

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

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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.

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Introduction

The European hake (*Merluccius merluccius*) is a demersal species that is widely distributed throughout the Northeast Atlantic, from Norway to Mauritania (Casey and Pereiro, 1995). It has supported valuable commercial fisheries, especially in Spain, France, and the UK. Since the 1970s, ICES has defined northern and southern hake stocks separated by the Cap Breton Canyon, which is supposed to act as a geographic barrier limiting exchanges between them, although there is no genetic proof that the two are distinct populations (Roldan *et al.*, 1998; Castillo *et al.*, 2004; Cimmaruta *et al.*, 2005). The northern stock extends from the southern Bay of Biscay to Norway (ICES Division IIIa, Subareas IV, VI, VII, and Divisions VIIIa, b, and d). Spain takes the largest part of the landings (59% of the total in 2007), followed by France (27%) and the UK (7%; ICES, 2008). Northern hake is targeted by several gear types in mixed fisheries (trawls, gillnet, and longline) throughout its distribution (CEC, 2001b). Annual landings declined during the 1960s from ~100 000 t to ~60 000 t, then remained relatively static until the 1990s, when they declined further to ~40 000 t, at which level they have remained since (Casey and Pereiro, 1995). A high fishing mortality and a succession of poor recruitments at the beginning of the millennium (CEC, 2001b) prompted management to introduce new technical measures and to implement a recovery plan (CEC, 2001a, 2002, 2004). Currently, there are signs that the stock may

be responding to these actions, and some of the explicit management objectives stated in the recovery plan have been achieved (ICES, 2008).

Despite many studies on hake, some of its biological characteristics, especially growth and migration, are poorly understood. Based on age determination using otoliths, hake were assumed to be slow-growing (Martin, 1991; ICES, 1993; Lucio *et al.*, 2000), but 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, 2006). These studies on adult hake growth and analysis of the daily growth increments in juvenile otoliths (Kacher and Amara, 2005) reveal that the growth rate is probably much faster than thought previously. Migration has been studied mainly through catch per unit effort (cpue) analysis (Belloc, 1935; Hickling, 1935; Casey and Pereiro, 1995; Poulard, 2001). Mature hake aggregate during their spawning season (Casey and Pereiro, 1995; Poulard, 2001) along the slope of the continental shelf from Portugal to Scotland (Alvarez *et al.*, 2004), then seem to disperse the rest of the year. Juveniles, on the other hand, concentrate in 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.*, 2001, 2004; Kacher and Amara, 2005). Spawning and nursery areas are far apart, and migration between them has not been documented, nor has any exchange of hake between the Celtic Sea and the Bay of Biscay.

The biological uncertainties listed above affect both stock assessment and prediction. Hake stock assessment is conducted annually using extended survivors analysis (XSA; Shepherd, 1999), which has proven useful in detecting trends and estimating stock abundance. However, the model requires input data based on age, whereas the data are collected based on length. Age-length keys are therefore constructed annually, at great cost despite carrying with them the uncertainty in implied age. XSA also assumes when fitting abundance indices that population and fishing activity are spatially uniformly distributed, although this assumption is likely to be violated for hake and may lead to unreliable assessment (Pelletier and Parma, 1994; Horbowy, 2005; Kraak et al., 2009).

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

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

Here, we develop a length-structured spatially explicit population model for the northern stock of European hake, aiming to improve biological knowledge of the stock by estimating unknown parameters, especially growth and migration. Our model is a state-space one (Figure 1): a spatially explicit and deterministic state model describes the population dynamics and fishing activity, and an observation model describes the uncertainties around the observation processes.

Methods

Data

Available data are aggregated at the level of ICES fishery units (ICES, 1991). Fishery units are characterized by fishing gear, fishing zone, and target species. Fishery units 2 (longline in shallow water in Subarea VII) and 6 (beam trawling in shallow water in Subarea VII) were not incorporated in the analysis because relatively few hake are caught there. Fishery unit 16 (all gears in Subareas IIIa, IV, V, and VI) was not considered because fishing activity takes place in a zone not studied in the model. Fishery unit 15 (miscellaneous) was also removed because of a lack of data. The remaining ten fishery units considered are subdivided into 18 national subunits (Table 1).

Estimates of the total landings by subunit and quarter are provided by national declarations of landings (Table 1). Sampling programmes at auctions provide length compositions of the landings per subunit on variable time-scales (either quarter or year; Table 1).

A proportion-at-length of discards is taken from the data for fishery unit 9, which generates most of the discards (ICES, 2008). This proportion was estimated from on-board observations (Système d'Informations Halieutiques: <http://www.ifremer.fr/sih>).

Three survey indices are available, 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. It was carried out twice annually in May and November from 1997 (and also in August 1997), but the index was considered to be unreliable for 2002. From 1997, the FR-EVHOES survey has been conducted in autumn, covering both the Bay of Biscay and the Celtic Sea using a random stratified sampling design and a GOV 36/47 trawl. The UK-WCGFS started in 1988 in the Celtic Sea and was terminated in 2004. As it was conducted annually in March, no hake aged 0 were caught.

Data from another 120 hake that were tagged and recaptured (de Pontual et al., 2003, 2006) are also used to fit the model; only fish spending at least 3 months at liberty after tagging and release (i.e. at least the time-step of the model) were selected. A maturity-at-length relationship (Piñeiro and Sainza, 2003) was used to compute $p_{\text{mat}}(c)$, the proportion of hake mature in length class c . Piñeiro and Sainza (2003) also provide a length-weight relationship with compute w_c , the weight of an individual hake in length class c . Natural mortality (M) is assumed to be known and constant at 0.2 year^{-1} (ICES, 2008).

State model: population dynamics and fishing activity

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

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

where $N(t, z, c)$ is the 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 time-step t , and L the number of length classes;

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

where $R(t, z, c)$ is the recruitment in zone z at length class c at time t ;

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

where $p_{\text{mat}}(c)$ is the proportion of mature fish in length class c , $m_{\text{imm}}(t, i, z)$ and $m_{\text{mat}}(t, i, z)$ the proportion of immature and mature hake, respectively, migrating from zone i to zone z during time-step t , and Z the number of zones;

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

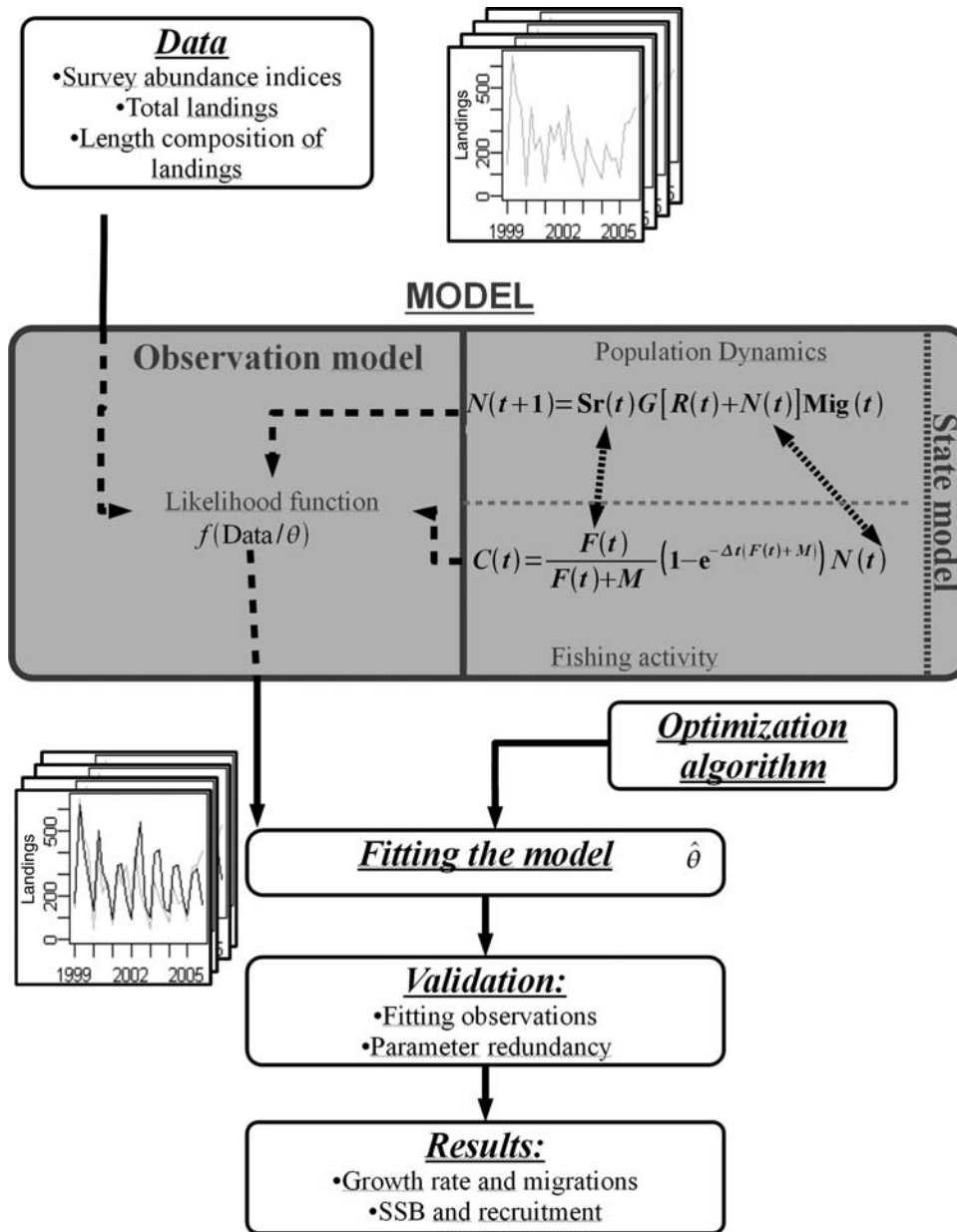


Figure 1. The modelling process used in the study.

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

The three processes, growth [Equation (1)], recruitment [Equation (2)], and migration [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, consistent with a preliminary sensitivity analysis (Drouineau *et al.*, 2008). For reasons of computation time, length classes were set at 2 cm intervals (from 3 to 109 cm, lower bound), rather than the 1 cm recommended by Drouineau *et al.* (2008). Space was divided into four 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.

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:

$$E(\Delta l|l) = (L_\infty - l)(1 - e^{-K\Delta t}),$$

$$V(\Delta l|l) = CE(\Delta l|l).$$

(5)

We assume that the hake in a length class are all of equal length (equal to the midpoint length of the class), so the probability $g_{i,j}$ of

Table 1. A list of the different subunits (FR, France; SP, Spain; EW, England and Wales, UK), and available length compositions of catches (Q, quarterly; Y, yearly).

Fishery unit	Description	Subarea	Subunit	1999	2000	2001	2002	2003	2004	2005
FU01	Longline in medium to deep water	VII	FU01EW	-	-	-	-	-	-	-
FU01SP			Q	Y	Q	Q	Q	Q	Q	Q
FU03	Gillnets	VII	FU03EW	Q	Q	Q	Q	Q	Q	Q
			FU03FR	-	-	-	-	-	-	-
FU04	Non- <i>Nephrops</i> trawling in medium-depth to deep water	VII	FU03SP	Q	Y	Q	Q	Q	Q	Q
			FU04EW	-	-	-	-	-	Y	Q
			FU04FR	-	-	-	-	-	-	-
FU05	Non- <i>Nephrops</i> trawling in shallow water	VII	FU04SP	Q	Y	Q	Q	Q	Q	Q
			FU05EW	Q	Q	Q	Q	Q	Q	Q
			FU05FR	Y	Y	Y	Q	Q	Q	Y
FU08	<i>Nephrops</i> trawling in medium-depth to deep water	VII	FU08FR	-	-	-	-	-	-	-
FU09	<i>Nephrops</i> trawling in shallow to medium-depth water	VIII	FU09FR	Y	Y	-	Q	Q	Q	Q
FU10	Trawling in shallow to medium-depth water	VIII	FU10FR	Y	Y	-	Q	Q	Q	Q
FU12	Longline in medium-depth to deep water	VIII	FU12FR	-	Y	-	Q	Q	Q	Q
			FU12SP	Q	Y	Q	Q	Q	Q	Q
FU13	Gillnets in shallow to medium-depth water	VIII	FU13FR	Y	Y	-	Q	Q	Q	Q
			FU13SP	Q	Y	Q	Q	Q	Q	Q
FU14	Trawling in medium-depth to deep water	VIII	FU14SP	Q	Y	Q	Q	Q	Q	

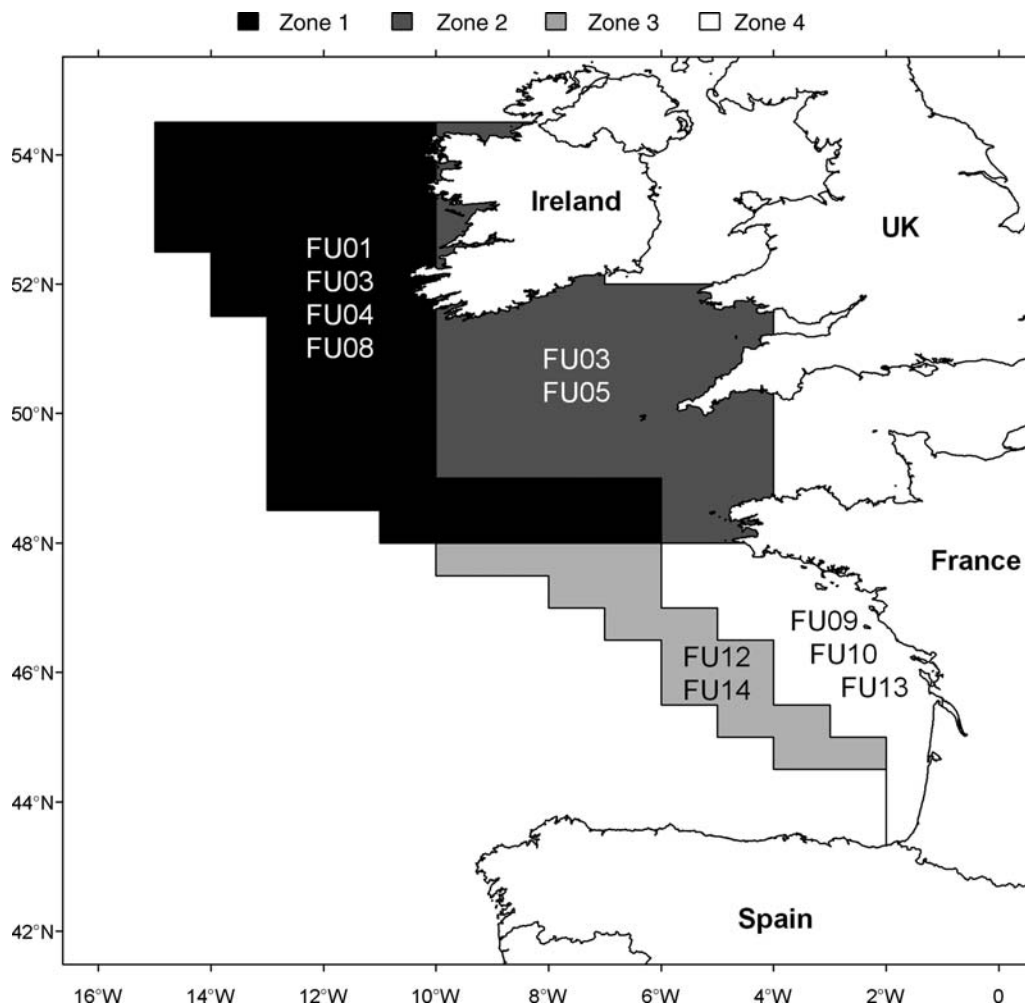


Figure 2. Maps of the four model zones and the respective fishing areas of each fishery unit.

transition from class i to class j is given by

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

where $E(\Delta l/l) = \alpha_{\Delta l/l} C$, $V(\Delta l/l) = \alpha_{\Delta l/l} C^2$, Δl is the width of the length classes (2 cm), and m_i is the midpoint size of the departure class i .

Following de Pontual *et al.* (2006), we assume that L_∞ is known (110 cm). Growth rate K and constant C [Equation (5)] need to be estimated, but spatial or seasonal heterogeneities in growth are not taken into account. A complete description of the growth model is given by Drouineau *et al.* (2008).

Recruitment

Hake recruit to two main shelf-nursery areas, one located in the Bay of Biscay (Zone 4; Figure 2), the other in the Celtic Sea (Zone 2; Figure 2; Casey and Pereiro, 1995; Kacher and Amara, 2005). Recruitment in the Bay of Biscay starts during the second quarter of the year and in the Celtic Sea during the third quarter. No clear relationship has been established between the two nursery areas, so we assume recruitment in the two areas to be independent. Length-at-recruitment is assumed to follow a normal distribution of mean L_0 and standard deviation σ_0 . Therefore, if p_c denotes the proportion of recruits in length class c , recruitment for each quarter is

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

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

where $R_{BB}(y)$ is the recruitment in the Bay of Biscay (Zone 4) in year y (corresponding to time-step t), and $R_{CS}(y)$ is the recruitment in the Celtic Sea (Zone 2) in year y .

Migration

As already stated, hake migration patterns are poorly known. Migration is assumed to be related to spawning, and juvenile and adult hake are clearly spatially segregated at certain times of the year. Therefore, we modelled the migration of mature and immature hake differently. Migrations are supposed to be seasonal and can be described by a proportion of mature fish 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 information on the life cycle in the literature (Table 2), leaving 23 coefficients unknown. However, given that $\sum_{i=1}^z mi_{imm}(t, z, i) = 1$ and $\sum_{i=1}^z mi_{mat}(t, z, i) = 1$, only 12 parameters need to be estimated.

Survival

Survival is the result of both natural and fishing mortality. It is computed from

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

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

Estimating fishing mortality and catch

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

Assuming a constant selection pattern between the subunits of a fishery unit is consistent with the assumption made by the ICES Working Group on hake, monk, and megrim (WGHMM; ICES, 2008), which often uses the length composition of the landings of a country to estimate the length composition of another

Table 2. Proportion of fish moving from a zone (in the rows) to another (in the columns) for each quarter.

Quarter	Immature fish					Reason	Mature fish					Reason
	1	2	3	4			1	2	3	4		
1	1	1	0	0	0	Immature fish are fixed	1	1	0	0	0	Western aggregation
	2	0	1	0	0	Immature fish are fixed	2	x	x	0	0	Western aggregation
	3	0	0	1	0	Immature fish are fixed	3	0	0	1	0	Reproduction in the Bay of Biscay
	4	0	0	0	1	Immature fish are fixed	4	0	0	1	0	Reproduction in the Bay of Biscay
2	1	1	0	0	0	Immature fish are fixed	1	1	0	0	0	Reproduction in the Celtic Sea
	2	0	1	0	0	Immature fish are fixed	2	1	0	0	0	Reproduction in the Celtic Sea
	3	0	0	1	0	Immature fish are fixed	3	x	0	x	x	Mature fish migrate to the shelf or to the Celtic Sea
	4	0	0	x	x	Recruitment drift	4	0	0	0	1	Mature fish migrate to the shelf
3	1	1	0	0	0	Immature fish are fixed	1	x	x	0	0	No constraint
	2	x	x	0	0	Recruitment drift	2	x	x	0	0	No constraint
	3	0	0	1	0	Immature fish are fixed	3	0	0	x	x	No constraint
	4	0	0	0	1	Immature fish are fixed	4	0	0	x	x	No constraint
4	1	1	0	0	0	Immature fish are fixed	1	x	x	0	0	No constraint
	2	0	1	0	0	Immature fish are fixed	2	x	x	0	0	No constraint
	3	0	0	1	0	Immature fish are fixed	3	0	0	1	0	Aggregation on the shelf slope
	4	0	0	0	1	Immature fish are fixed	4	0	0	x	x	Aggregation on the shelf slope

x, to be estimated.

country within the same fishery unit. Moreover, the data do not show any major inconsistencies between the length compositions of the landings of subunits within a fishery unit.

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

$$F_{su}(t, z, c) = q_{su}s_{fu}(c)E_{su}(t) \frac{\text{Surface}(z)}{S_{fu}}, \tag{10}$$

if $z \in \text{metierzone}_{fu}$.

The ratio $\text{Surface}(z)/S_{fu}$ distributes the total fishing effort among the different model zones of the métier zone. The selection pattern is modelled either by a sigmoid, e.g. Froysa *et al.* (2002), to mimic an increasing selection pattern (fishery units using a 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 subunits:

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

Catches are computed using the traditional Baranov equation and reallocated to each subunit. Discards are not taken into account except for the métier corresponding to Fishery unit 9, i.e. catches and landings are assumed to be equivalent for all subunits except fishery unit 9, where a fraction is discarded.

Total landings $Y_{su}(t)$ by weight by subunit and time-step are then computed:

$$Y_{su}(t) = \sum_{z \in \text{metierzone}} \sum_{c=1}^C w_c(1 - \text{dis}_{su}(c))C_{su}(t, z, c), \tag{12}$$

where $C_{su}(t, z, c)$ is the number of fish of length class c caught by subunit su in zone z during time-step t , and $\text{dis}_{su}(c)$ the proportion of fish of length class c discarded by subunit su . For all subunits, $\text{dis}_{su}(c) = 0$, except for fishery unit 9, for which a discard ogive was estimated from on-board observations.

The length composition of the landings is also computed over a period $f_{su}(\text{period}, c)$:

$$f_{su}(\text{period}, c) = \frac{\sum_{t \in \text{period}} \sum_{z \in \text{metierzone}} C_{su}(t, z, c)}{\sum_{t \in \text{period}} \sum_{z \in \text{metierzone}} \sum_{c=1}^C C_{su}(t, z, c)}. \tag{13}$$

Survey abundance indices

Abundance indices per survey and zone are summarized in Table 3. The number of individuals $C_{\text{surv}}(t, z, c)$ of class c

caught by a survey surv during time-step t in zone z is given by the product of the catchability q_{surv} , the sampling effort in terms of time spent fishing, $E_{\text{surv}}(t, z)$, the number of hake in the zone $N(t + \tau_3, z, c)$, and the selection pattern $s_{\text{surv}}(c)$. A ratio of surface is also used to make indices comparable between zones (SurfaceMin refers to the surface of the smallest zone sampled by the survey; this choice is arbitrary):

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

We assume that the selection pattern of FR-EVHOE and UK-WCGFS is constant, equal to 1. FR-RESSGASCS used a commercial trawl, so we modelled the selection pattern using a sigmoid function. We then computed total abundance estimates $IA_{\text{surv}}(t, z)$ and length compositions $f_{\text{surv}}(t, z, c)$:

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

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

Initial numbers by class and zone

Theoretically, initial numbers by class and zone ought to be estimated, but that would imply estimating 216 parameters. Instead, we assumed that the population at the beginning of the simulation period was at equilibrium with the fishing mortality and the recruitment for the first year, and ran a pre-simulation over the 10 years before the simulation in which (i) the initial numbers were zero, and (ii) the population was subject to fishing mortality and recruitment of the first year during the 10 years of pre-simulation. The final numbers in each class and zone after the pre-simulation period were used as initial numbers for the simulation.

Observation model and likelihood function

The likelihood function [Equation (17)] is equal to the sum of four components: (i) total landings in weight per subunit and time-step [Equation (18), $\log L Y_{\text{obs}_{su}}(\theta)$], (ii) total survey abundance estimates [Equation (19), $\log L IA_{\text{surv}}(\theta)$], (iii) length composition of the landings per subunit and of the survey abundance estimates [Equation (20), $\log L P_s(\theta)$], and (iv) tagging

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

Survey	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	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	X			X	X			
UK-WCGFS quarter 4																								X				X	

data [Equation (22), $\log L_{\text{tag}}(\theta)$]:

$$\log L(\theta) = \sum_{\text{su}} \log L Y_{\text{obs, su}}(\theta) + \sum_{\text{surv}} \log L IA_{\text{surv}}(\theta) + \sum_s \log L P_s(\theta) + \sum_{\text{tag}} \log L_{\text{tag}}(\theta). \quad (17)$$

Contributions of total landings $Y_{\text{su}}(t)$ and total survey abundance estimates

The total catches per survey per zone and the total landings of the subunits are assumed to follow gamma distributions (Froysa et al., 2002), with a constant coefficient of variation (CV). The loglikelihood ($\log L$) of observed total landings for a subunit is therefore

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

and the loglikelihood of total survey abundance estimates is

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

where λ is a constant proportional to the inverse of the CV; we fix $\lambda = 100$, which corresponds to a CV of 10%. This value is relatively high, but we chose to give it small weight in the absence of more information.

Contributions of the length composition of landings and survey abundance estimates

We used a robust likelihood such as that proposed by Fournier et al. (1990) to account for the length composition of the landings. The loglikelihood of a sample s of landings from subunit su collected during a period is then

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

where

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

where n_s is the number of hake sampled. To limit the influence of large samples, n_s was limited to 500, and the same assumption was made for the length composition of survey abundance estimates.

Contribution of tagging data

Initial length l_0 , time at liberty after release ΔT , and the growth increments ΔL of tagged hake were available. In terms of length-at-release, we assumed that all released hake were fully recruited to commercial gear (mainly fishery unit 9), because the size at release was always sufficiently large (27.5 cm) for that assumption to be made. The increments were first extrapolated to obtain an increment ΔL_q corresponding to a quarter period at

liberty ΔT_q :

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

This transformation was required because the constant C [Equation (5)] of the growth model is only valid for quarterly increments. To understand this issue, consider that a fish of size l_0 spends two quarters at 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. Hence, $V(\Delta L) \neq CE(\Delta L|l)$.

The contribution of a tagged fish (tag) to the loglikelihood is therefore

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

where $\mu_{\text{tag}} = (L_\infty - l_{0, \text{tag}})(1 - e^{-K\Delta t})$ and $v = \mu_{\text{tag}}/C$.

Parameter estimation

In all, 73 parameters were estimated (Table 4) by maximum likelihood. The loglikelihood maximization was carried out using an evolutionary strategy algorithm (Schwefel, 1995) and a quasi-Newton algorithm provided in the autodif library (<http://www.otter-rsch.com/>). The evolutionary strategy algorithm was used as a first step in providing a starting point for the quasi-Newton algorithm.

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

Results

Growth

The estimated growth rate ($K = 0.24 \pm 0.01$ cm; Figure 3; best correlation 0.38 with FU04EW catchability) and the resulting growth curve were close to the curve estimated from tagging data (de Pontual et al., 2003, 2006) and higher than those

Table 4. Unknown parameters of the model.

Parameter origin	Parameters	Notation	Number	
Population	Annual recruitment	$R_{\text{BB}}(y)$	$2(\text{years} + 2) = 16$	
		$R_{\text{CS}}(y)$		
		L_0		
		σ_0		
		Growth		K, C
Migration		m_{imad}	12	
		m_{imm}	12	
Fishing activity	Catchability per subunit	q_{su}	18	
		Selectivity pattern	s_{fu}	20
		Catchability	q_{surv}	3
Survey	Selectivity pattern (FR-RESSGASCS)	s_{surv}	2	
Total			73	

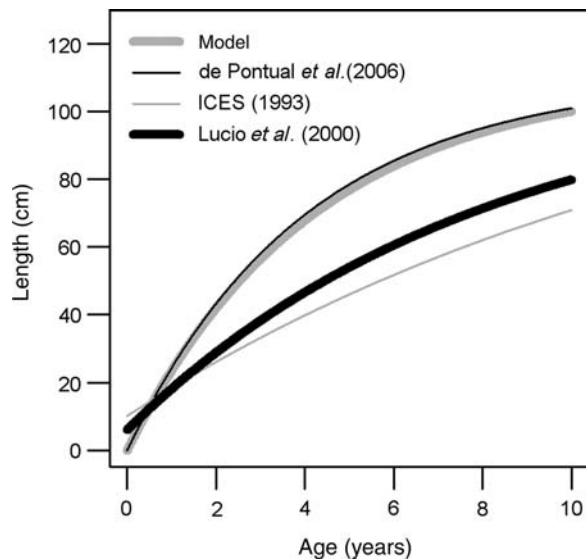


Figure 3. Estimated growth curves from tagging data (black line), otolith reading (black bold line and grey line), and the model (grey bold line).

estimated by otolith readings. This lends further credence to the notion that hake grow faster than previously thought.

The positions of the peaks in length compositions of landings (Figure 4) fit the model well, supporting the idea that there is an appropriate growth model. Subunits of fishery unit 13 (gillnets on the shelf of the Bay of Biscay) fitted badly, but data from that fishery unit are very doubtful (only a small proportion of the log-books were available) and fishers have a very specific strategy there (targeting large hake on the shelf). It is important to realize that the length compositions of the landings are the most reliable data and fit the model well, supporting our estimate of growth rate.

The length compositions of survey catches (Figure 5) were not as well represented by the model, but peaks in length compositions are generally well estimated. It is not surprising that those data are not as well reproduced by the model because commercial catch samples are larger and more numerous.

Distribution of spawning-stock biomass and migrations

Mature fish are mainly concentrated over the margin of the shelf of both the Celtic Sea and the Bay of Biscay (Figure 6). The model failed to show a seasonal pattern, whereas the literature describes seasonal heterogeneities in the distribution of mature hake in the Celtic Sea (Hickling, 1935; Poulard and Léauté, 2002).

Few estimates of migration rate were not close or equal to zero (Figure 6): hake leave the shelf and migrate to its edge when maturing, where they remain until they die. More surprisingly, no major migration from the Bay of Biscay to the Celtic Sea was estimated by the model, although that is sometimes mentioned in the literature (Casey and 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 the catchabilities of subunits FU05EW and FU05FR (correlation 0.60).

Some seasonal offsets are observed between simulated and observed peaks of landings for UK subunit 4 (Figure 7, left) and

French subunit 4 (Figure 7, right), which can be explained partly by the seasonal differences observed in the peaks of cpue between subunits of the same fishery units (Figure 8). Those types of offset are only observed for those fishery units.

Discussion

Despite the abundance of scientific literature on European hake, much of its biology remains poorly understood. The model we have proposed improves knowledge of some of the biological processes by estimating growth rates and migration rates.

The estimated growth rate is close to the estimate derived from tagging data, though much higher than estimates from otolith reading. Moreover, peaks in the length frequencies from both the commercial fishery (except fishery unit 13) and scientific surveys are well captured by the model. This result confirms the hypothesis of the species being fast-growing (de Pontual et al., 2003, 2006; Kacher and Amara, 2005). Following de Pontual et al. (2003, 2006), we assumed that L_{∞} was known and fixed, at 110 cm, to avoid problems of correlation between K and L_{∞} and to compare our results directly with estimates from the tagging study; however, a different value of L_{∞} would likely give a different estimate of the growth rate. Shackell et al. (1997) proposed a method to obtain reliable estimates of growth parameters that might be appropriate in further developing our model. Natural mortality was also fixed at an arbitrary level, consistent with ICES assumptions, and that too may have influenced the estimation of growth rate. For fishery unit 13, the model is unable to fit the length composition of the catches, likely for three main reasons: (i) poor data for that fishery unit, (ii) fishers specifically target large hake in an area close to the coast within the nursery area, a spatial scale not taken into account in our model, and (iii) inconsistencies in the length compositions of the catches in fishery units 9 and 13 and in the assumed selectivity models (fishery unit 9 does not yield any large hake, but fishes the same zone as fishery unit 13 and has a sigmoid selectivity function). Finally, we chose to fix selectivity at a constant level for two scientific surveys to limit the number of unknown parameters. Although survey indices relate to a specific geographic zone and a quarterly period makes this assumption more credible, this assumption may influence the estimated growth rates. A sensitivity analysis to this hypothesis needs to be carried out in a future version of the model.

Analysing the length composition of scientific surveys, the notable drop between the first two peaks is not well captured by the model (Figure 5). Although we are not satisfied by the estimate of growth variability (which seems to be overestimated), the model succeeds in differentiating the two groups, which is a positive aspect when trying to estimate a growth rate. We tried to fit the model only to survey data, but doing that does not notably change the length frequency fits, confirming that our growth model does not describe growth variability well. Other relationships between mean growth increments and the variance or other types of model (age-length-structured models) should perhaps be explored in future.

The spatial distribution of the spawning-stock biomass (SSB) estimated by the model is consistent with other observations, but the model cannot reproduce the seasonal aggregations of mature hake on the shelf of the Celtic Sea, as described by Poulard (2001). Seasonal lags between simulated and observed peaks in the landings of some fishery units (Figure 7) can be explained either by poor estimation of those rates of migration,

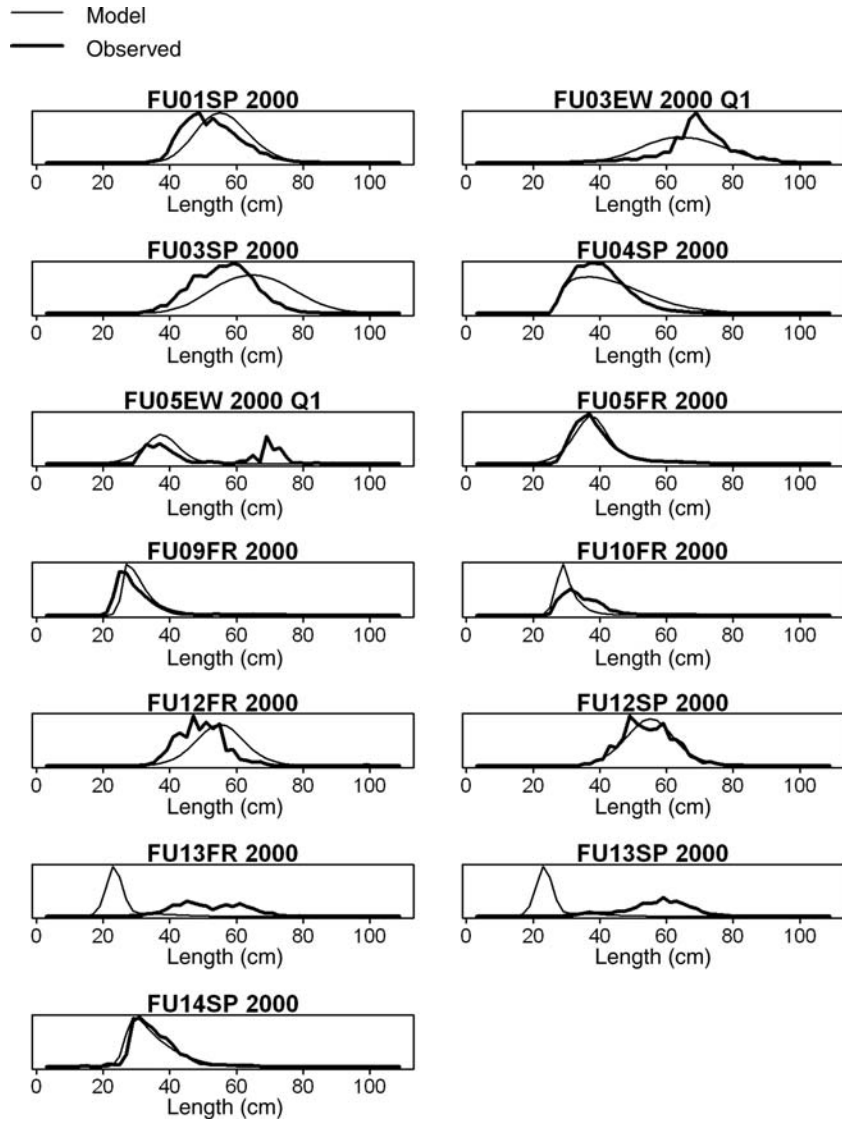


Figure 4. Observed (bold solid line) and estimated (solid line) length composition of the landings for the different subunits in 2000. Length compositions for the other years are not presented here because they are similar to those for 2000. There is a good fit for all fishery units, except fishery unit 13, which does not fit at all.

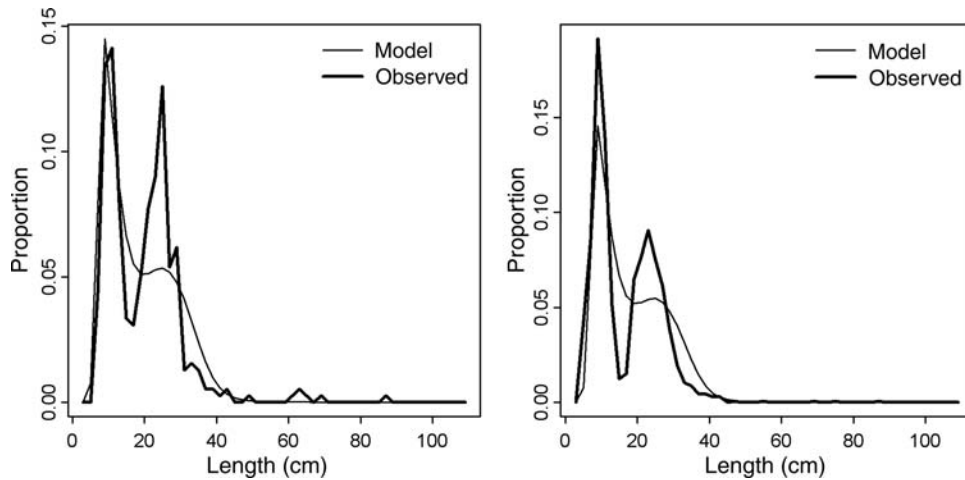


Figure 5. Observed (bold solid line) and estimated (solid line) length compositions of survey catches: from UK-WCGFS 2003 in zone 4 (left) and from FR-EVHOE 2005 in zone 2 (right).

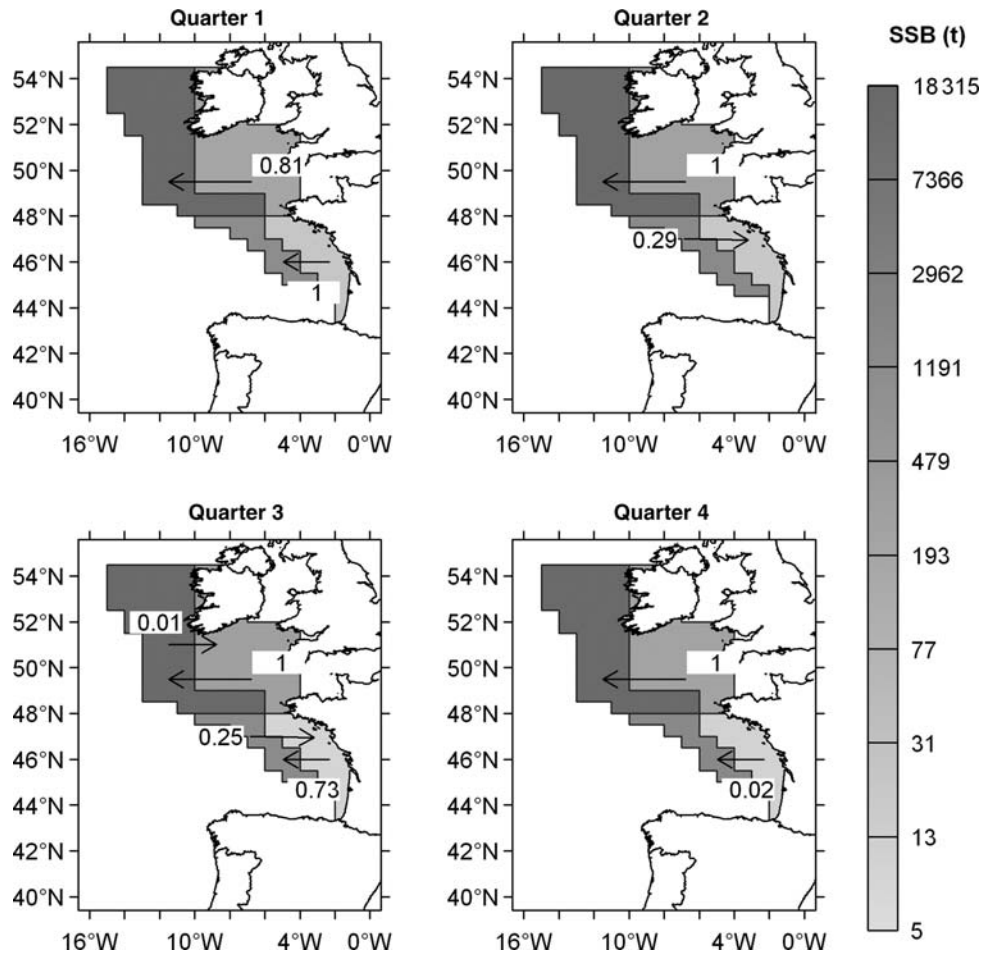


Figure 6. Distribution of SSB (t per area) in 2005 and the estimated migration rates of mature hake. The SSB estimates should be considered as relative and indicating spatial distribution, rather than absolute.

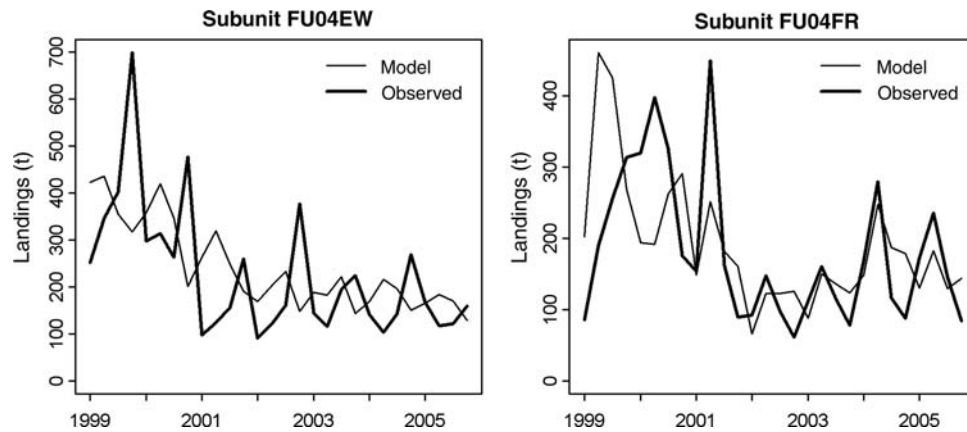


Figure 7. Seasonal distributions of the landings for UK (left) and French (right) subunit 4.

by effort data being poor, or by some catchability–season interactions not being well-described in the model. In that respect, the use of VMS data would probably allow the spatial fishing effort allocation to be improved. 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 the two areas because in the literature only

large mature males are assumed to make this migration. The migration of large males is likely to be insignificant compared with that of large numbers of smaller mature males, so it is unsurprising that the model has difficulty in capturing such a pattern.

The model has demonstrated a heterogeneity in hake spatial distribution, underscoring the importance of spatial management measures such as marine protected areas. Parameter estimates

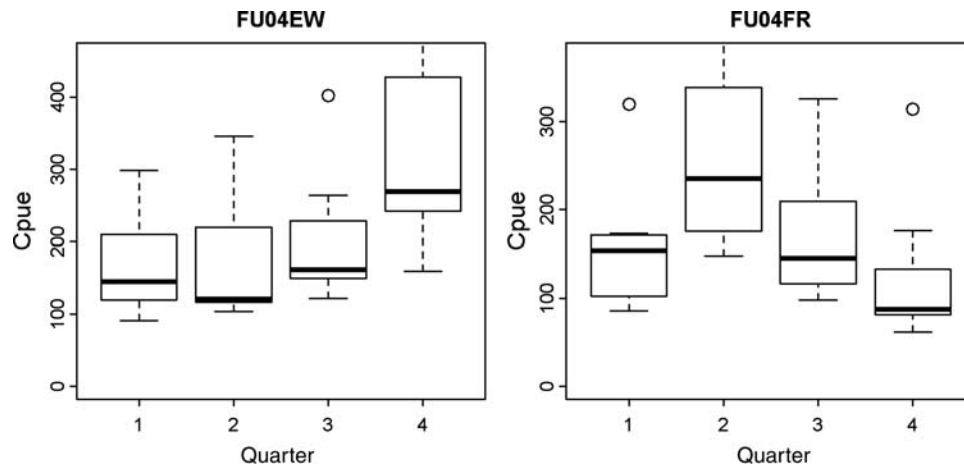


Figure 8. Seasonal distributions of observed cpue for UK (left) and French (right) subunit 4, open circles representing outliers.

may, for example, be used to improve the work of *Drouineau et al.* (2006), which attempted to assess the influence of some management scenarios on the mixed hake/*Nephrops* fishery in the Bay of Biscay. Moreover, the variability in the spatial distribution of SSB indicated in our fit contradicts some of the assumptions of XSA. It might be interesting to assess the impact of a non-uniform spatial distribution of SSB on XSA estimates.

Tagging data were only used to improve the estimation of growth rate. However, they are still limited (in number and space), so have limited impact on the outcome (the results are similar when the model is fitted without the tagging data). A large-scale tagging campaign might provide information on both migration and growth, and if so, a tag-attrition model (*Kleiber et al.*, 1987) describing the tagged subpopulation could take those data into account. Alternatively, tagging data may be used as a first step towards estimating the growth transition matrix, and then fitting it to the rest of the model (*DeLong et al.*, 2001). A pluri-seasonal survey with a greater spatial distribution would also provide valuable information on migration and the spatio-temporal distribution of the SSB.

Two assumptions may have a notable impact on the results. First, we assumed constant catchability and selection pattern during the studied period, resulting in variations in fishing mortality per national subunit over time only being captured by variations in fishing effort. To relax this assumption, departures from the observed effort data have been considered through a yearly random walk of subunit catchabilities, but the resulting model is overparametrized, and the algorithm does not converge to a unique solution. However, this assumption may have a minor effect on the estimation of growth rate, for which we believe that the length composition of samples and hence the selectivity of the different fishery units and scientific survey play the main role. Moreover, catchability variations are more likely at an annual than a seasonal scale, so the assumption likely has a greater impact on the estimation of the annual trend in SSB than on the estimation of its spatial distribution and seasonal migration within a year. Second, the assumption of equilibrium for the initial year is also strong, but was required to make the model identifiable. Sensitivity analyses should be made in developing our model further to quantify the impact of such an assumption, though the impact of the assumption will decrease in future as the time-series lengthens. Again we believe that the assumption

has an important impact on the year-on-year evolution of SSB, but probably less of an impact on the seasonal distribution of SSB and hence the estimated migration rates.

We paid particular attention to the construction of the likelihood function, trying to construct a function that described the observation processes well. However, some approximations were sometimes required to make the model robust, especially for length compositions of the samples. Notwithstanding, the approximation we used has been used in many models (*Fournier et al.*, 1998; *Maunder and Watters*, 2003) and has provided reliable results. Moreover, we tried where possible to avoid using a subjective weighting of datasets, so datasets are weighted through their variance by likelihood construction. In terms of length compositions, the variance (and consequently the likelihood weight) is a direct function of the number of hake sampled. For tagging data, the variance (and hence the likelihood weighting) is provided directly by our assumption on growth increment distribution [Equation (5)]. For total landings and total survey abundance, it was impossible to derive an objective measure of the variance, so in the absence of evidence, we selected a CV of 10%, which probably downweights the influence of those data.

To conclude, our results seem to us to be encouraging and to provide quantitative estimates of biological parameters that are consistent with existing qualitative knowledge. Some uncertainties remain, however, so the results should still be considered as preliminary, at least until further sensitivity tests have been completed. Here, we chose to focus on the estimation of some biological parameters (growth and migration), but to some extent, the model may also be able to provide an assessment of stock size because it also estimates catchability and recruitment. Uncertainties on data and biological processes would then be more effectively described than currently (*ICES*, 2008), and expensive and unreliable age-length data would be less of a requisite. Moreover, the model and the results may be an appropriate basis from which to develop length-structured models for other species for which age-length conversions are uncertain (e.g. anglerfish *Lophius* spp. and Norway lobster *Nephrops norvegicus*).

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