liberty period ΔT_q :

$$(21) \quad \Delta L_q = \frac{\Delta L (1 - \exp^{-K \cdot \Delta T_q})}{1 - \exp^{-K \cdot \Delta T}}$$

This transformation is required because the constant C (equation 5) of the growth model is only valid for quarterly increments. To understand this point, consider a fish of size l_0 spends two quarters in liberty, the growth increment $\Delta L/l_0$ is the sum of two quarterly

increments $X_1 = \Delta L_1 / l_0$ and $X_2 = \Delta L_2 / l_0 \cap \Delta L_1$ which are not independent, Consequently, $V(\Delta L) \neq C \cdot E(\Delta L / l)$.

The contribution of a tagged fish *tag* to the loglikelihood is therefore:

$$(22) \quad \log L_{tag}(\theta) = -\log(\Gamma(v)) + v \cdot \log(v \cdot \Delta L_{q,tag}) - v \cdot \log(\mu_{tag}) - \log(\Delta L_{q,tag}) - \frac{v \cdot \Delta L_{q,tag}}{\mu_{tag}}$$

$$\text{with } \mu_{tag} = (L_{\infty} - l_{0,tag}) (1 - \exp^{-K \cdot \Delta t}) \text{ and } v = \frac{\mu_{tag}}{C}$$

2.8. Parameters estimation

Seventy three parameters are estimated (Table 4) by maximum likelihood.

The loglikelihood maximisation was carried out using an evolutionary strategy algorithm (Schwefel, 1995) and a quasi-Newton algorithm provided in autodif library (<http://www.otter-rsch.com/>). The evolutionary strategy algorithm was used in a first step to provide a starting point to the quasi-Newton algorithm.

Variance covariance and the correlation matrices were computed to check parameters redundancy: Hessian matrix was approximated by a finite difference approximation and inverted to get the variance-covariance matrix.

3. Results

3.1. Growth

The estimated growth rate ($K=0.24 \pm 0.01$ cm Figure 3, highest correlation 0.38 with FU04EW catchability) and resulting growth curve is very close to the curve estimated from tagging data (de Pontual *et al.*, 2003 ; de Pontual *et al.*, 2006) and higher than those estimated by otoliths reading. This lends further weight to the suggestion that hake grow much faster than previously thought.

The positions of the peaks in length compositions of landings (Figure 4) are well fitted by the model supporting the idea of an appropriate growth model. Sub-units of fishery unit 13 (gillnets on the continental shelf of the Bay of Biscay) are badly fitted, however, data from this fishery unit are very doubtful (only a small proportion of the logbooks were available) and fishermen have a very specific strategy (targeting large hake on the continental shelf). It is important to mention that length-composition of landings are the most reliable data and are very well fitted by the model, giving weight to our growth rate estimate.

Length compositions of survey catches (Figure 5) are not as well represented by the model, however peaks in length compositions are generally properly estimated. It is not surprising that those data are not as well reproduced since samples from commercial catches are larger and more numerous.

3.2. Distribution of spawning stock biomass (SSB) and migrations

Mature fishes are mainly concentrated over the margin of the continental shelf of both Celtic Sea and Bay of Biscay (Figure 6). The model did not show any seasonal pattern whereas the literature describes seasonal heterogeneities in the distribution of mature fishes in the Celtic Sea (Hickling, 1935 ; Poulard et Léauté, 2002).

Few migration rates estimates were not close or equal to zero (Figure 6): hakes leave the continental shelf and migrate to the margins when maturing, where they remain till the end of their lives. More surprisingly, no major migration from the Bay of Biscay to the Celtic Sea is estimated by the model though it is sometimes mentioned in the literature (Casey et Pereiro, 1995). However, a few migration rates were correlated with other parameters: $mi_{mat}(t,3,3)$ is highly correlated with $mi_{mat}(t,4,3)$ during quarter 3 (correlation -0.84), and $mi_{mat}(t,1,1)$ during quarters 3 and 4 which are correlated with catchabilities of subunits FU05EW and FU05FR (correlation 0.60).

Some seasonal offsets are observed between simulated and observed peaks of landings for the English sub-unit 04 (Figure 7 left) and French sub-unit 04 (Figure 7 right) which can be partly explained by the observed seasonal differences in peaks of catches per unit of effort between sub-units of the same fishery units (Figure 8). Those kinds of offsets are only observed for this fishery unit.

4. Discussion and perspectives

Despite the abundant scientific literature on European hake, part of its biology remains poorly known. The proposed model improves the knowledge on some biological processes by estimating growth and migration rates.

Growth rate estimate is close to estimate resulting from tagging data and much higher than estimates from otoliths reading. Moreover, peaks in length-frequency data from both commercial fishery (except fishery unit 13) and scientific surveys are properly captured by the model. This result confirms the hypothesis of a fast growing species formulated by de Pontual *et al.* (2003), de Pontual *et al.* (2006) and Kacher et Amara (2005). Following de Pontual *et al.* (2003) and de Pontual *et al.* (2006), we assumed that L_{∞} was known and fixed, equal to 110cm, to avoid problems of correlation between K and L_{∞} and to directly compare our results to estimates from the tagging study; however, a different value of L_{∞} is likely to give a different growth rate estimate. Shackell *et al.* (1997) proposed a method to get reliable growth parameters estimates that might be appropriate in further development of our model. Natural mortality was also fixed to an arbitrary level but consistent with ICES assumptions and may have influenced growth rate estimation. Concerning fishery unit 13, the model is not able to properly fit length composition of catches which may be related to three main reasons: (i) poor data for this fishery unit, (ii) specific fishing target of the fishermen who target large individual in specific zone (close to the coast) within the nursery area corresponding to a spatial scale not taken into account in the model and (iii) inconsistencies of length compositions of catches of fishery unit 09 and 13 and the

assumed selectivity models (fishery unit 09 does not capture any large hakes while it fishes in the same zone than fishery unit 13 and has a sigmoid selectivity function). Finally, we chose to fix selectivity at a constant level for two scientific surveys in order to limit the number of unknown parameters. Though the fact that survey indices relate to a specific geographical zone and quarterly time period makes this assumption a bit more believable, this assumption may affect growth rate estimates. A sensitivity analysis to this hypothesis should be carried out in a further version of the model.

Analysing length-composition of scientific survey, we see that the big drop between the two first peaks is not exactly captured by the model (Figure 5). Although we are not fully satisfied by the estimate of growth variability (overestimated), the model succeeds in differentiating the two groups which is a very positive aspect when trying to estimate the growth rate. We tried to fit the model only on survey data, and it does not change a lot the length frequencies fits, which confirms that our growth model does not perfectly describe growth variability. Other relationship between mean growth increments and variance or other kind of models (age-length structured models) should perhaps be explored in the future.

Spatial distribution of the spawning stock biomass estimated by the model is quite consistent with previous observations. However, the model is not able to reproduce the seasonal aggregations of mature fishes on the continental shelf of the Celtic Sea described by Poulard (2001). Seasonal lags between simulated and observed peaks of landings for some fishery units (Figure 7) can be explained either by a poor estimation of those migration rates, by poor effort data or by some catchabilities-seasons interactions not properly described in the model. In that aspect, the use of VMS data would probably enable to improve spatial fishing effort allocation. Although the model does not estimate any significant migrations from the Bay of Biscay to the Celtic Sea, it would be premature to conclude that there is no exchange between those two areas since only large mature males are assumed to accomplish this migration in the literature, it is likely to be insignificant compared to the migrations of large numbers of smaller mature males and it is therefore not surprising that the model has difficulties to capture such pattern.

The models demonstrated the heterogeneity in the population spatial distribution. This result underlines the potential interest of spatial management measures such as marine protected areas. Parameter estimates may for example be used to improve the work done by Drouineau *et al.* (2006) aiming at assessing the influence of some management scenarios on the hake/Nephrops mixed fishery of the Bay of Biscay. Moreover, the high variability in the spatial distribution of the spawning stock biomass indicated in our fit is in contradiction with some of the assumptions of Extended Survivors Analysis. It would be especially interesting to assess the impact of non uniform spatial distribution of the spawning stock biomass on XSA estimates.

Tagging data were only used to improve the growth rate estimation. However they are still limited (in number and space) and therefore have a limited impact on the result (results are very similar when the model is fitted without tagging data). A large scale tagging campaign would provide relevant information on both migration and growth. In that case, a sub-model tag-attrition model (Kleiber *et al.*, 1987) describing the tagged sub-population would be relevant to take into account those

data. Alternatively, tagging data may be used in a first step to estimate the growth transition matrix and then to fit the rest of the model (DeLong *et al.*, 2001). A pluri-seasonal survey with a larger spatial distribution would also provide valuable information on migrations and spatio-temporal distribution of the spawning stock biomass.

Two assumptions may have an important impact on the results. First, we assumed a constant catchability and selection pattern during the studied period. This results in assuming that variations of fishing mortality per national sub-unit over time are only captured by variations of fishing effort. To relax this assumption, departures from the observed effort data have been considered through a yearly random walk of sub-units catchabilities, but resulting model is overparametrized and the algorithm did not converge to a unique solution. However, this assumption may have a minor effect on the estimation of growth rate, in which we think the length composition of samples and therefore the selectivity of the different fishery units and scientific survey play the main role. Moreover, catchability variations are more likely to occur at yearly scale than at a seasonal scale within a year, and therefore the assumption has probably a larger impact on the estimation of the yearly trend in spawning stock biomass, than on the estimation of its spatial distribution and seasonal migrations within a year.

Second, the assumption of equilibrium for the initial year is also quite strong but was required to keep the model identifiable. Sensitivity analysis could be carried out in further development of our model to quantify the impact of such an assumption. The impact of the assumption will decrease in the future when the time series will get longer. Once again, we think that the assumption has an important impact on year to year evolution of the spawning stock biomass, but probably a smaller impact on seasonal distribution of spawning stock biomass and consequently on the estimation of migration rates.

We paid special attention to the construction of the likelihood function. We tried to build a likelihood function that describes as properly as possible the observation processes. However, some approximations were sometimes required to keep the model robust, especially for length compositions samples. However, the approximation we have used has been used in many models (Fournier *et al.*, 1998 ; Maunder et Watters, 2003) and has proved to provide reliable results. Moreover, we tried as much as possible to avoid using subjective weighting of data sets, consequently, data sets are weighted through their variance by likelihood construction. Considering length-compositions sample, the variance (and consequently a likelihood weight) is a direct function of the number of sampled fishes. Concerning tagging data, the variance (and consequently a likelihood weight) is directly given by our assumption on growth increments distribution (equation 5). Concerning total landings and total survey abundances, it was not possible to have an objective measure of the variance, therefore, in the absence of evidence, we chose a CV of 10% which probably down weight those data.

To conclude, the results seems rather encouraging and provide quantitative estimates of biological parameters which are consistent with existing qualitative knowledge. Some uncertainties remain and therefore results should still be considered with caution. In this paper, we choose to mainly focus on the estimation of some biological parameters (growth and migrations), however to some extent, the model may also relevant to carry out an assessment of the stock

since it also estimates catchabilities and recruitments. Uncertainties on data and biological processes would then be more properly described than currently (ICES, 2008), and expensive and unreliable age-length would not be required any more. Moreover, the work presented in this paper may be a relevant basis to the development of length-structured models for other species for which the age-length conversion is uncertain (anglerfish *Lophius sp.*, *Nephrops...*).

Acknowledgements

We are grateful to Mike Smith (CEFAS) and José Castro (IEO) for providing us the data which were required for our study. We also thank the three referees for their relevant comments which largely improve this article.

Tables

Table 1 : List of the different sub-units (FR : France, SP : Spain, EW : England), and of available length composition of catches. Q=quarterly Y=yearly.

Fishery unit	Description	Sub-areas	Sub-unit	1999	2000	2001	2002	2003	2004	2005
FU01	Long-line in medium to deep water	VII	FU01E W							
			FU01SP	Q	Y	Q	Q	Q	Q	Q
FU03	Gillnets	VII	FU03E W	Q	Q	Q	Q	Q	Q	Q
			FU03FR							
			FU03SP	Q	Y	Q	Q	Q	Q	Q
FU04	Non-Nephrops trawling in medium to deep water	VII	FU04E W						Y	Q
			FU04FR							
			FU04SP	Q	Y	Q	Q	Q	Q	Q
FU05	Non-Nephrops trawling in shallow water	VII	FU05E W	Q	Q	Q	Q	Q	Q	Q
			FU05FR	Y	Y	Y	Q	Q	Q	Y
FU08	Nephrops trawling in medium to deep water	VII	FU08FR							
FU09	Nephrops trawling in shallow to medium water	VIII	FU09FR	Y	Y		Q	Q	Q	Q
FU10	Trawling in shallow to medium water	VIII	FU10FR	Y	Y		Q	Q	Q	Q
FU12	Long-line in medium to deep water	VIII	FU12FR		Y		Q	Q	Q	Q
			FU12SP	Q	Y	Q	Q	Q	Q	Q
FU13	Gill nets in shallow to medium water	VIII	FU13FR	Y	Y		Q	Q	Q	Q
			FU13SP	Q	Y	Q	Q	Q	Q	Q
FU14	Trawling in medium to deep water	VIII	FU14SP	Q	Y	Q	Q	Q	Q	Q

Table 2 : Proportion of fishes moving from a zone (in line) to another (in column) for each quarter. « x » stands for “to be estimated”.

quarter	immatures						matures					
	1	2	3	4	reason	are	1	2	3	4	reason	are
1	1	1	0	0	0	Immatures are fixed	1	1	0	0	0	Western aggregation
	2	0	1	0	0	"	2	x	x	0	0	"
	3	0	0	1	0	"	3	0	0	1	0	Reproduction in Bay of Biscay
	4	0	0	0	1	"	4	0	0	1	0	"

quarter	immatures						matures					
	1	2	3	4	reason	are	1	2	3	4	reason	are
2	1	1	0	0	0	Immatures are fixed	1	1	0	0	0	Reproduction in Celtic Sea
	2	0	1	0	0	"	2	1	0	0	0	"
	3	0	0	1	0	"	3	x	0	x	x	Matures migrate to the shelf or to the Celtic Sea
	4	0	0	x	x	Recruitment drift	4	0	0	0	1	Matures migrate to the shelf

quarter	immatures						matures					
	1	2	3	4	reason	are	1	2	3	4	reason	are
3	1	1	0	0	0	Immatures are fixed	1	x	x	0	0	No constaint
	2	x	x	0	0	Recruitment drift	2	x	x	0	0	"
	3	0	0	1	0	Immatures are fixed	3	0	0	x	x	"
	4	0	0	0	1	"	4	0	0	x	x	"

quarter	immatures						matures					
	1	2	3	4	reason	are	1	2	3	4	reason	are
4	1	1	0	0	0	Immatures are fixed	1	x	x	0	0	No constaint
	2	0	1	0	0	"	2	x	x	0	0	"
	3	0	0	1	0	"	3	0	0	1	0	Aggregation on the shelf slope
	4	0	0	0	1	"	4	0	0	x	x	"

Table 3 : List of available indices (X) per year, zone and survey.

zone	1999				2000				2001				2002				2003				2004				2005			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
FR-EVHOE quarter 4	X	X		X	X		X		X	X		X	X		X		X	X		X	X	X	X	X	X	X	X	X
FR- RESSGASCS quarter 2				X								X																
FR- RESSGASCS quarter 4				X								X																
UK-WCGFS quarter 1	X	X			X	X	X		X	X			X	X	X		X	X							X	X		
UK-WCGFS quarter 4																							X					X

Table 4 : Unknown parameters of the model.

Parameters origin	Parameters	Notation	Number
Population	Yearly recruitments	$R_{BB}(y)$	2 x Y+2 =16
		$R_{CS}(y)$	
		L_0	
		σ_0	
	Growth	K, C	2
	Migrations	Mi_{mat}, Mi_{imm}	12
Fishing activity	Catchability per sub-unit	q_{su}	18
	Selection pattern	s_{fu}	20
Survey	Catchability	q_{surv}	3
	Selection pattern (FR-RESSGASCS)	s_{surv}	2
TOTAL			73

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Figures

Figure 1 : Modelling process used in the study.

Figure 2 : Maps of the four model zones and respective fishing areas of each fishery unit.

Figure 3 : Estimated growth curves from tagging data (black line), otoliths reading (black bold line and grey line) and from the model (grey bold line).

Figure 4 : Observed (bold solid line) and estimated (solid line) length composition of landings for the different sub-units 2000. Length compositions for other years are not presented here because similar to 2000: good fit for all fishery units, except fishery unit 13 which is not fitted at all.

Figure 5 : Observed (bold solid line) and estimated (solid line) length compositions of survey catches : UK-WCGFS 2003 in zone 4 (left) and from FR-EVHOE 2005 in zone 2 (right).

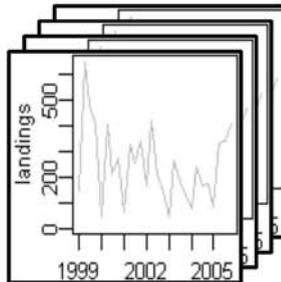
Figure 6 : Distribution of the spawning stock biomass (in tons per area) in 2005 and estimated mature fishes migration rates. Spawning stock biomass estimates should not be considered as an absolute value but as a relative value indicating spatial distribution.

Figure 7 : Seasonal distributions of observed catch per unit of effort for English (left) and French (right) sub-units IV.

Figure 8 : Seasonal distributions of observed catch per unit of effort for English (left) and French (right) sub-units IV.

Data:

- Survey abundance indices
- Total landings
- Length composition of landings



MODEL

Observation model

Likelihood function
 $f(\text{Data}/\theta)$

Population Dynamics

$$N(t+1) = Sr(t)G[R(t) + N(t)]\text{Mig}(t)$$

$$C(t) = \frac{F(t)}{F(t) + M} (1 - \exp^{-\Delta t(F(t) + M)}) N(t)$$

Fishing activity

State model

Optimization algorithm

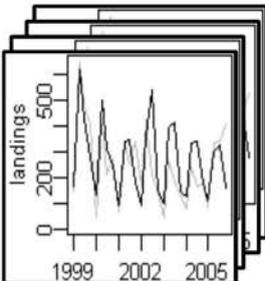
Fitting the model $\hat{\theta}$

Validation:

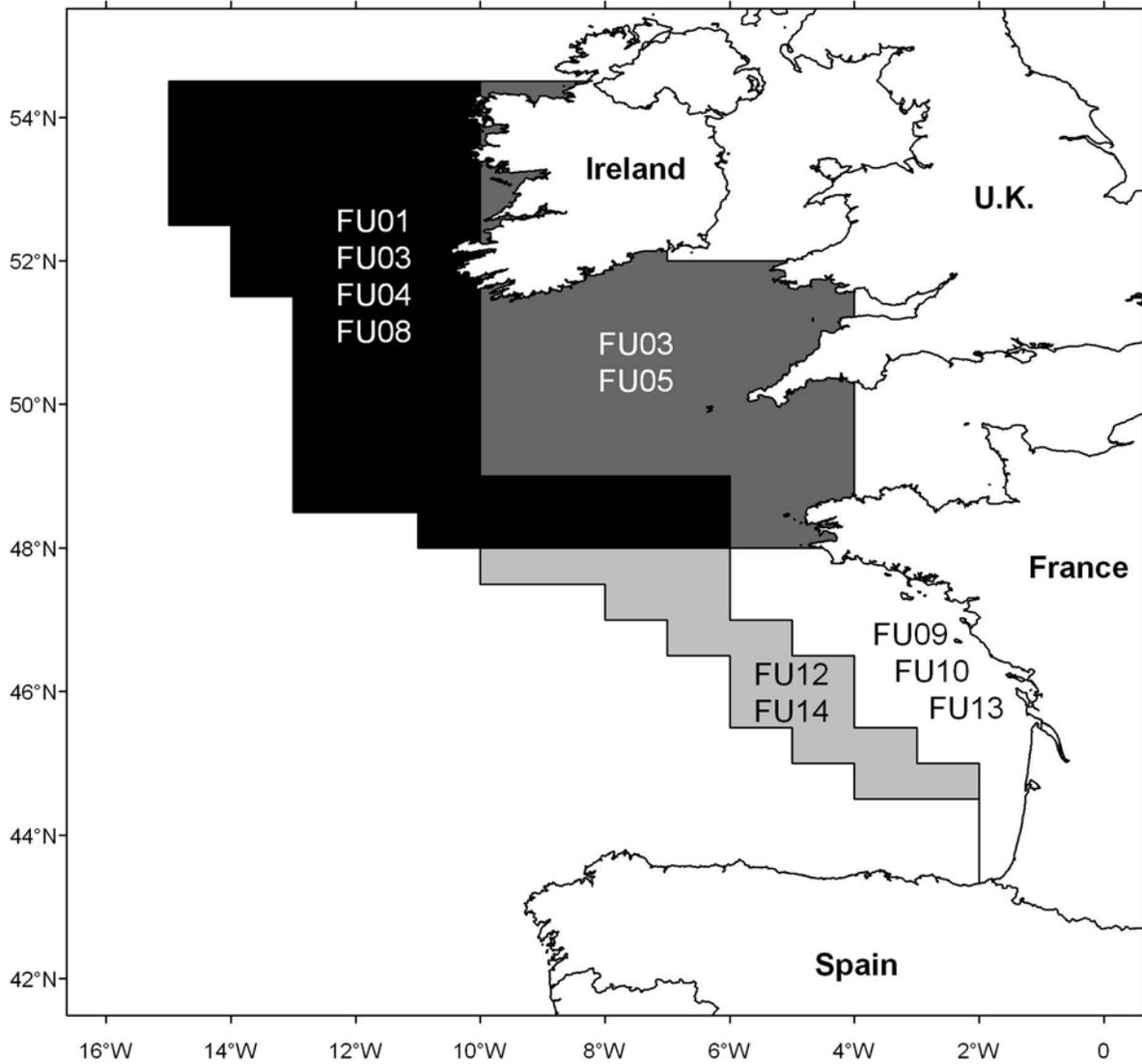
- Fitting observations
- Parameters redundancy

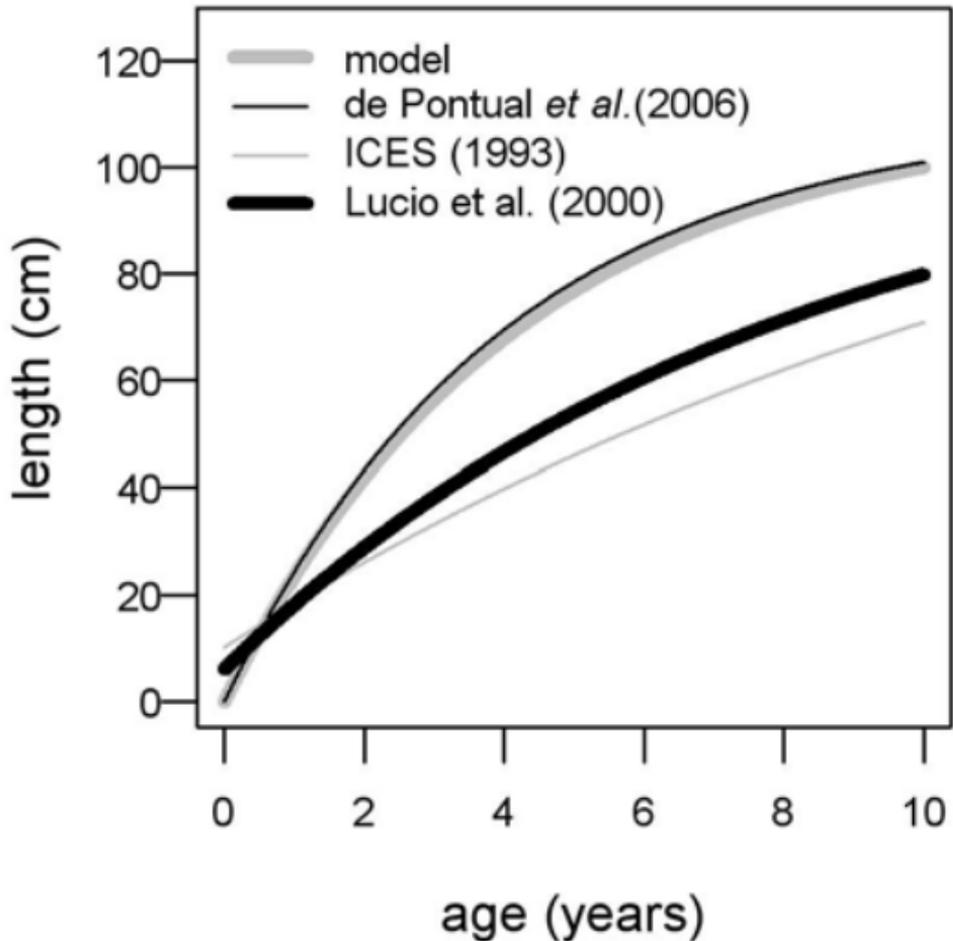
Results:

- Growth rate and migrations
- SSB and recruitment



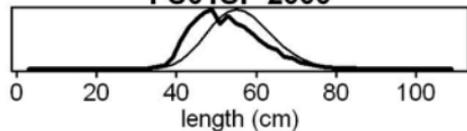
■ zone 1 ■ zone 2 ■ zone 3 □ zone 4



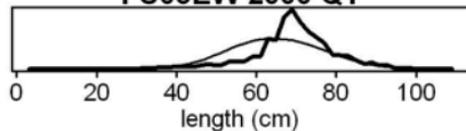


— model
— observed

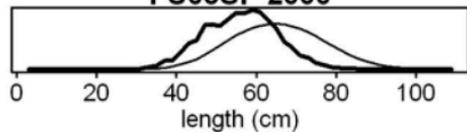
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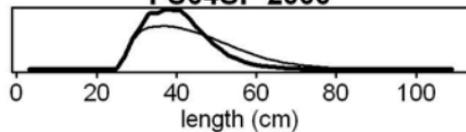
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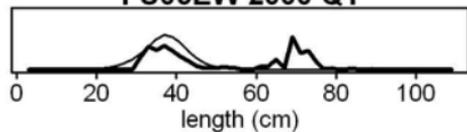
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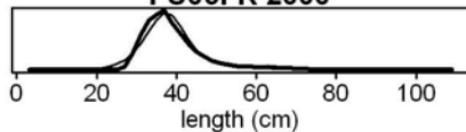
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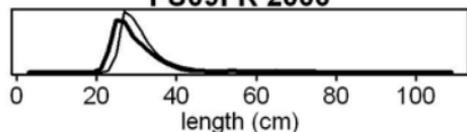
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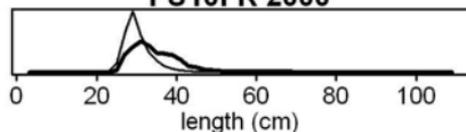
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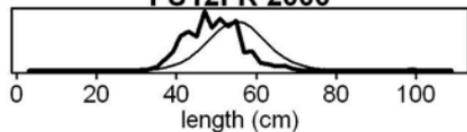
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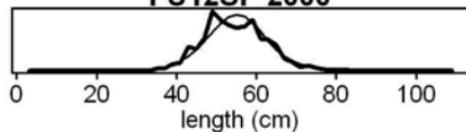
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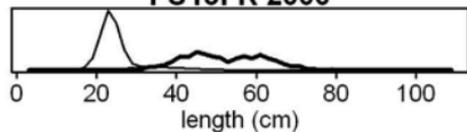
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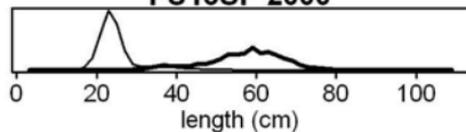
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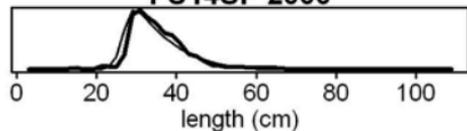
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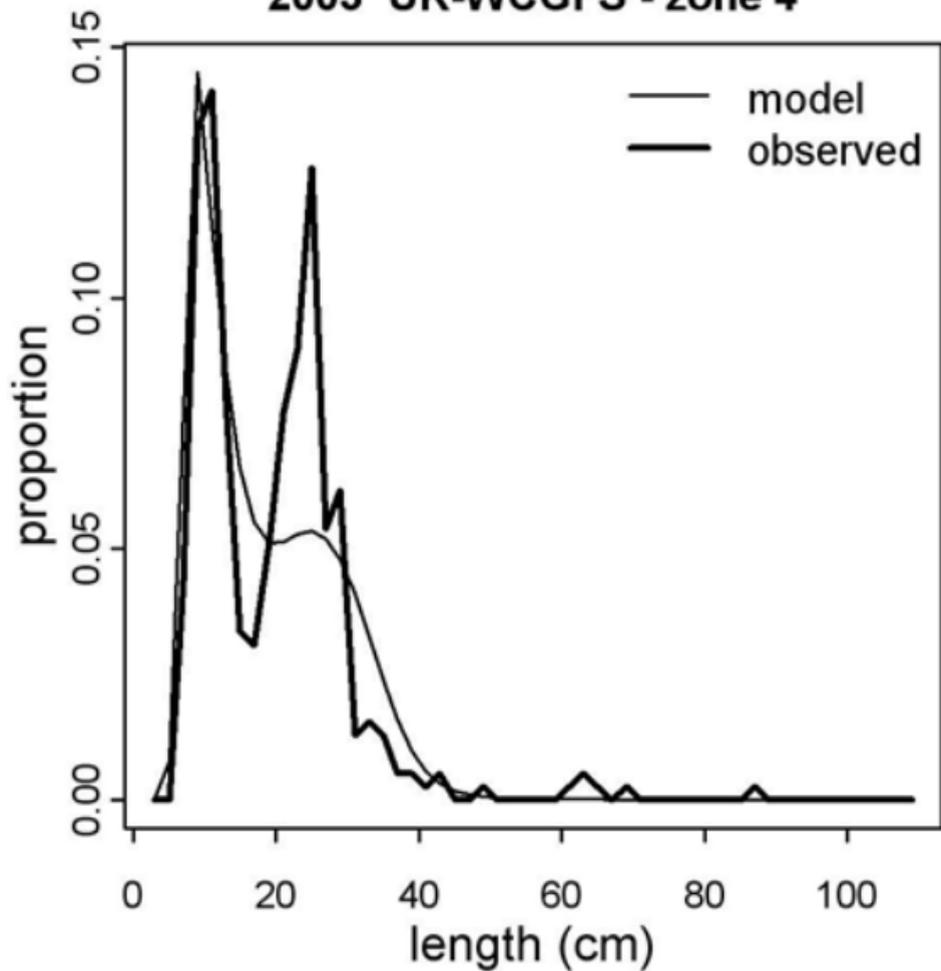
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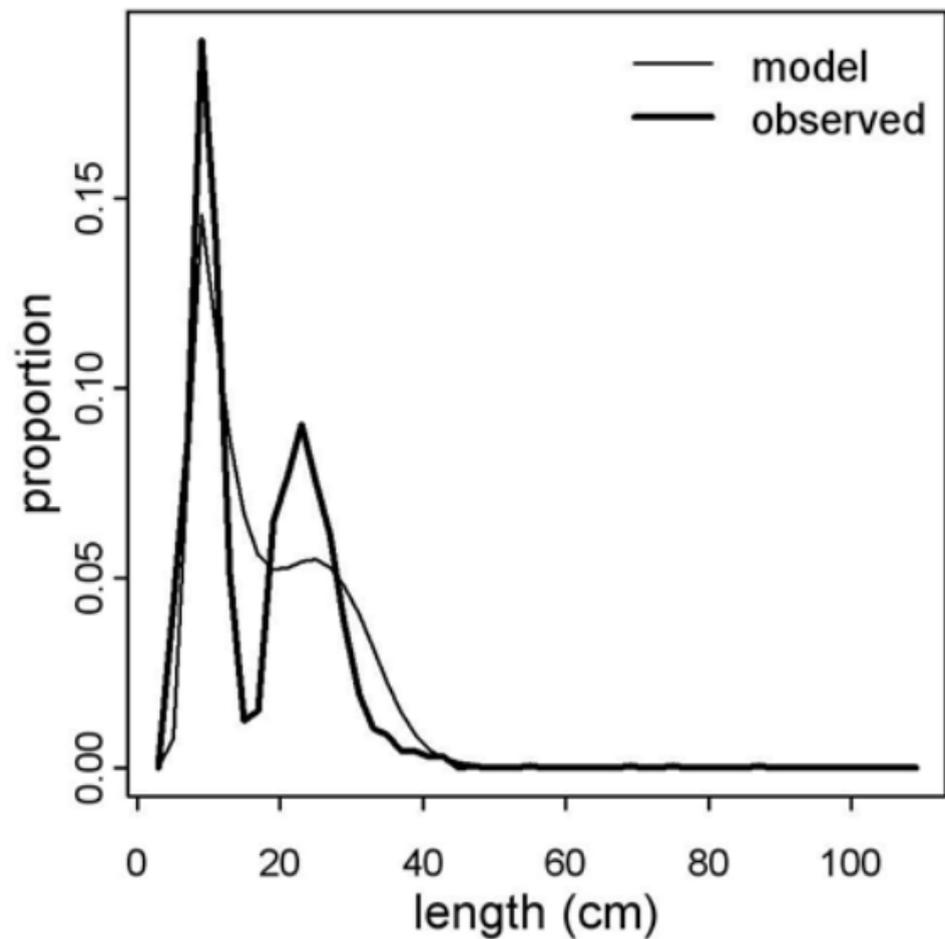
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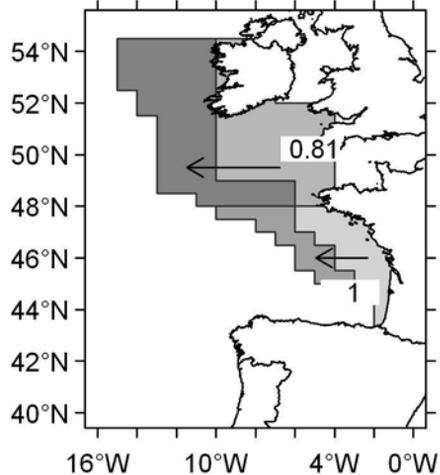
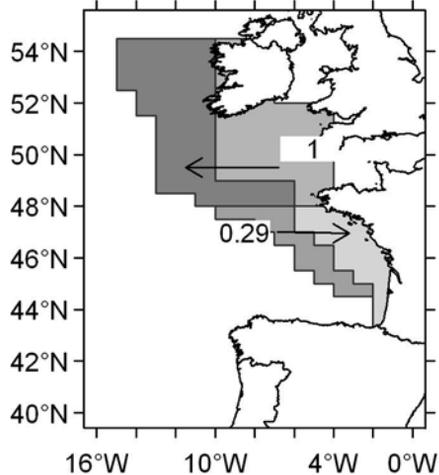
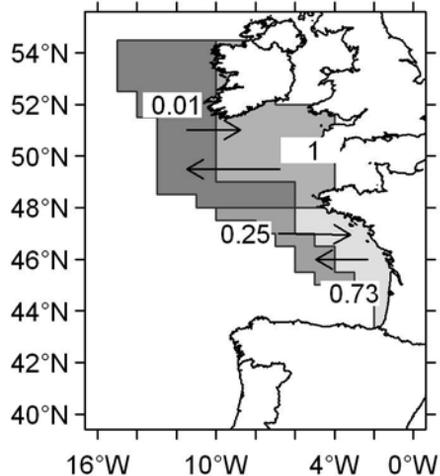
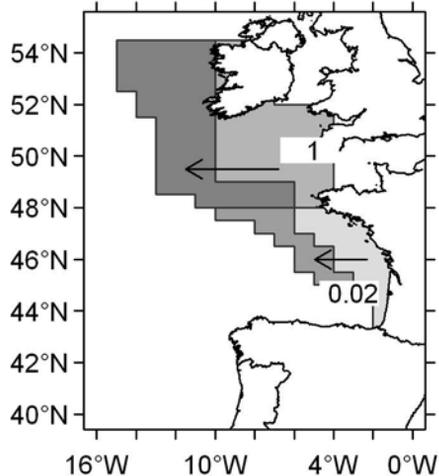
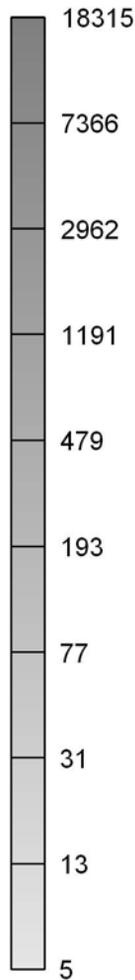


2003 UK-WCGFS - zone 4

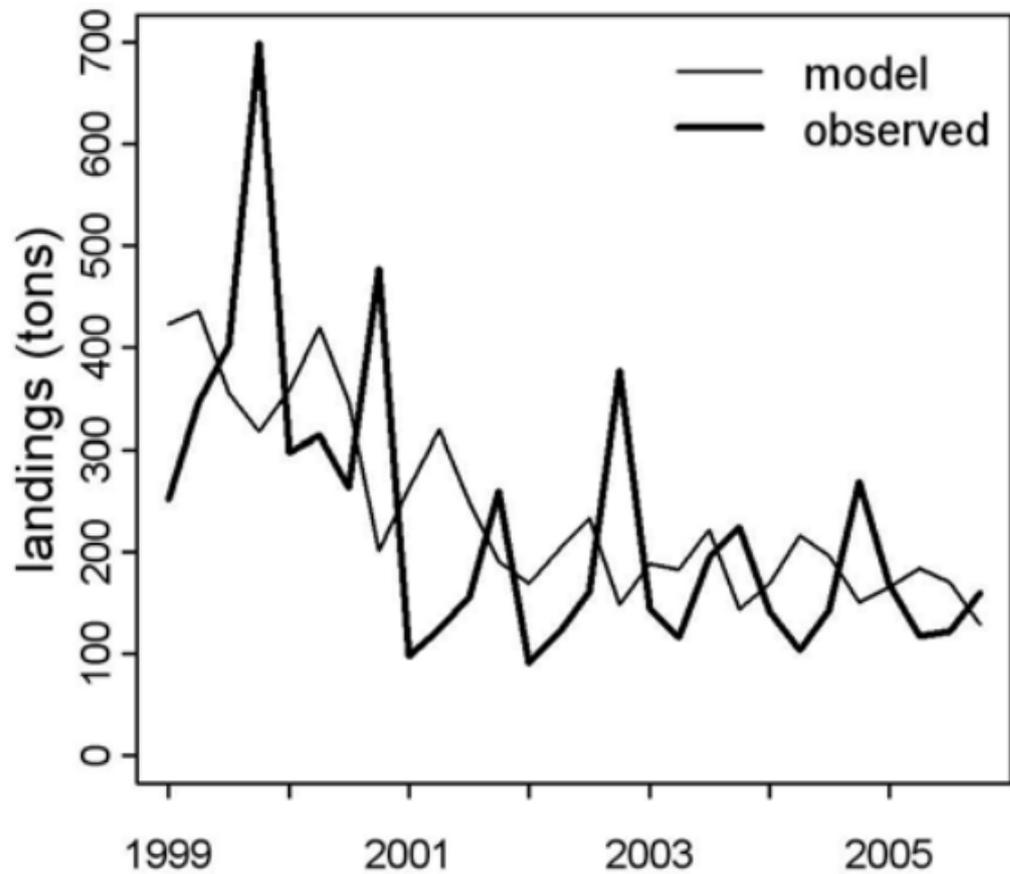


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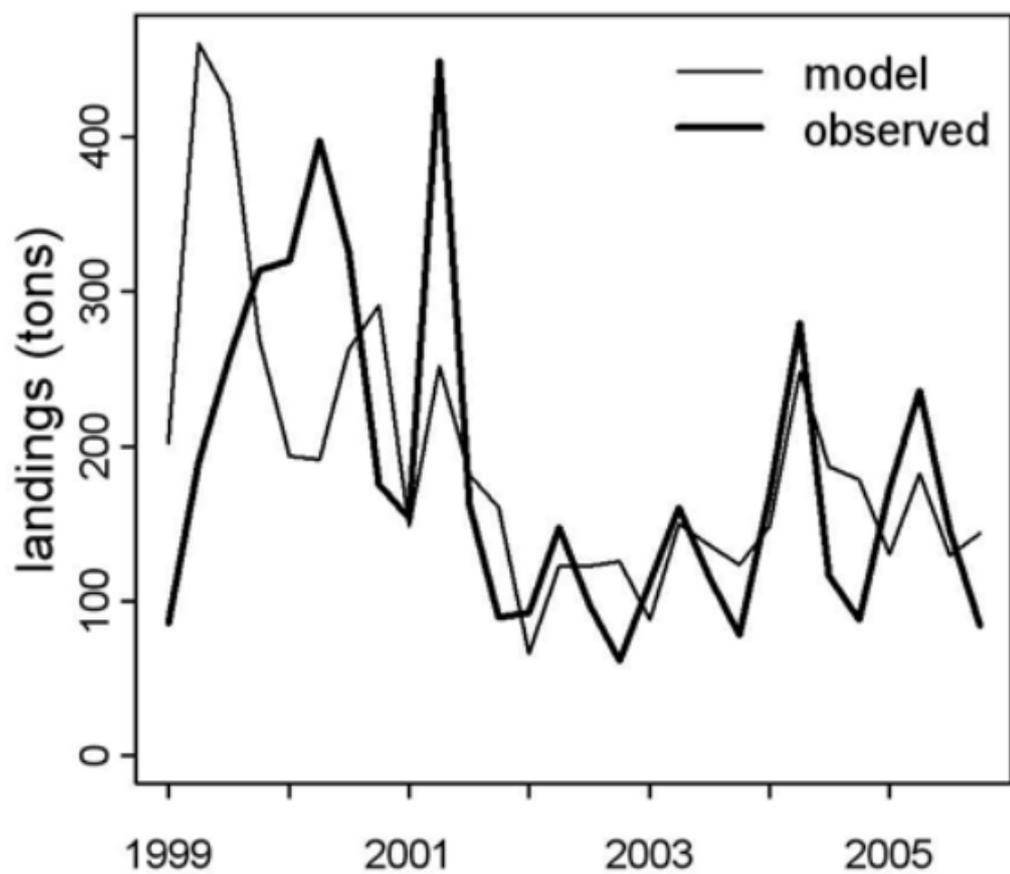


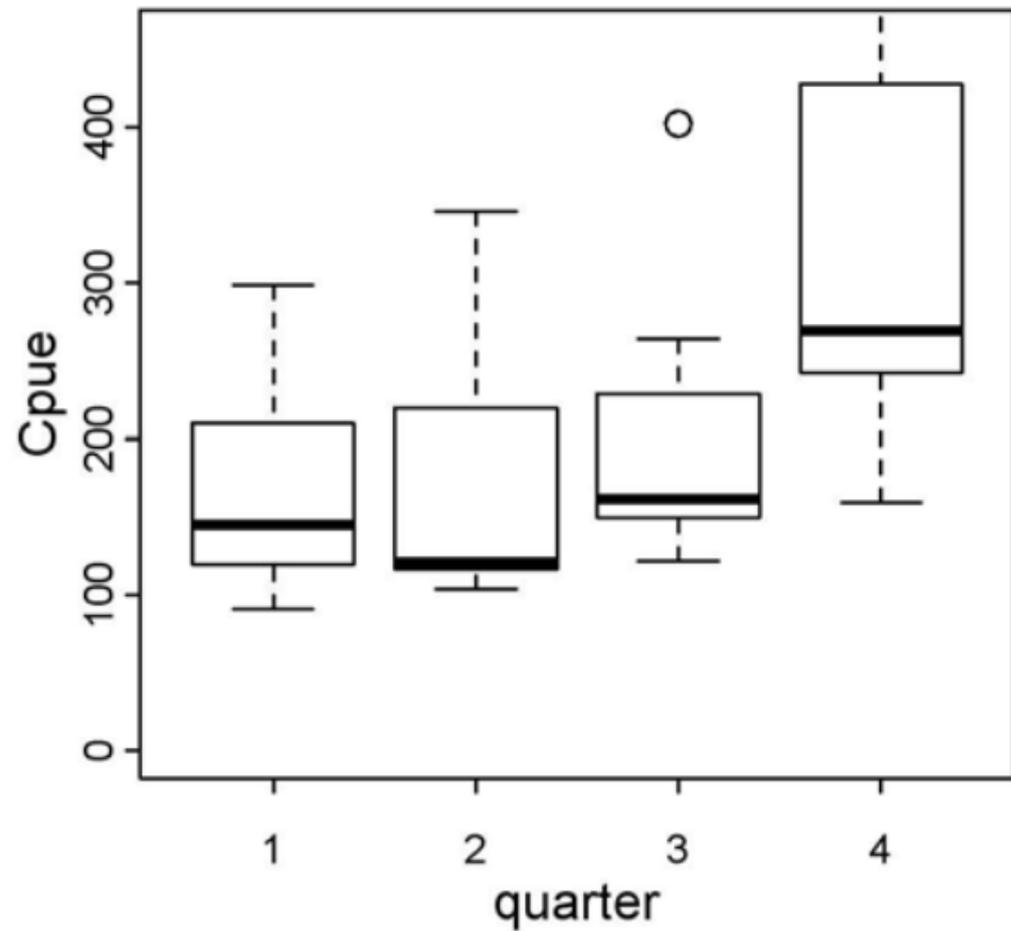
quarter 1**quarter 2****quarter 3****quarter 4****SSB (t)**

sub-unit FU04EW



sub-unit FU04FR



FU04EW**FU04FR**