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Update of the English Channel cuttlefish stock assessment with a Bayesian two-stage biomass model

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ABSTRACT

A two-stage biomass model is developed in the Bayesian framework that allows us to assimilate various sources of information. A method that makes use of ancillary length frequency data is developed to provide an informative prior distribution for the intrinsic biomass growth rate parameter and its annual variability. The new Bayesian model provides substantial improvement to the existing stock assessment method used by ICES. Considering a time-varying *g* parameter improves model fit and improves the ecological realisms of the model according to the sensitivity of the cuttlefish population dynamics to environmental fluctuations. We present results of the English Channel cuttlefish stock assessment updated with the new Bayesian model. The model also provides predictions of the unexploited biomass in winter based on survey data, and help managing the stock in case of strong depletion.

Keywords: stock assessment, short-lived species, data-limited, cuttlefish, Sepia officinalis, English Channel, two-stage biomass model, Bayesian

INTRODUCTION

Most of cephalopods fisheries are only occasionally assessed, despite trials of various models (Pierce and Guerra 1994). There is no generalized method to conduct stock assessment for short-lived species, which makes it difficult to compare outputs of the assessments or to infer information from one stock to another. There is a need for a

precautionary approach when no routine stock assessment is conducted (Rodhouse *et al.* 2014).

The cuttlefish stock in the English Channel has already been assessed occasionally with a Thomson and Bell model based on monthly catch-at-age data (Royer *et al.* 2006), but the method was too much data-demanding for a routine stock assessment. In order to achieve routine stock assessment, a two-stage biomass model (Roel and Butterworth 2000) was adapted to this stock (Gras *et al.* 2014). A simplification of cuttlefish life-cycle was used, assuming two different stages among the exploited population: recruitment and full exploitation. The model was fitted to time-series of catches and abundance indices by a least-square error method, and uncertainties were estimated by bootstrapping the estimates.

However, the model suffers several caveats. First, it is fitted to data sources using a classical least-square procedure that might not be adapted to fully quantify uncertainties in estimates and predictions and that suffers from a lack of flexibility to change model assumption and/or to assimilate other sources of available information or data.

Second, the model is based on a very strong hypothesis of a fixed biomass growth parameter that embeds a natural mortality and a mean growth coefficient both considered constant in time and known without uncertainty. An annual natural mortality rate of 1.2 was set, and a mean growth coefficient of 2.2 was calculated based on historical data (Medhioub 1986). However, a sensitivity analysis showed a high sensitivity of model outputs to this biomass growth rate parameter. Gras *et al.* (2014) advocate for the use of more recent data to provide a more accurate estimate of the biomass growth rate parameter. Moreover, using a constant biomass growth rate might not be suitable for short-lived species strongly sensitive to environmental factors.

Third, the initial two-stage biomass model represents the biomass of group 1+ individuals only, and basic assumptions are made on the data to fit this hypothesis. The model assumes that the exploited population can be observed at two different stages: recruitment and full exploitation. Recruited biomass (B_1) is estimated with abundance indices from the Bottom Trawl survey (BTS) and the Channel Ground Fish Survey (CGFS). Spawning stock biomass (B_2) is estimated with Landings Per Unit Effort (LPUE) from French and UK bottom trawl fisheries. In this initial model, CGFS time-series is assumed to be based mainly on group 1+ individuals, but regarding the length frequencies, this assumption could be criticized. Indeed, this survey occurs in October, when cuttlefish migrates offshore. Part of the group 0 individuals is 3 months old at this period of the year, forming the lower part of the survey length frequencies. The same assumption is made for BTS data, which is more acceptable, as this survey happens around July, at hatching time. A monthly percentage is applied on French LPUE, based on commercial category information from sales data.

In this work, we elaborate on the two-stage biomass model adapted for cuttlefish, and we bring three substantive new contributions:

(i) First, the model is developed in a Bayesian framework (Gelman 2004), thus allowing for a comprehensive quantification of the different sources of uncertainty (Punt and Hilborn 1997, Parent and Rivot 2013) and for the use of informative prior on some key parameters (Hilborn and Liermann 1998).

(ii) Second, we develop a method to build an informative prior on the biomass growth rate that takes advantage of various sources of data. The method allows us to provide an informative prior for the average growth rate together with a credible range of variability among years.

(iii) Third, we improve the demographic realism of the model by explicitly considering that two separate age classes (0+ and 1+) can compose the exploited biomass.

We present results of the English Channel cuttlefish stock assessment updated with the new Bayesian two-stage biomass model. We also discuss the possible use of a model based only on survey data to predict the unexploited biomass in winter and help managing the stock.

MATERIALS AND METHODS

The model is written in a Bayesian state-space modelling framework (Gelman 2004) that integrates stochasticity in both the process equations for the population dynamics (process errors) and the observation equations (observation errors), hence the hierarchical framework of the modeling (Rivot *et al.* 2004, Buckland *et al.* 2007, Parent and Rivot 2013). We first describe the process equation for the biomass dynamic. Second, we describe the observations equations. Third, we provide details about the data processing and the method used to build an informative prior on the biomass growth rate parameter (denoted *g* in the following). Last, we detail our strategy to analyse the sensitivity of the results to the hypotheses made on the time-variations of critical parameters, to the age-structure and the data sources. All parameters used in the model are summarized in Table 4.

The two-stage biomass model



Figure 1: Simplified life cycle of the English Channel stock of cuttlefish.

The model is based on a simplification of cuttlefish life cycle: we consider an exclusive 2 years lifespan, with mass mortality occurring short after spawning in July. Each fishing season extends from 1^{st} July (one year-old individuals are recruited to the fishery) to 30^{th} June of the following year (one year later, remaining individuals are mature and have

spawned). Total catch of cuttlefish (C_y) is assumed to happen as a pulse in the middle of the fishing season (on 2nd January). We use subscript *y* to refer to the fishing season.

Spawning stock biomass $B_{2,y}$ of fishing season y is expressed as:

$$B_{2,y} = \left[B_{1,y}e^{g_y}(1-E_y)\right]e^{z_{1,y-0,5\times sigma_B2}}$$
(1)

where E_y is the exploitation rate, $B_{1,y}$ is the biomass at the beginning of the fishing season, g is the intrinsic biomass growth rate parameter and $\mathcal{E}_{1,y}$ the lognormal random noise term with variance $sigma_B2$.

The unexploited biomass estimated on 1^{st} January ($B_{1,jan,y}$) without catch removals is calculated as follows:

$$B_{1,jan,y} = B_{1,y}e^{\frac{3y}{2}}$$
(2)

Observation equations

Expected mean of the catches are calculated as the product of the biomass in the middle of the fishing season, $B_{1,y}e^{\frac{g_y}{2}}$ with the exploitation rate E_y . Catches are then considered observed with lognormal observation errors $\varepsilon_{2,y}$ with variance *sigma_C*.

$$C_{y} = E_{y}B_{1,y}e^{\frac{g_{y}}{2}}e^{\varepsilon_{2,y-0,s\times sigma_{c}}C}$$
(3)

BTS and CGFS survey index are considered as indirect observation of the biomass $B_{1,y}$ with catchabilities q_{bts} and q_{cgfs} and lognormal observation errors with unknown variance $sigma_AI_I$, drawn in a non-informative prior distribution (see Table 2):

$$\begin{cases} U_{y}^{bts} = q_{bts}B_{1,y}e^{s_{s,y-0,s\times sigma}AI} \\ U_{y}^{cgfs} = q_{cgfs}B_{1,y}e^{\frac{g_{y}}{4}}e^{s_{4,y-0,s\times sigma}AI} \end{cases}$$

$$(4)$$

where U_y^{bts} is the BTS survey index for fishing season y, U_y^{cgfs} the CGFS survey index for fishing season y, $\varepsilon_{3,y}$ and $\varepsilon_{4,y}$ the lognormal observation errors with variance *sigma_AI*.

French standardized LPUE (U_{v}^{fr}) is modelled as follows:

$$U_{y}^{fr} = \frac{1}{2}q_{fr} \left[B_{1,y} + B_{1,y} e^{g_{y}} \left(1 - E_{y} \right) \right] e^{z_{\xi,y-0,\xi \times sigma_{x}} AI}$$
(5)

where q_{fr} is the catchability of French trawlers and $\varepsilon_{5,y}$ the lognormal observation errors with variance *sigma_AI*. Setting the same variance for BTS, CGFS and French LPUE observation errors is a model hypothesis allowing to reduce the number of estimated parameters.

Both BTS abundance indices and UK catch data were obtained from the Center for Environment Fisheries and Aquaculture Science (CEFAS). French CGFS abundance indices, French catch and effort data, and length data were obtained from the French Research Institute for Exploitation of the Sea (IFREMER).

As BTS survey occurs around July, hatchlings are born very recently inshore, and should therefore represent a very small proportion in biomass. BTS abundance indices are therefore used to model both global biomass and 1+ biomass.

CGFS survey occurs each year on October. At this time of the year, part of the population of group 0 individuals is already 3 months old, meaning that the abundance indices timeseries can't be directly used to infer information on group 1+ individuals. The following procedure was used to derive a CGFS abundance index of group 1+ individuals. The package mixdist was used on CGFS length frequency data to calculate mean length and

percentage in number of individuals older than one year-old ($^{40}N_{1+}$). Mean length was converted into mean weight using Dunn (1999) length-weight relationship. Percentage in weight of 1+ individuals was calculated as follows:

$$\%w_{1+} = [\%N_{1+} * \overline{w}_{1+}] / [\overline{w}_{1+} * \%N_{1+} + \overline{w}_0 * (1 - \%N_{1+})]$$
(6)

where \overline{w}_0 and \overline{w}_{1+} are the mean weight of group 0 and group 1+ individuals. $\%w_{1+}$ was then applied to CGFS catch data to calculate abundance indices for 1+ individuals. On average, 1+ individuals represented 91.5% of CGFS catch in weight, with a CV of 0.056. As length data for CGFS survey are available from 2005 only, we used this value to calculate previous abundance indexes for 1+ individuals.

To calculate French LPUE, commercial data were used to know the percentage in weight of one year-old cuttlefish (animals above 300g) by year and month, and a Delta-GLM was applied with ICES statistical rectangle, vessel power, year and month as factors. Percentages were also applied to total catch data (from both French and UK vessels) to select individuals older than one year-old (1+).

As we didn't have information on the proportion of one year-old cuttlefish among English catch, we couldn't calculate UK LPUE time-series specific to group 1+ individuals. Furthermore, French LPUE are considered to better capture spatial and temporal variability than UK LPUE for the English Channel stock. Indeed, French otter bottom trawlers operate almost every month in all ICES rectangles (Denis and Robin 2001), which is not the case for UK trawlers (Dunn 1999b). We chose to favour data quality rather than quantity, and decided therefore not to use UK LPUE.

We calculated Bayesian posterior predictive *p*-values to evaluate the fit of the posterior distribution of the model. The aim is to quantify the discrepancies between data and model, and assess whether they could have arisen by chance, under the model's own assumptions (Gelman *et al.*, 2014). *p*-values concentrating near 0 or 1 indicate that the observed pattern would be unlikely to be seen in replications of the data if the model were true.

Building an informative prior distribution for the biomass growth rate parameter g

The biomass growth rate parameter g is defined as the balance between the mean growth coefficient (*Gr*), and the natural mortality rate (*M*) as follows:

$$g = Gr - M$$
(7)

To build a prior for group 1+ individuals (prior_g₁₊), we first calculate the mean growth coefficient for 1+ individuals (Gr). We apply the package mixdist on length frequency data obtained from the French Onboard Observer Program (ObsMer). Number of individuals sampled each year is indicated in Table 1. Mean length of 1+ individuals is calcu-

lated in October and December, as cohort split-up is of better quality for these months. Dunn (1999) length-weight relationship is used to convert mean length into mean weight

 (\overline{w}_{1+}) . Variability of mean weight values is plotted on Figure 2. The goodness-of-fit is checked, and years where one of the cohort split-up model has a *p*-value above 0.05 are not used in the growth rate calculation.

Table 1: Number of individuals sampled in ObsMer. Years followed by "*" were not used for growth rate calculation.

Year	October	December
2005	277	252
2006	1035	186
2007*	245	138
2008	409	220
2009	526	161
2010*	1304	220
2011*	655	153
2012	755	796
2013	1035	334
2014	1001	1488



Figure 2: Variability of mean weight values of 1+ individuals after cohort split-up of ObsMer data. Full lines represent years where *p*-value of cohort split-up model was not significant, and dotted lines represent years used for growth rate calculation.

For each year where cohort split-up is reliable, the growth rate Gr_y is calculated (equation 8) and Gr is calculated as the median value of all Gr_y.

$$Gr_{y} = \log(\overline{w}_{1+,December}/\overline{w}_{1+,October}) * 6$$
(8)

To calculate the mean growth coefficient of 1+ individuals (Gr), ObsMer data were used. Cohort split-up was reliable for seven years from 2005 to 2014. Length data obtained from mixdist package had a CV of 0.058 in October and 0.054 in December. We found a value of 1.542 for Gr, with CV of 0.64.

Natural mortality (*M*) is calculated with Caddy (1996) gnomonic time division method. This method assumes that M is a simple function of mean lifespan and is constant. A vector of natural mortality at age is calculated: life-span is divided into several intervals whose duration increases proportionally to the age, and mortality is constant for each interval. The time-division is called gnomonic, and for each interval, a constant number (β) is obtained when multiplying the instantaneous mortality rate by the interval duration. Initial death rate is assumed to be high, and after a few months, a plateau is obtained. An initial number of individuals must be chosen, and 2 survivors must remain after 2 years to assure population replacement.

The mortality function is fitted with an initial number of hatchlings (*N*₁) derived from fecundity estimates. Previous studies on cuttlefish fecundity can help choosing values for the initial number of individuals. Mangold-Wirz (1963) reported that females *Sepia officinalis* may lay from about 150 to 4000 eggs depending on their size. Richard (1971) estimated numbers of 150 to 500 eggs by counting mature ova only, and a mean number of 2000 eggs was observed in laboratory culture (Hanley *et al.* 1998). Four values of N₁ are tested: 500, 1000, 1500 and 2000.

The two years life span are divided into a number *i* of smaller time intervals Δ_i . A value of 2/365 is set for the first interval Δ_1 . For each interval:

$$N_{i+1} = N_i * \exp(-M_i * \Delta_i)$$
(9)

where M_i is the mortality rate for the interval of duration Δ_i .

$$M_i * \Delta_i = \beta$$
(10)

where β is a constant. To calculate *M*, the SOLVER routine of EXCEL is used.

To estimate natural mortality of 1+ individuals, we choose the number of time intervals such that the last time interval ends at t = 2 years and lasts approximately 12 months. After the division of the lifespan into 10 gnomonic time intervals, SOLVER is used to calculate the decline in numbers such that 2 spawners survive by two years of age.

We tested four possible values of initial number of individuals (N_1) for 10 gnomonic timeintervals (Table 2). With 10 time-intervals, the pre-spawning interval was 11.5 months, so the resulting mortality was related to 1+ individuals.

Table 2: Results of natural mortality for different values of N_1 and different pre-spawning intervals.

N_1	а	β	М	Pre-spawning	Number of gnomonic time-
				interval (months)	intervals
500	0.926	0.552	0.574	11.5	10
1 000	0.926	0.621	0.646	11.5	10
1 500	0.926	0.662	0.688	11.5	10
2 000	0.926	0.691	0.718	11.5	10

Once mean growth coefficient and natural mortality were calculated, we could obtain mean value g used for the construction of prior on the g parameter (Table 3). The choice of the CV value of 0.4 used to build priors on g parameter was motivated by three considerations: the high CV of Gr, model convergence issues with a CV of 0.6 for prior construction, and density-dependent mortality which might balance the high CV and justify a choice of 0.4.

Table 3: Summary of natural mortality, mean growth coefficient and *g* parameter.

Age	Mean mortality	Mean individual growth	g parameter mean value
class			
1+	0.657	1.542	0.89

We use the mean g value obtained to construct an informative prior on the biomass growth rate:

$$log(prior_g_{1+,y}) \sim N(log(0.89), 6.74)$$
(11)

where the precision of 6.74 results from a CV of 0.4 (inter-annual variability), allowing a certain variability of g but keeping the prior informative enough for model fit.

Table 4: Summary of model parameters values and priors.

Parameter	Definition	Value/Prior
prior_g _{1+,y}	g for 1+ individuals	$Log(prior_{g_{1+,y}}) \sim N(0.89, 6.74)$
<i>B</i> _{1,y}	Initial biomass	$Log(B_{1,y}) \sim N(15\ 000,\ 4.5)$
E_y	Exploitation rate	~ Beta(1.5, 1.5)

q.bts	BTS catchability	Log(q.bts) ~ Unif(-15, 3)
q.cgfs	CGFS catchability	Log(q.cgfs) ~ Unif(-15, 3)
q.fr	LPUE.FR catchability	Log(q.fr) ~ Unif(-15, 3)
sigma_B2	Precision for <i>B</i> ₂	25.5 (for CV=0.2)
sigma_AI	Precision for all abundance indices	~ Gamma(0.05, 0.05)
sigma_C	Precision for total catch	2 500.5 (for CV=0.02)

Model construction

The model used to update the English Channel cuttlefish stock assessment (M1) is based on a time-varying *g* parameter and BTS, CGFS and LPUE.FR time-series, and captures the dynamics of 1+ individuals only. A second model is constructed (M2), based only on BTS and CGFS time-series. After comparing outputs of models M1 and M2, we run a retrospective analysis to evaluate model predictive capacity. We construct model M2r1 which is similar to M2, but catch of the last fishing season (2014) is replaced by the mean of the 5 previous years of catch. For model M2r2, all data from 2014 are deleted, and catch value used for 2013 is the mean of the 5 previous years of catch. Model M2r3 is constructed with the same logic, deleting data from 2013.

RESULTS

Results from the full model M1

Results are plotted with years at the beginning of the fishing seasons on the x-axis. Therefore, for a fishing year y, estimates of B_1 are on July y, estimates of $B_{1,jan}$ are on January y+1, and estimates of B_2 are on June y+1. Catch of group 1+ (Figure 3a) show high between-years variability with no clear trend until 2006. From 2006 to 2014, a decreasing trend can be identified.

All observed abundance indices are within the range of 95% Bayesian credible intervals for French LPUE (Figure 3b) and BTS (Figure 3c). For CGFS (Figure 3d), only 2011 observed abundance index is outside the Bayesian credible intervals.

Variability is greater for French LPUE than for the survey abundance indices. One possible explanation is that French LPUE abundance indices cover the entire fishing season, whereas the calculation for CGFS and BTS is based on data from a single month each year.



Figure 3: Comparison of posterior median estimates with observed values for catch (a) and LPUE (b), BTS (c) and CGFGS (d) abundance indices. Solid lines: posterior medians. Shaded areas: 95% Bayesian credible intervals.

Biomass estimates B_1 and $B_{1,jan}$ show a slight decreasing trend from 2002 to 2013 (Figure 4a). Biomass estimates of B2 show no clear trend (Figure 4b). Estimates of *g* from model M1 fluctuate between 0.63 and 0.92 from 1992 to 2008 with no particular trend. Median *g* estimate increases from 0.8 in 2009 to 1.2 in 2011. The highest value is estimated to 1.47 in 2014 (Figure 4c). Exploitation rate varies between 0.34 and 0.57 from 1992 to 2008, and a drop to 0.2 occurs in 2009 (Figure 4d). Highest values are obtained for years 2001 and 2011 (respectively 0.57 and 0.55) and are associated with low estimates of recruited biomass B_1 and spawning stock biomass B_2 in 2001, and high estimate of *g* in 2011.



Figure 4: Posterior medians estimates of recruited biomass and unexploited biomass on 1st January (a), spawning stock biomass (b), growth rate (c) and exploitation rate (d) for model M1. Shaded areas: 95% Bayesian credible intervals.

Posterior predicted *p*-value for catch is 0.5, showing a good capacity of the model to reproduce similar results when data are replicated. This is explained by the small value of CV used for catch data. The model tends to slightly overestimate BTS abundance indices (*p*-value > 0.5) and slightly underestimates CGFS and LPUE.FR abundance indices (Table 5).

Table 5: Posterior predictive *p*-values for model M1.

	Catch	BTS	CGFS	LPUE.FR
Model M1	0.5	0.61	0.46	0.46

Results from model M2 and predictive capacity of the model

We compare results of the full model M1 and model M2 based only on survey abundance indices, to evaluate the impact of suppressing French LPUE abundance indices. Biomass estimates B1 and B1.jan (Figures 5a and 5b) follow the same trend for models M1 and M2, but model M2 outputs show a greater decreasing trend between 2002 and 2014 than

model M1. This result is due to the French LPUE abundance indices which are higher than survey abundance indices for the five last fishing seasons (Figures 3b, 3c and 3d).

Estimates of biomass growth parameter (Figure 5c) and exploitation rate (Figure 5d) show that model M2 estimates less extreme values for g and more extreme values for E than model M1. In 2011 and 2014, g estimates are above 1.1 for model M1 and under 0.9 for model M2, whereas E estimates are above 0.7 for model M2 and under 0.6 for model M1. For these years, survey abundance indices are low, therefore the estimated biomass at the beginning of the fishing season is low. But as catches are not low, model M2 estimates high exploitation rate, whereas model M1 estimates higher g value thanks to the information brought by French LPUE.



Figure 5: Comparison of B_1 (a), $B_{1,jan}$ (b), g (c) and E (d) for models M1 and M2. Solid lines: posterior medians for model M1. Dotted lines: posterior medians for model M2. Shaded areas: 95% Bayesian credible intervals (Light grey for model M1 and grey for model M2).

The retrospective analysis conducted on the unexploited biomass (Figure 6a) shows a good predictive capacity of model M2 for this variable. Results obtained for the exploitation rate (Figure 6b) are less conclusive, as 2013 exploitation rate estimates from M2 and M2r2 differ greatly.



Figure 6: Retrospective analysis of $B_{1,jan}$ (a) and E (b) for model M2. Grey shaded areas: 95% Bayesian credible intervals.

Model M2 posterior predicted *p*-value is 0.5 for catch and 0.51 for CGFS abundance indices, showing a good capacity of the model to reproduce similar results when data are replicated. The model tends to slightly overestimate BTS abundance indices (*p*-value > 0.5), and this is amplified for models M2r1, M2r2 and M2r3. Models M2r2 and M2r3 tend to slightly underestimate CGFS abundance indices (Table 6).

Table 6: Posterior predictive *p*-values for models M2, M2r1, M2r2 and M2r3.

	Catch	BTS	CGFS
Model M2	0.5	0.56	0.51
Model M2r1	0.5	0.57	0.51
Model M2r2	0.5	0.6	0.48
Model M2r3	0.5	0.62	0.45

DISCUSSION

Quality and limits of the data and the model

We present a Bayesian implementation of a two-stage biomass model adapted to the English Channel stock of cuttlefish. The initial model (Gras *et al.*, 2014) was based on CGFS and BTS abundance indices, as well as LPUE from both French and UK trawlers. The model was sensitive to the fixed biomass growth parameter *g*, whose value was based on individual growth estimated with historical mean weight at age data and assumption of a natural mortality equals to 1.2. The first aim of the present study was to build an informative prior for the *g* parameter and to test a model with a time-varying *g*. For the stock used in this study, we had data available to calculate abundance indices

time-series specific to 1+ individuals. We were also able to build a prior on g parameter specific to 1+ individuals, using ObsMer length frequency data. This data source contains a risk of bias because the sampling plan is not entirely achieved, and the percentage of achievement varies between years. But these data are only used to construct a prior on g, which is then updated during model runs.

Our choice to focus on 1+ individuals was based on two main arguments. A previous study (Royer *et al.* 2006) indicates the presence of two micro-cohorts of cuttlefish among the English Channel, with a first recruitment around October, and a second around April. But the presence of two micro-cohorts observed during the study is not always verified, which makes it difficult to use CGFS length data to calculate a mean growth coefficient. Furthermore, environmental conditions might have stronger impact on group 0 individuals than on group 1+ individuals. Indeed, temperature and nutrient availability are known to affect both growth and natural mortality of cuttlefish, particularly in the juvenile phase (Moltschaniwskyj and Martinez 1998).

Other stock assessment methods have already been used on the English Channel stock of cuttlefish. A Leslie-De Lury depletion model has been applied by Dunn (1999a) based on data from UK beam trawl fleet only. French landings were not taken into account, although higher than English landings. Trials with a monthly VPA have also been conducted by Royer *et al.* (2006). But because of the inconsistence of size structures, this stock assessment method could not be applied routinely. Using complex models requires more data, and human resources to gather data and run the model. The two main advantages of the two-stage biomass model are its simplicity, allowing a routine update of the stock assessment, and its suitability in case of short-lived species and lack of reliable age-data (Roel and Butterworth 2000, Roel *et al.* 2009, Giannoulaki *et al.* 2014). A Bayesian model allowing time-variability of the *g* parameter is closer to reality, and brings additional information about the biomass growth parameter.

Management implications

Following Gras *et al.* (2014) conclusions, we did not find any stock-recruitment relationship. In their work, they do not detect any trend in exploitation rates between 1992 and 2008. Our study adds 6 years of data, and results differ as we detect a decreasing trend of exploitation rate from 2001 to 2009. Our results show that the highest exploitation rates occur in 2001 and 2011, with a slightly higher exploitation rate in 2001. Exploitation level from 2001 should be a limit reference point for future management. This recommendation was also specified in (Gras *et al.* 2014).

Because of the short lifespan of cuttlefish and the strong effect of environmental conditions on recruitment, usual management applied to finfish cannot be considered. Inseason assessment and management might be necessary to avoid overexploitation risk (Rosenberg *et al.* 1990, Pierce and Guerra 1994). In France, the minimum landing weight of cuttlefish is 100 g and otter trawl nets are not allowed to use mesh size <80mm. For pot fishery, there is also a limited number of fishing licenses. In Normandy, trawlers are allowed to fish cuttlefish spawners 6 weeks in spring inside the 3 nautical miles as an exemption which is decided each year around April. Another exemption allows them to target hatchlings 2 weeks in summer. BTS survey occurs in July/August and CGFS in October. It is therefore possible to have the abundance indices in winter and estimate the unexploited biomass $B_{1,jan}$ with model M2. Therefore, based on the prediction of $B_{1,jan}$, these exemptions could be avoided in case of very low biomass predicted for the fishing season considered. This would give adult cuttlefish better chances to spawn and would increase juveniles' survival chances.

Targeting juveniles leads to a loss in production for the following year, and discarding juveniles would still not be a solution. The survival rate of discarded cuttlefish has indeed been studied by (Revill *et al.* 2015). They found an immediate survival rate of 31% for cuttlefish smaller than 15 cm dorsal mantle length, and additional mortality occurred later. The exemption of the 3 nautical miles law is systematically granted in Normandy, which might result in a loss of production as well as a destruction of juvenile habitats.

In a context of global warming, we can fear a strong impact of sea temperature on cuttlefish growth and life cycle. Indeed, with the warming of the sea, we can expect higher growth rates and shorter life span (Forsythe *et al.* 1994). But at the same time there might be an effect of size at hatching on the resultant size-at-age. Due to the exponential nature of growth, the effect of hatchling size is more apparent at higher growth rates. There is a decrease in hatchling size as temperatures increase (Vidal *et al.* 2002), therefore the smaller initial size of cephalopods might balance the higher growth rates induced by increased temperatures (Pecl *et al.* 2004). These conclusions are valid for cephalopods in general, but more specific studies were conducted on *S. officinalis*. (Safi 2013) found an effect of incubation's environmental conditions on hatchling sizes, with larger juveniles obtained when eggs were incubated in colder waters. But the difference observed with different incubation temperatures was compensated when individuals grew in the same biotic and abiotic conditions. With the combined effect of sea temperature increase and pollution, changes in both growth and mortality could be expected. A time-varying *g* will bring additional information allowing to detect these changes.

Applicability of the model on other stocks

By using a Bayesian framework, we intended to incorporate uncertainty at different levels of the model, in order to propagate uncertainty to final outputs. We also intended to build a simple and general model which could be easily modified for an application on other stocks. We wanted to use the English Channel cuttlefish stock as a case study for this kind of stock assessment models. As some stocks suffer from a severe lack of data, it might not be possible to calculate abundance indices separated by age class, in which case both group 0 and 1+ individuals could be modelled as a single group. The issue remains the calculation of the g parameter. The use of a meta-analysis could help improving precision around this parameter and transfer information to stocks where no data are available for the calculation of g.

Some trials of stock assessment have been conducted on other cuttlefish stocks. An assessment of *S. officinalis* stock in the Bay of Biscay was conducted by (Gi Jeon 1982). He used a VPA with a monthly time-scale and two age groups, based on data from years 1978-1979. A Schaefer dynamic production model was implemented for the Dakhla (2001-2006), Cape Blanc (1990-2006) and Senegal-the Gambia stocks (1993-2006) (FAO/CECAF 2007). Results obtained for Cape Blanc stock were judged unreliable because of the bad model fit. Results obtained for the two other stocks showed a situation of overexploitation. As both catch and abundance indices from survey and CPUE are available, a two-stage biomass model can be applied on these stocks to estimate *g* parameter.

Other species of cuttlefish have also been subject to assessment trials in India (Nair *et al.* 1993, Rao *et al.* 1993), in the Arabian Sea coast of Oman (Mehanna *et al.* 2014), in the Gulf of Suez (Mehanna and Amin 2005, Mehanna and El-Gammal 2010). But these studies use length-based cohort analysis, which requires the assumption of a stable age-length relationship. Cephalopod growth rates are known to be highly variable (Pierce and Guerra 1994), and the use of Von Bertalanffy growth model for cephalopods might not be valid (Forsythe and Heukelem 1987, Saville 1987).

Some European cuttlefish stocks monitored by the International Council for the Exploration of the Sea Working Group on Cephalopod Fisheries and Life History have not been yet subject to an assessment, but data are available to try the two-stage biomass model. For the Bay of Biscay stock of *S. officinalis*, a series of French standardized LPUE can be calculated, and data are available from Ifremer EVHOE survey. But data from EVHOE survey might not be reliable abundance indices because it occurs offshore in November, therefore catching cuttlefish only if the migration already happened. Another stock of *S. officinalis* is found in ICES divisions VIIIc and IXa, exploited mainly by Spain and Portugal, with most of the catches occurring in division IXa. A time-series of Spanish trawlers LPUE is available, as well as a time-series of survey abundance indices in division IXa South. For stocks in warmer waters, we could expect a higher value of *Gr.* Indeed, cuttlefish seems to experience faster growth in warmer waters, even at small scale (Richard 1971). Cuttlefish experiences for example a slower growth rate in the English Channel than in South Brittany, and a water temperature effect is suspected (Le Goff and Daguzan 1991). The initial two-stage biomass model (Roel and Butterworth 2000) was developed for a squid with a one-year life cycle. Care must be taken when adapting the model to other stocks, as the assumption of an exclusive two-year life cycle is no longer valid. The model should be modified to take into account a proportion of the population experiencing a one-year life cycle.

For several cuttlefish stocks, there might be enough available data to apply a two-stage biomass model. For others, this model might not be appropriate, but as data are sometimes available to calculate growth, information could be extended to establish for example a relationship between growth, latitude of the stock and length of the life-cycle. But care should be taken to establish data reliability, and to distinguish parameters which can be assimilated to Gr or to g.

One of the consequences of overfishing is the decrease of many fish stocks, impacting the whole ecosystem. As cephalopod predators' abundance decrease, biotic changes might benefit cephalopods. At the same time, changes in environmental conditions as well as density-dependent mortality might impact these stocks. Doubleday *et al.* (2016) show that cephalopod populations have increased globally and may have benefited from a changing ocean environment. Using a model with a time-varying *g* parameter could allow the detection of long-term changes in either growth or natural mortality for the stock considered. It might not be possible to identify the role played by mortality or growth, or to know whether biotic or abiotic factors had the most impact. But it could help identifying a general tendency in the evolution of the ecosystem toward a favorable situation or an unfavorable situation for a specific stock.

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