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Original Article

A two-stage biomass model to assess the English Channel cuttlefish (*Sepia officinalis* L.) stock

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The English Channel cuttlefish (*Sepia officinalis*) is the most abundant cephalopod resource in the Northeast Atlantic and one of the three most valuable resources for English Channel fishers. Depletion methods and age-structured models have been used to assess the stock, though they have shown limitations related to the model assumptions and data demand. A two-stage biomass model is, therefore, proposed here using, as input data, four abundance indices derived from survey and commercial trawl data collected by Ifremer and Cefas. The model suggests great interannual variability in abundance during the 17 years of the period considered and a decreasing trend in recent years. Model results suggest that recruitment strength is independent of spawning–stock biomass, but appears to be influenced by environmental conditions such as sea surface temperature at the start of the life cycle. Trends in exploitation rate do not reveal evidence of overexploitation. Reference points are proposed and suggestions for management of the sustainable utilization of cuttlefish in the English Channel are advanced.

Keywords: abundance indices, English Channel, exploitation rate, *Sepia officinalis*, SST, stock–recruitment relationship, trawl survey, two-stage biomass model.

Introduction

Cephalopods are highly productive species that represent abundant and valuable fishery resources, but which also present a challenge to fishery managers because of their biological characteristics (short life, variable growth, and recruitment). The interest of fishers in cephalopod stocks increased during the latter part of the twentieth century owing to the increasing demand for high-quality protein for human consumption and the worldwide depletion of finfish stocks (Caddy, 1983; Roper *et al.*, 1984; Boyle and Rodhouse, 2005; Royer *et al.*, 2006). At a European scale, cephalopod resources have traditionally been exploited in the Mediterranean Sea by Spanish, Italian, and Greek fishers as well as in the Atlantic Ocean by Portuguese and Spanish fishers. Since the 1980s, interest in the resources by other European countries led to an increase in landings from 30 000 t in 1950 to 120 000 t in 2010 (Pierce *et al.*, 2010). In the English Channel, fishers commenced targeting three cephalopod species (*Sepia officinalis*, *Loligo forbesii*, and *Loligo vulgaris*) during the 1980s (Dunn, 1999a; Royer *et al.*, 2002, 2006).

The English Channel cuttlefish stock is the most commercially important cephalopod stock exploited in the Northeast Atlantic (Pierce *et al.*, 2010). In the list of all English Channel fishery resources, cuttlefish is ranked third by both weight and value (Portail CHARM III—Interreg IV, 2012). Annual landings (averaging 11 000 t from 2000 to 2010) are caught mainly by France and the UK. French fishers catch between 56 and 75% of the resource, and the rest is taken by UK fishers. Belgian and Netherlands fishers can also exploit cuttlefish in the English Channel, but their activity is relatively small compared with the two main countries. Cuttlefish is an important source of income for fishers considering that, during 2000–2010, the declared turnover varied around €15 million for French fishers and €5 million for UK fishers (Portail CHARM III—Interreg IV, 2012).

The most common model used to assess cephalopod stocks worldwide is the depletion method (Rosenberg *et al.*, 1990; Hilborn and Walters, 1992; Brodziak and Rosenberg, 1993; Pierce and Guerra, 1994; Basson *et al.*, 1996; Agnew *et al.*, 1998; Dunn, 1999b; Royer *et al.*, 2002; Young *et al.*, 2004; Payne *et al.*, 2006; Pierce *et al.*, 2010). In the Falkland Islands, the depletion model has been used to assess two species, *Illex argentinus* and *Doryteuthis gahi*. The economic importance of these fisheries and the results obtained have led to the model being used to define management rules for these two stocks (Rosenberg *et al.*, 1990; Basson *et al.*, 1996; Agnew *et al.*, 1998). The model has also been applied in trials in the Northeast Atlantic to the veined squid (*Loligo forbesii*) (Royer *et al.*, 2002; Young *et al.*, 2004) and English Channel cuttlefish fisheries (Dunn, 1999b). However, the depletion model developed by Dunn (1999b) was only based on UK landings, which represent only a third of the total landings (Portail CHARM III—Interreg IV, 2012).

An age-structured model is the most common method used to assess finfish stocks, particularly those that have a long lifespan (several years; Hilborn and Walters, 1992). It has also been adapted to various cephalopod stocks, such as *Illex illecebrosus* in the Northwest Atlantic (Hendrickson and Hart, 2006) and *Octopus vulgaris* (Jouffre *et al.*, 2002) off Mauritania. In the English Channel, virtual population analysis (VPA) was first adapted by Royer *et al.* (2002) on a monthly time-step to assess the loliginid squids *Loligo forbesii* and *L. vulgaris*. Royer *et al.* (2006) then adapted the same methodology to the English Channel cuttlefish stock. VPA is a very powerful way to assess long lifespan species, but it is time- and data-demanding (Mesnil, 2003; Trenkel, 2008), particularly when it is developed on a monthly basis. In addition, as for other cephalopod species, age determination of English Channel cuttlefish is difficult, length frequencies being unsuitable as a basis. Statoliths are the only hard structures that yield the real age of specimens, but interpreting daily rings is difficult and virtually impossible in animals >240 d old (Bettencourt and Guerra, 2001; Challier *et al.*, 2002, 2006). Although fascinating results were obtained (Royer *et al.*, 2006), no routine assessment has been implemented using age data owing to the difficulties associated with data collection.

In recent years, the ICES Working Group on Cephalopod Fisheries and Life History (WGCEPH) has expressed a wish to provide scientific advice on the stock status of European exploited cephalopod stocks (ICES, 2011, 2012). However, and despite the publication of stock assessment exercises based on historical data (Dunn, 1999b; Royer *et al.*, 2006), no routine assessment has been implemented to date to manage the English Channel cuttlefish stock. Currently, in the trawl fishery, cuttlefish benefits from local management measures and from more general laws that regulate trawling, such as bans on using mesh size <80 mm in otter trawl nets and on operating inshore (inside 3 nautical miles). In terms of the latter, there are currently two exemptions, one in spring and one in summer, to exploit spawners (during 6 weeks) and hatchlings (during 2 weeks) in French inshore waters, respectively. Also, fishers are not allowed to land animals <100 g (Council Regulation No 2406/96). Local management measures cover effort and spatial segregation in the coastal zone, which is, for instance, implemented in Lower Normandy for both trapfishing and inshore trawling (Pierce *et al.*, 2010).

Because of their short lifespan and specific biological features, cephalopod stocks are difficult to assess with classical stock assessment methods or by adapting some of the classical tools. An alternative method exists, however, in terms of using a two-stage biomass model that assumes that an exploited population is made of two stages, recruited and fully recruited (Roel and Butterworth, 2000; Mesnil, 2003; Trenkel, 2008; Roel *et al.*, 2009). This model is less data-demanding, but takes into account recruitment strength (Ibaibarriaga *et al.*, 2008) and gives consistent results relative to the VPA (Mesnil, 2003). It can also take into account more than one time-series of abundance indices (Roel and Butterworth, 2000) and uses weight data rather than the number of specimens caught. It also takes into account observation error, which means errors associated with the survey and commercial fishery indices, so process error is ignored (Ibaibarriaga *et al.*, 2008).

Here, we propose a two-stage biomass model for the assessment of English Channel cuttlefish. As a first step, survey and commercial data are used to derive cuttlefish abundance indices, which are then standardized using the Delta-GLM methodology. For the second step, standardized abundance indices are used as input data to fit the two-stage model and to highlight the spatial distribution and migration patterns of cuttlefish in the English Channel. A sensitivity test is performed to show how the model responds to variations in externally fixed parameters. For the third step, outputs of the model are used to show trends in cuttlefish abundance and to derive two indicators to help managers trace the impact of fishing on the stock. Finally, the results of this stock assessment exercise are discussed in the framework of management.

Materials and methods

The English Channel area and cuttlefish stock boundaries

The English Channel connects the Celtic Sea and the North Sea (Figure 1). It is an important fishing ground for both of its bordering countries, France and the UK. The Cotentin Peninsula, situated in the middle of the Channel, is the boundary between shallower waters to the east and deeper waters to the west that host different benthic communities (Pingree, 1980; Dauvin, 2012) and fish stocks. As a consequence, ICES has divided the Channel into two main zones: (i) Division VIId for the eastern part and (ii) Division VIIe for the western part. For data purposes, they are respectively divided into 14 and 19 ICES rectangles of $1^\circ \times 0.5^\circ$. The Channel is subjected to considerable anthropogenic activity, including maritime traffic, extraction of marine aggregates, and fishing (Ulrich *et al.*, 2002; Carpentier *et al.*, 2009).

The English Channel cuttlefish population is distributed throughout, its entire life cycle takes place within, and abundance in the adjacent seas (North and Celtic seas) is low. The English Channel cuttlefish has so far been considered to be a single stock (Le Goff and Daguzan, 1991; Dunn, 1999a; Wang *et al.*, 2003; Royer *et al.*, 2006). Cuttlefish inshore/offshore migrations, however, illustrate seasonal connections between east and west (Boucaud-Camou and Boismery, 1991). Population genetic studies carried out by the European Project Cephalopod Recruitment from English Channel Spawning Habitats (CRESH; 2009–2012) used microsatellites to identify population structure based on samples collected from different spawning areas in the English Channel. Preliminary results indicate that the cuttlefish is in fact one stock (P. Shaw, pers. comm.), so on that basis, the assumption of a single stock is maintained.

Métiers exploiting English Channel cuttlefish

The English Channel cuttlefish stock is exploited by a series of métiers that fish the species at almost all stages of its life cycle (Denis and Robin, 2001). Exploitation begins a few weeks after hatching during a limited 2-week period at the end of August when trawlers target juveniles within the 3-mile inshore zone by way of an exemption from the law protecting the coastal zone. After migrating to offshore wintering grounds, juvenile cuttlefish are partially recruited to the offshore French trawl fishery. The annual cohort is totally recruited to both French and UK bottom-trawl fisheries when it returns inshore to

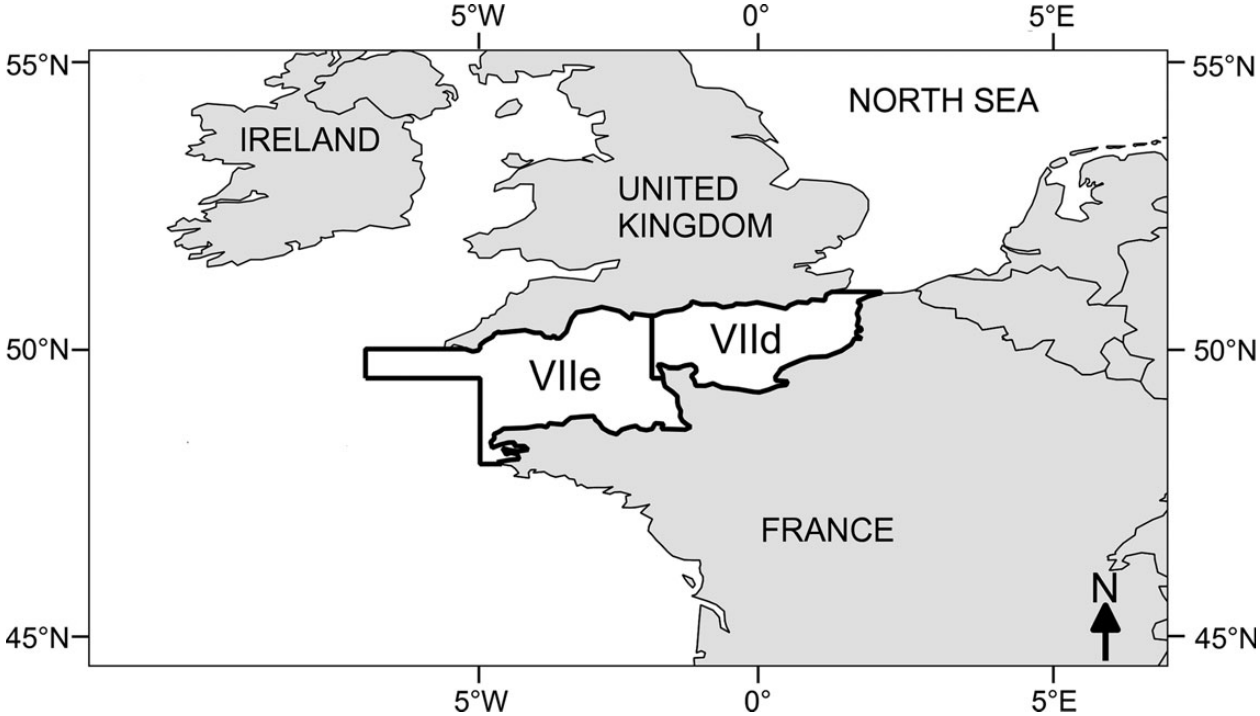

Figure 1. The English Channel, Northeast Atlantic, showing ICES Divisions VIId and VIIe.

feed in summer 1 year after hatching. Multispecies trawlers mainly use otter trawls in France and beam trawls in the UK. During the spawning period at the end of the 2-year life cycle when the animals are inshore along both French and UK coasts, fishers exploit them using traps (Dunn, 1999a; Denis and Robin, 2001; Royer, 2002; Royer *et al.*, 2006). Another exemption from the law allows French bottom trawlers to exploit the spawners for 6 weeks in spring in the 3-mile inshore zone.

Database extractions and the abundance time-series

Commercial and survey data were extracted from Cefas and Ifremer databases for the period 1992–2008. In the eastern English Channel (ICES Division VIId), Cefas carries out a bottom-trawl survey (BTS) in July each year on a research vessel, currently the RV "Cefas Endeavour" equipped with a 4-m beam trawl. Ifremer also carries out a survey in the eastern English Channel every October, the Channel Ground Fish Survey (CGFS), using RV "Gwen Drez" equipped with a very high vertical opening otter trawl (10 m wide and 3 m high). Both surveys take 30 min (on bottom) hauls to catch demersal species at each station, as defined in the established protocol (Coppin *et al.*, 2002; Carpentier *et al.*, 2009). In the BTS survey protocol, 75 stations are identified in ICES Division VIId and >100 stations by the CGFS in the same area. These two fishery-independent data series yield two time-series of abundance indices, the first one during the recruitment period and the second 3 months later, i.e. post-recruitment. Both organizations (Ifremer and Cefas) also collect landings data (all gears) and trawler landings and effort. The latter are considered adequate to derive abundance indices from commercial fishing activity: landings per unit effort (lpue) variations and their spatial/temporal components (Pierce *et al.*, 1998). Such fishery-dependent data can be used to estimate cuttlefish abundance when fishery-independent data are not available.

In this paper, the term "age 0 specimens/cuttlefish" is used for cuttlefish <1 year old, the terms "recruitment" or "recruited specimens/cuttlefish" for cuttlefish at the time of their first birthday, and the term "1-year-old specimens/cuttlefish" for cuttlefish during their second year of life after their first birthday.

Table 1. Weight classes of French commercial categories (European regulation 2406/96 about marketing standards describes commercial categories 1–3. A fourth category appears irregularly because there is no minimal landing size for cuttlefish in France).

Commercial category	Weight class (g)
1	>500
2	300–500
3	100–300
4	<100

The two-stage biomass model requires abundance indices of 1-year-old cuttlefish as input data. Examination of the length composition data collected by the BTS survey indicates that the cuttlefish caught consist mainly of 1-year-olds. On that basis, a BTS index of abundance for that age group was constructed. In October during the CGFS survey, juveniles are 3–4 months old and constitute <5% of the catch weight. Records of the CGFS survey are also assumed to be estimates of 1-year-old abundance. The UK fishery is considered to catch only 1-year-olds, and French fishers to catch cuttlefish aged both 0 and 1 year. At French landing sites, cuttlefish are sorted by commercial category (Royer, 2002; weight ranges are described in Table 1). For the analysis conducted here, cuttlefish of commercial categories 1 and 2 were considered to be 1 year olds and the other categories as age 0. In the landings data, 1-year-old cuttlefish represent ca. >80% of the total take. As the Ifremer *Sytème d'Information Halieutique* (SIH) does not provide landings by commercial category, we estimated the monthly percentage of 1-year-old cuttlefish in the sales data from all English Channel landing sites and used it to estimate the weight of 1-year-old cuttlefish caught in the English Channel overall. However, spatial origin of the landings is not given in the sales data.

Dunn (1999a) and Denis *et al.* (2002) showed that English Channel fishers did not discard cuttlefish in the 1990s, but the French National Onboard Observer Programme, as part of the European Union Data Collection Framework, currently collects discard data (protocol available at http://sih.ifremer.fr/Acquisition-des-donnees/Observations-a-la-mer/Documentation/Manuels-et-protocoles; European Union, 2008). Data were extracted from this database for the period 2004–2008.

Finally, a series of sea surface temperature (SST) observations was extracted from the National Oceanographic and Atmospheric Administration (NOAA) database from 1991 to 2008 for the English Channel area (between 5°W and 2°E and between France and the UK). Data were averaged on a quarterly basis to test the effect of SST (as a proxy of environmental conditions) on cuttlefish recruitment strength.

Scientific and commercial data extracted from the Cefas and Ifremer databases were computed to obtain abundance indices in kilograms of cuttlefish per hour of trawling:

$$S_y^{\text{obs}} = \frac{C_n}{E_n} \tag{1}$$

or

$$U_y^{\text{obs}} = \frac{C_n}{E_n} \tag{2}$$

where S_y^{obs} and U_y^{obs} are, respectively, the survey and the lpue abundance indices observed for year y, C_n and E_n are, respectively, the catch in kilograms of cuttlefish and the effort (h) trawled in trip n. Survey abundance indices were estimated by ICES rectangle and averaged for the whole eastern English Channel. As Hilborn and Walters (1992) suggest, fitting a GLM is the most powerful way to derive abundance indices from commercial lpue data. This method is currently used to standardize fish stock abundance indices and has already been used to estimate cephalopod abundance indices (Diallo and Ortiz, 2002; Royer *et al.*, 2002, 2006). In addition, the numerous null values observed in the dataset were taken into account using a Delta-GLM method (Stefansson, 1996; Syrjala, 2000; Le Pape *et al.*, 2003, 2007; Fletcher *et al.*, 2005; Martin *et al.*, 2005; Rochette *et al.*, 2010; Acou *et al.*, 2011), which combines a binomial error GLM and a Gaussian error GLM to explain first presence/absence and second the abundance of the resource. Variability in lpue is thus explained by four variables (year y, month m, ICES rectangle r, and engine power of the vessel p) which are introduced in both models:

$$\log it(U_{y,m,r,p}^{\text{obs}})_{0/1} = \alpha_y + \beta_m + \gamma_r + \delta_p + \omega_{y,m,r,p} \tag{3}$$

and

$$\ln(U_{y,m,r,p}^{\text{obs}})_{>0} = \ln(\alpha_y) + \ln(\beta_m) + \ln(\gamma_r) + \ln(\delta_p) + \varepsilon_{y,m,r,p} \tag{4}$$

where $\omega_{y,m,r,p}$ and $\varepsilon_{y,m,r,p}$ are the observation errors for the year y, month m, ICES rectangle r, and engine power of the vessel p. Standardized lpue ($U_{y,m,r,p}^{\text{st}}$) values are then estimated using the formula:

$$U_{y,m,r,p}^{\text{st}} = \frac{e^{\log it(U_{y,m,r,p}^{\text{obs}})_{0/1}}}{1 + e^{\log it(U_{y,m,r,p}^{\text{obs}})_{0/1}}} \times e^{\ln(U_{y,m,r,p}^{\text{obs}})_{>0}} \times e^{\frac{\sigma^2 \cdot \ln(U_{y,m,r,p}^{\text{obs}})_{>0}}{2}} \tag{5}$$

where σ is the standard error of the Gaussian error GLM. To avoid varying weights from one time-series to another in the model-fitting procedure, each observed abundance index was rescaled by dividing it by the mean of the time-series concerned, such that

$$S_y = \frac{S_y^{\text{obs}}}{(1/17)\sum_{y=1992}^{y=2008} S_y^{\text{obs}}} \tag{6}$$

$$U_y = \frac{U_{y,m,r,p}^{\text{st}}}{(1/17)\sum_{y=1992}^{y=2008} U_{y,m,r,p}^{\text{st}}} \tag{7}$$

where S_y is the rescaled survey abundance index and U_y is the standardized rescaled lpue value. Survey abundance indices and standardized lpue give the average spatial distribution and the trend observed in the resource abundance. Maps of standardized abundance indices can thus be used to illustrate the inshore/offshore movements of the cuttlefish during the fishing season. The four time-series of abundance indices are then used as input data to fit the two-stage biomass model.

Cuttlefish life cycle and its simplification to model its biomass

The English Channel cuttlefish (*Sepia officinalis*) is semelparous, hatches inshore in summer, and performs offshore/inshore migrations to wintering grounds in the centre of the western Channel and to coastal feeding and spawning grounds in spring and summer. The population lifespan is 2 years, and spawners die after reproducing. Recruitment into the fishery begins in October of the first year, and the annual cohort is fully recruited at the start of the second summer of life (1 year after hatching; Boucaud-Camou *et al.*, 1991; Boucaud-Camou and Boismery, 1991; Dunn, 1999a).

In a simplified version of the cuttlefish life cycle (Figure 2), fishing seasons begin on 1 July of year y (when the cohort born 1 year earlier is recruited) and end on 30 June 1 year later. In this paper, the subscript y refers to the year when the cohort is recruited. The model, therefore, describes the population dynamics of 1-year-old cuttlefish from recruitment to the end of life. During

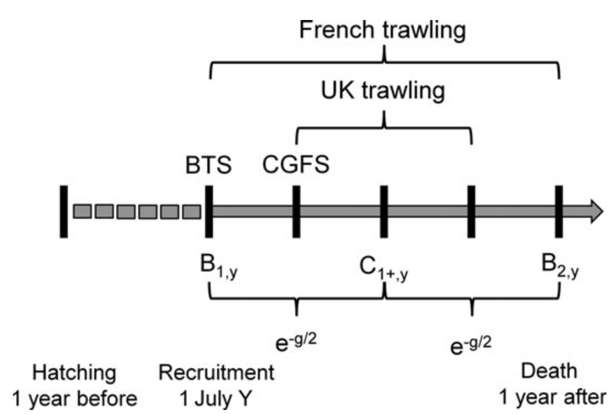

Figure 2. English Channel cuttlefish biomass dynamics. Recruitment to the fishery is assumed to take place at the start of the second year of a cohort's life and death at the end of it. The cuttlefish biomass is modelled from recruitment on 1 July to the end of the cycle on 30 June the following calendar year. Recruited biomass (B_1) experiences growth and natural mortality which are subsummed in the parameter g. The catch consists of specimens in their second year of life ($C_{1+,y}$) and occurs as a pulse in the middle of the fishing season defined from July to June the following year. UK fishing takes place in autumn and winter, but French fishing throughout the year.

the second year of life, the recruited biomass of cohort y ($B_{1,y}$) is influenced by catch, growth, and the natural mortality parameter g. Just like Pope's simplified procedure in cohort analysis (Pope, 1972), the catch of 1-year-old specimens is recruited in July of year y and $C_{1+,y}$, is assumed to happen as a pulse in the middle of the fishing season (i.e. at 31 December of year y). Considering that recruitment is assumed to take place in July of every year, the final biomass $B_{2,y}$ at the end of the life cycle can be modelled as:

$$B_{2,y} = [(B_{1,y}) \cdot e^{-g/2} - C_{1+,y}] \cdot e^{-g/2} \tag{8}$$

Abundance indices can then be used to fit the model. The BTS index is used to estimate abundance at the start of the fishing season as:

$$S_y^1 = k_1.B_{1,y} \cdot e^{\xi_y} \tag{9}$$

where S_y^1 is the BTS survey index for year y, k_1 is the BTS survey catchability, and ξ_y is the observation error for year y. The CGFS survey, which takes place 3 months after recruitment, can also be used to estimate B_1 as:

$$S_y^2 = k_2 \cdot B_{1,y} \cdot e^{-g/4} \cdot e^{\zeta_y} \tag{10}$$

where S_y^2 is the CGFS survey index for year y, k_2 is the CGFS survey catchability, and ζ_y is the observation error for year y.

Abundance indices derived from commercial trawling were also fitted. Assuming that the catch is taken as a pulse in mid-year, the abundance indices are modelled based on the mean biomass in the fishing season. The UK standardized lpue (U_y^{uk}) can hence be modelled by the following equation:

$$U_y^{uk} = \frac{1}{2} q_{uk} \cdot [B_{1,y} \cdot e^{-g/4} + (B_{1,y} \cdot e^{-g/2} - C'_{1+,y}) \cdot e^{-g/4}] \tag{11}$$

where q_{uk} is the catchability of the UK fleet and $C'_{1+,y}$ is the landings from July to April, considering that the UK does not exploit cuttlefish in either spring or summer. French otter trawlers exploit cuttlefish throughout the year, and the standardized abundance index (U_y^{fr}) for this fleet can, therefore, be modelled by the following:

$$U_y^{fr} = \frac{1}{2} q_{fr} \cdot [B_{1,y} + (B_{1,y} \cdot e^{-g/2} - C_{1+,y}) \cdot e^{-g/2}] \tag{12}$$

where q_{fr} is the catchability of the French fleet. The model is finally fitted by minimizing the sum of squares residuals (SSR) as:

$$\mathrm{SSR} = \sum_{y=1992}^{y=2008} \ln\left(\frac{S_y^1}{\hat{S}_y^1}\right)^2 + \sum_{y=1992}^{y=2008} \ln\left(\frac{S_y^2}{\hat{S}_y^2}\right)^2 + \sum_{y=1992}^{y=2008} \ln\left(\frac{U_y^{uk}}{\hat{U}_y^{uk}}\right)^2 + \sum_{y=1992}^{y=2008} \ln\left(\frac{U_y^{fr}}{\hat{U}_y^{fr}}\right)^2 \tag{13}$$

Estimation of the biomass growth parameter

The parameter g is fixed externally to avoid overparametrization. It is made up of the natural mortality rate M (which is assumed to be known and equal to 1.2, the same assumption as made by Royer *et al.*, 2006) and the growth rate G (both estimated on an annual basis) as:

$$g = M - G \tag{14}$$

The parameter G is derived from the mean weight at age using historical data collected by the University of Caen (Medhioub, 1986) as:

$$G = \sum_{a=12}^{a=22} \ln\left(\frac{\omega_{a+1}}{\omega_a}\right) \tag{15}$$

where ω is the cuttlefish weight at age a from the beginning of the modelled period in July (when cuttlefish are 12 months old) to the end of the modelled period in June of the next year (when cuttlefish are 23 months old). The data used are not necessarily representative of the cohorts studied, but were the only information available to provide some indication of adult growth rate (G) and ultimately of g. That resulted in an estimate for g of −1.01. In order to test the sensitivity of the model, a variation of natural mortality and individual growth was tested. As cuttlefish are active predators (Rodhouse and Nigmatullin, 1996), a variation of $\pm 8\%$ of M was applied. As in all cephalopod species, individual growth is variable and related to environmental parameters (Mangold, 1966; Guerra and Castro, 1988; Boucaud-Camou *et al.*, 1991; Boucaud-Camou and Boismery, 1991; Coelho and Marthins, 1991; Le Goff and Daguzan, 1991; Gauvrit *et al.*, 1997; Dunn, 1999a), so a variation of $\pm 18\%$ of G was considered. As a result, the two-stage model was run for values of $g = -0.5$ (with $M = -1.3$ and $G = 1.8$) and −1.5 (with $M = -1.1$ and $G = 2.6$) to test the sensitivity of the model results to the assumption of $g = -1.01$.

Statistical error estimation using bootstrap methodology

Model variability was estimated using a bootstrap method. Using the original dataset (a table with four abundance indices over 17 years), a dataset of residuals was estimated. A sampling with replacement of the residuals was performed 1000 times (without taking into account the time-series), and each generated residual dataset was added to the predicted abundance indices to recreate 1000 tables of four abundance index time-series over 17 years. The model was then fitted using each of the 1000 generated datasets, and outputs were used to compute averages and confidence intervals for the estimated biomass and abundance indices (B_1, B_2, S^1, S^2, U^{uk}, and U^{fr}).

Indicators of cuttlefish stock status

The biomass model provides estimates of initial and final biomass that correspond to recruitment at the start and end of the life cycle. Visual examination of a stock–recruitment plot suggested no relationship between the two. Further, there is no indication that recruitment would be reduced as biomass declines. Therefore, only a mean and its confidence interval were computed for the recruitment time-series. As no stock–recruitment relationship was identified, B_{lim} is defined as the minimum spawning–stock biomass (SSB; B_2) observed on the series. The effect of the SST during the four quarters preceding recruitment was also tested using a linear model.

As a preliminary means of evaluating the impact of fishing, an exploitation rate (E_y) is defined as the ratio of landings from the fishing season starting in year y (C_{1+y}) to the estimated biomass of cuttlefish at the end of year y:

$$E_y = \frac{C_{1+,y}}{B_{1,y} \cdot e^{-g/2}} \qquad (16)$$

Results

Trends in cuttlefish landings

Trends in cuttlefish landings during the 17-year period 1992–2008 can be split into two subperiods (Figure 3), before and after 2004, the year when total landings peaked. During the first period (1992–2004), French and UK landings increased from 4350 to 17 400 t. During the second period, total landings decreased to 8650 t, primarily because French landings dropped. During the same period, UK landings remained stable.

Discards

Discard data collected in the framework of the OBSMER programme are presented in Table 2. From 2004 onwards, when the validated data begin, discards do not exceed 5% of total catch. In the English Channel, cuttlefish landings can, therefore, be considered as equivalent to the actual quantum extracted.

Abundance indices

The two-stage biomass model fits survey abundance indices and commercial lpue trends well (residuals do not show any particular pattern), so it seems suitable to estimate the English Channel cuttlefish biomass (Figure 4). The four abundance indices used in this work show great interannual variability in cuttlefish abundance over the whole study period. From the beginning of the time-series in 1992 and up to 2001, abundance indices do not show any trend, but they then dropped. From 2002 to the end of the time-series in 2008, abundance indices continue to decrease.

Spatial distribution of cuttlefish abundance

Maps of standardized abundance indices derived from commercial fisheries are presented in Figure 5 by ICES rectangle from the third quarter, when recruitment takes place in the fishery, to the second quarter, when 1-year-old cuttlefish start to reproduce. French lpue data derived from the otter trawl fleet are presented on the left side of Figure 5, and the UK lpue data derived from its beam trawl fleet are shown on the right side. Both abundance index maps show equivalent spatial patterns during the fishing season. Spatial variations in cuttlefish abundance illustrate inshore/offshore migrations, as described previously (Boucaud-Camou and Boismery, 1991; Dunn, 1999a). Only one zone, the Norman-Breton Gulf, is characterized by high cuttlefish abundance throughout the year. UK maps of abundance show that cuttlefish exploitation by UK beam trawlers is mainly during autumn and winter. In summer (quarter 3), cuttlefish abundance is high inshore and low offshore even if some offshore rectangles of the western English Channel yield moderate abundance. In autumn (quarter 4), when cuttlefish migrate to offshore wintering grounds, maps of lpue reveal abundance inshore and offshore. In winter (quarter 1), notable cuttlefish abundance is mainly offshore in the western English Channel, although there is some moderate abundance along the UK coast. Finally, in spring (quarter 2), when cuttlefish return inshore at the beginning of April, abundance is generally greatest inshore.

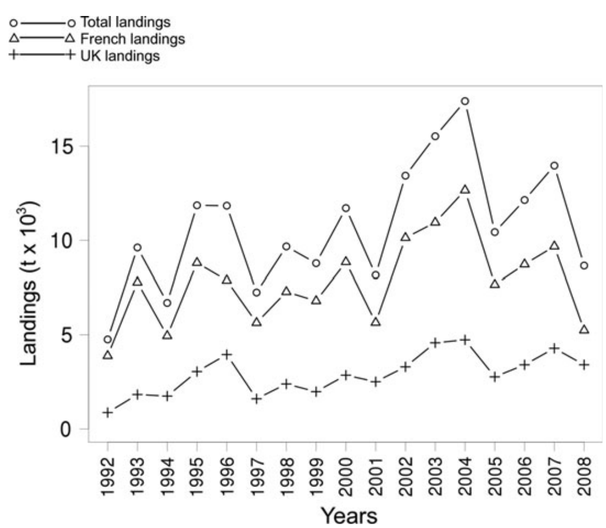

Figure 3. Annual total, French, and UK cuttlefish landings in the English Channel from 1992 to 2008.

Biomass trends

The recruited biomass (B_1) and SSB (B_2) trajectories (Figure 6), as estimated by the model, fluctuate widely without trend between 1992 and 2001, when biomass began to decline. It continued to do so until 2008 when the time-series ends.

Sensitivity analysis

Results of the sensitivity analysis to the estimate of g (Table 3) show that, on the one hand, changes in g have no consequences on either estimated recruitment (B_1) or BTS catchability (k_1). On the other hand, modifying g influences all the other parameters either slightly (such as the CGFS catchability, biomass in January, and exploitation rate) or highly (such as French and UK fleet catchabilities or SSB). The influence of variation in g is understandably greater on parameters estimated at the end of the life cycle than on those estimated at the start.

Indicators of the fishing impact on the cuttlefish stock

In terms of stock and recruitment of English Channel cuttlefish, we did not observe data points in the density-independent (left) part of the graph (Figure 7). Lower SSB (B_2) values are not followed by less recruitment (B_1) the following year. We have, therefore, estimated an average recruitment of 15 300 t (confidence interval of the mean: $\pm$1228 t), where SSB ranges between 11 000 t and a maximum of 43 000 t. A significant positive correlation was identified between SST in the third quarter (summer) of the year before recruitment and the estimated recruited biomass (B_1; Table 4).

Table 2. Cuttlefish discards in the French Channel fishery described by on-board observers of the OBSMER programme. For each year, the table presents the percentage of the catch discarded, the total landings observed, the number of trips observed during which cuttlefish were landed, and the number of hauls where cuttlefish were observed.

Year	Percentage discards	Landings observed (kg)	Number of trips	Number of hauls
2004	2	8522	20	143
2005	4	4187	16	105
2006	2	4317	10	51
2007	3	2394	9	61
2008	5	4360	32	176

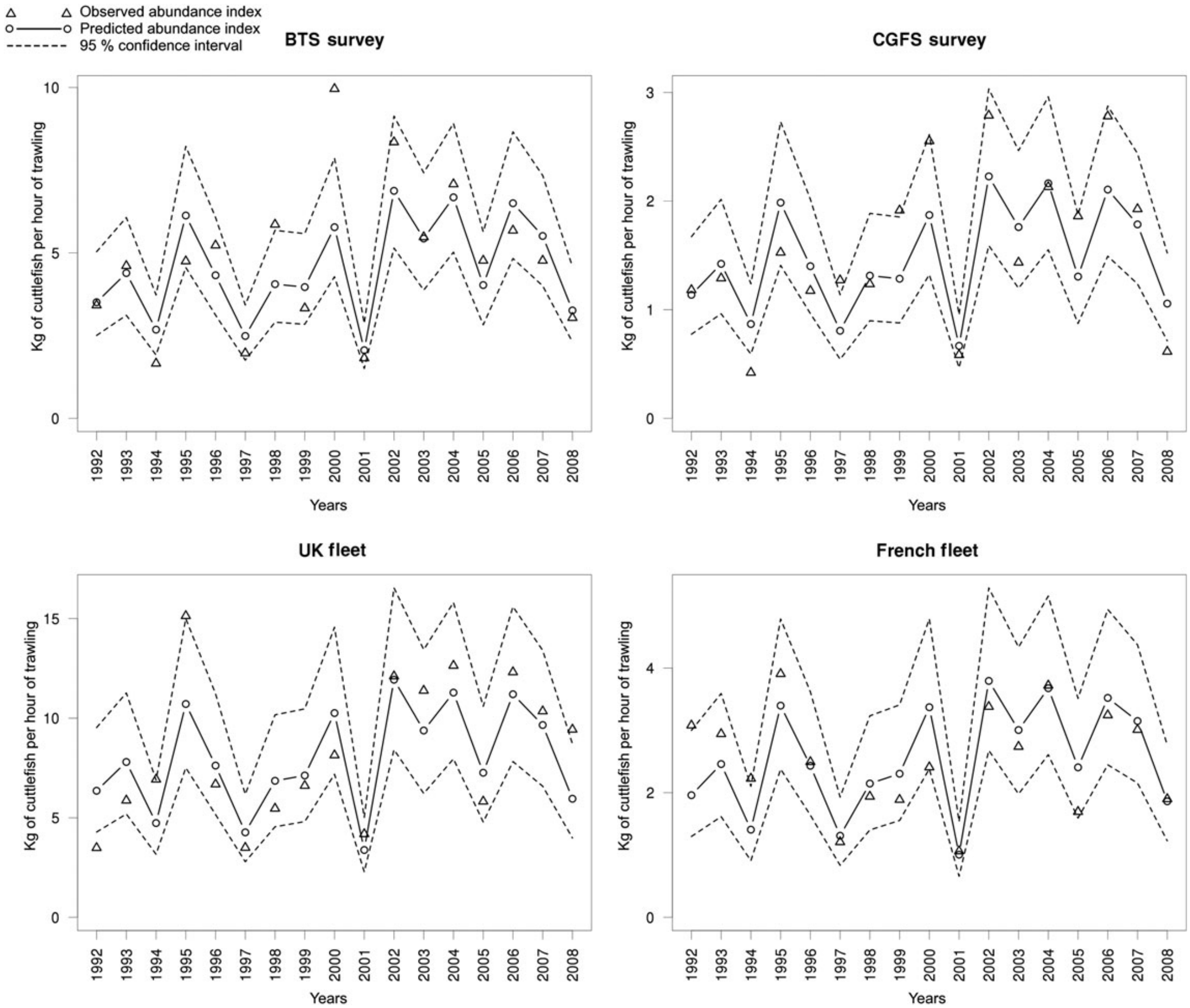

Figure 4. Time-series of the observed and predicted abundance indices with 95% confidence interval from 1992 to 2008. Predicted standardized abundance indices obtained from the fitting procedure were back-transformed (i.e. multiplied by the mean of each abundance index time-series) to fit the observed abundance indices.

However, there was no correlation with SST during the other three quarters before recruitment.

The time-series of the exploitation rate (Figure 8) does not show any significant trend during the study period. With the exception of 2001, it varies between 26 and 39%, with an average of 33%. In 2001, however, the exploitation rate peaked at 44%. The sensitivity tests to higher g values result in higher exploitation rates (see Figure 8). It is worth noting that the peak in exploitation rate is followed (taking into account a time-lag) by above-average recruitment.

Discussion

The two-stage biomass model developed here evaluates the English Channel cuttlefish stock over a 17-year period. An earlier study modelled cuttlefish in the same area over a 7-year period using a monthly VPA (Royer *et al.*, 2006). The two-stage biomass model is based on a schematic description of the life cycle and exploitation, which was also the case with the depletion models (Pierce and Guerra, 1994; Dunn, 1999b; Young *et al.*, 2004). Although age-structured VPA approaches appear to be more realistic, the approach used here is less data-demanding, and routine updates can be made more easily.

This work has shown great interannual variability in cuttlefish biomass, a common feature of cephalopod resources (Boletzky, 1983; Boumaaz and Dridi, 2002; Boyle and Rodhouse, 2005). The start of the study period is characterized by stability in abundance, but the end of the period shows a decreasing trend. The maximum and minimum abundance estimates observed in 2000 and 2001 were consistent with the results provided by the age-structured model developed by Royer *et al.* (2006). Closer comparisons of the two-stage biomass results with the work of Royer *et al.* (2006) are not easy because VPA uses numbers at age.

Despite the negative trend in observed and predicted estimates of abundance, no stock–recruitment relationship has been identified. However, a significant positive correlation between SST in the summer preceding recruitment and subsequent recruitment has been found, suggesting that temperature in the first summer of a cohort may be very influential.

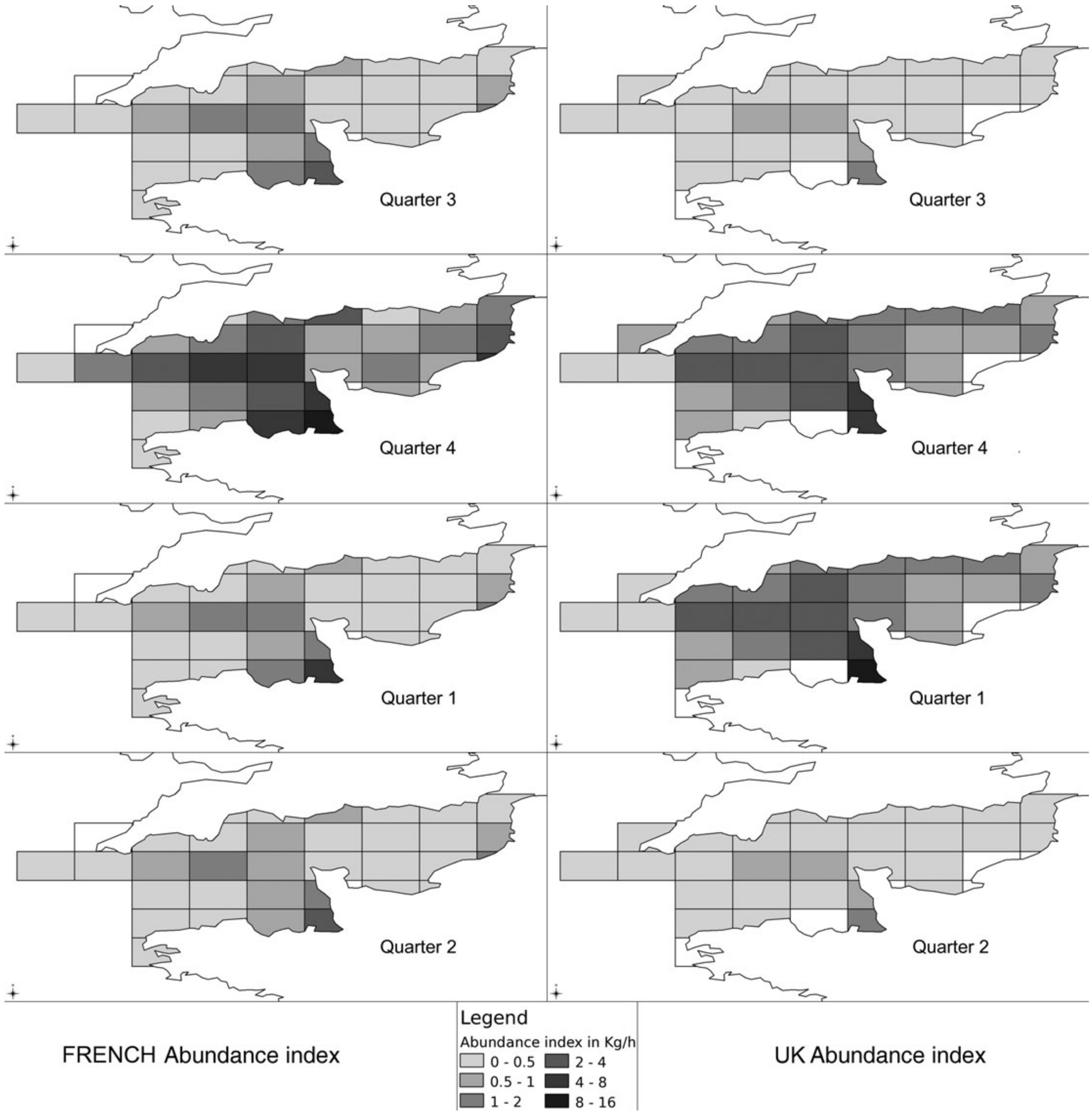

Figure 5. Spatial distribution of cuttlefish abundance by ICES rectangle and by quarter computed with the French and UK lpue values.

Finally, outputs of the two-stage biomass model allow estimation of the exploitation rate, which could be used as a management tool if a limit exploitation rate can be identified for the stock. Both the Cefas and Ifremer surveys, from which the data were taken for this analysis, target demersal fish species, particularly flatfish, in the eastern English Channel (ICES Division VIId). No survey currently exists to assess the demersal communities in the western English Channel (ICES Division VIIe), however. Moreover, the timing of the CGFS survey (which takes place in October each year) may not be entirely appropriate to derive population abundance indices for cuttlefish, because they are carried out when cuttlefish are about to leave the eastern English Channel for overwintering grounds in the western Channel (Boucaud-Camou and Boismery, 1991). Hence, the results are likely to be sensitive to the onset of migration. However, the fishery-dependant abundance series derived from landings of different trawls (French otter trawls, UK beam trawls) describe similar interannual variations. Finally, a significant improvement to the two-stage biomass model could be to estimate the parameter *g* based on recent data (for instance, making use of the extensive information collected under the European Data Collection Framework). Doing so could provide opportunity to apply a *g* varying from 1 year to another and/or from one season to another. Recommendations on this possibility have been formulated recently by the ICES WGCEPH (ICES, 2011, 2012).

Boletzky (1983) showed that environmental conditions play an important role in determining cuttlefish spatial distribution, abundance, and recruitment. In the English Channel, the water column is rarely stratified, and SST, which is positively correlated there with sea bottom temperature (SBT), can be assimilated into the water column temperature. From a spatial perspective, SST drives

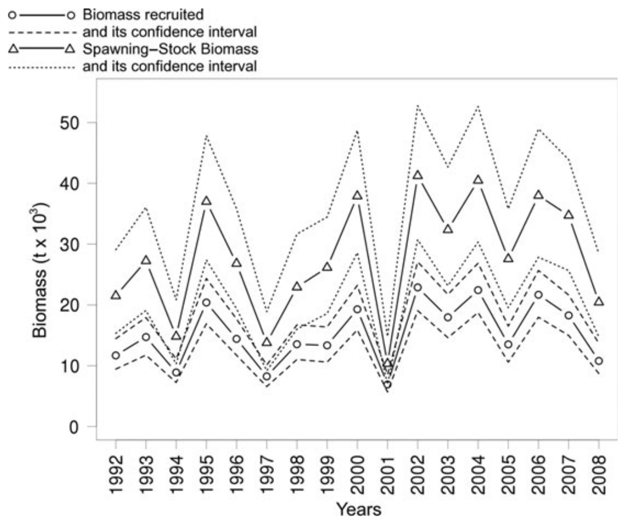

Figure 6. Temporal trends in biomass recruited (B_1, solid line with circles) and SSB (B_2, solid line with triangles) with 95% confidence intervals (dashed lines).

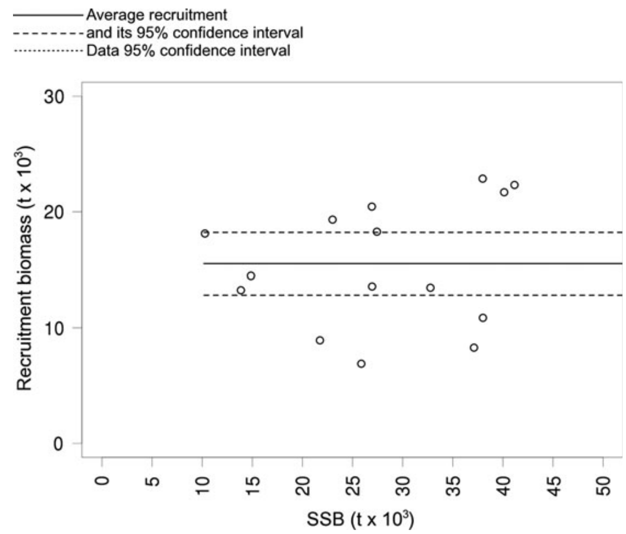

Figure 7. Stock and recruitment data (points), average annual recruitment (solid line), and 95% confidence interval (dashed lines).

Table 3. Percentage of variation in the outputs for a variation of 50% of *g*.

Output	$g = -0.5$ (%)	$g = -1.5$ (%)
B_1	<1	<1
k_1	−1	−0.1
k_2	13	−11
q_1	36	−26
q_2	46	−34
B in January	−22	27
Exploitation rate	28	−21
B_2	−49	81

Table 4. *p*-value and r^2 for the linear model carried out with English Channel SST measured during the four quarters preceding recruitment (summer $Q3_{y-1}$, autumn $Q4_{y-1}$, winter $Q1_y$, and spring $Q2_y$) and the recruitment strength ($B_{1,y}$).

Explaining variable SST	*p*-value	r^2
$Q3_{y-1}$	0.008	0.38
$Q4_{y-1}$	0.056	0.22
$Q1_y$	0.323	0.06
$Q2_y$	0.631	0.01

cuttlefish seasonal migration from inshore to their offshore wintering grounds. From a temporal perspective as well, Wang *et al.* (2003) highlighted the positive correlation between SST and cuttlefish abundance. During the juvenile phase, low temperatures and sub-optimal nutrition reduce growth rate and increase natural mortality (Moltschaniwskyj and Martinez, 1998). This could explain the correlation identified between SST during the first months of cuttlefish life and the recruitment strength ultimately estimated. For English Channel cuttlefish, the start of the life cycle is a critical period during which environmental conditions are clearly playing a vital role in determining recruitment strength.

In the English Channel cuttlefish, the first life stages following hatching are spent inshore in various spawning/nursery grounds along the French and UK coasts. Even if there are other hotspots, Torbay (UK), the west coast of the Cotentin Peninsula, and the Bay of Seine (France) are considered to be the most important (Boucaud-Camou and Boismery, 1991; Dunn, 1999a; Challier, 2005). These nursery grounds consist of benthic habitats of different nature, including seagrass/seaweed beds and rocky shores, so prey abundance and biodiversity may well differ from other areas and so might the environmental conditions. As the juvenile phase plays a critical role in determining recruitment strength, further research may be able to quantify the contribution to recruitment of each spawning/nursery area. Such findings could then help to identify the conditions that favour productivity of the cuttlefish resource.

The exploitation rate is a promising indicator of stock status. For English Channel cuttlefish, the apparent lack of a clear stock–recruitment relationship and the absence of a trend in exploitation rate suggest that the fishing impact is currently not detrimental to the current stock. The rate reached 44% in 2001, but even that high rate did not seem to have short-term consequences on recruitment. Equivalent levels of exploitation rate (i.e. several years >40%) were also experienced by the Bay of Biscay anchovy (*Engraulis encrasicolus*) without any short-term consequences, but a dramatic drop was observed over the long term and was evident by 2005 (ICES, 2008). In the Falkland Islands, the populations of *Doryteuthis gahi* and *Illex argentinus* tolerated an escapement ratio (number of animals escaping from the fishery over the total number of animals which should have survived without fishing) >40% (which could be considered as an exploitation rate of a maximum of 60% of the cohort; Basson *et al.*, 1996; Agnew *et al.*, 1998) in a series of years before two important drops in 2004 and 2010 (FAO, 2012). By maintaining an exploitation rate <40%, the English Channel cuttlefish fishery could be considered as not showing evidence of overexploitation, though it does seem to be fully exploited. The exploitation rate estimates presented here and based on the two-stage biomass model do provide an overview of current cuttlefish stock status. In order to better understand the stock and exploitation dynamics, however, further work needs to explore spatial and métier interactions, such as carried out by Royer *et al.* (2006).

Even if the current rate of exploitation of the English Channel cuttlefish stock does not seem to have had detrimental consequences

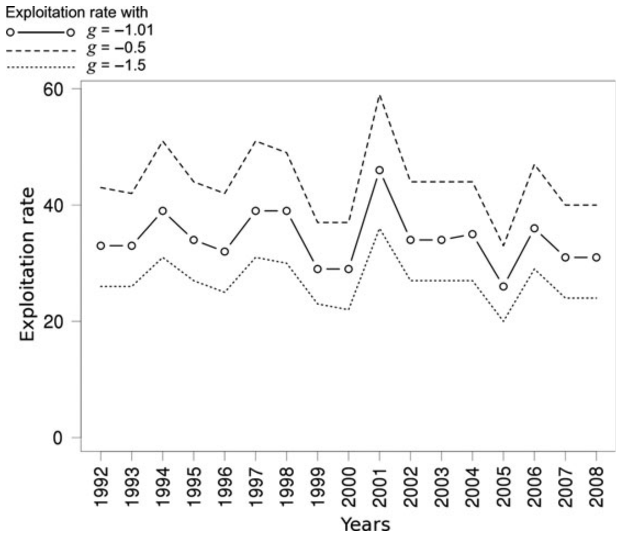

Figure 8. Temporal trends in exploitation rate of the cuttlefish resource from 1992 to 2008 for the model base case ($g = -1.01$) and two sensitivity tests ($g = -0.5$ and $g = -1.5$).

on the resource, such fishing pressure can influence life history traits. Fishing activity, by increasing mortality on larger animals, could favour slow growth and early maturation (Bianchi *et al.*, 2000; Shin *et al.*, 2005; Kantoussan *et al.*, 2009). Such fishing effects have been observed in various Northeast Atlantic demersal stocks (Shin and Rochet, 1998; Grift *et al.*, 2003; Engelhard and Heino, 2004; Olsen *et al.*, 2004). With its short life cycle of 1–2 years, depending on temperature (Mangold, 1966; Guerra and Castro, 1988; Boucaud-Camou *et al.*, 1991; Boucaud-Camou and Boismery, 1991; Coelho and Marthins, 1991; Le Goff and Daguzan, 1991; Gauvrit et al., 1997; Dunn, 1999a), the English Channel cuttlefish could well have been subjected to life history trait modification induced by high fishing pressure.

In European waters, finfish resources, which generally have long lifespans, are usually managed by total allowable catch (TAC). However, the English Channel cuttlefish is a short lifespan species, so the biomass consists largely of recruits. In addition, recruitment strength and abundance are highly variable and presumably much influenced by environmental conditions that are difficult to predict (Pierce *et al.*, 2008). As suggested by Basson *et al.* (1996) for *Doryteuthis gahi* in the Falkland Islands, however, perhaps the best way of managing the English Channel cuttlefish stock would be to control fishing effort during the fishing season rather than by setting a TAC, especially given that this would have to be agreed at the start of the calendar year.

Such a form of management would be facilitated if reference points were available to provide a diagnostic on the state of the resource (Mesnil, 2012; Brooks, 2013). That was the strategy developed in the Falkland Islands to manage squid stocks using the proportional escapement ratio (Beddington *et al.*, 1990; Rosenberg *et al.*, 1990; Basson *et al.*, 1996; Agnew *et al.*, 1998). In the case of English Channel cuttlefish, however, after fitting a two-stage biomass model, outputs could help in providing a diagnostic using an exploitation rate to assess the fishing impact on the current cohort. From 1992 to 2000, an average exploitation rate of 33% seemed to have been sustainable because SSB did not seem to be impacted. On the contrary, when the exploitation rate reached 44% in 2001, the SSB did seem to suffer. Even if the 2003 recruitment does not seem to have been impaired, we cannot anticipate the consequences in the long term of such a sustained high rate of exploitation. According to the precautionary principle, and based on experience in other cephalopod fisheries (Beddington *et al.*, 1990; Rosenberg *et al.*, 1990; Basson *et al.*, 1996; Agnew *et al.*, 1998), we strongly suggest maintaining the exploitation rate on cuttlefish at a level of <40%.

The decreasing trend in estimated cuttlefish biomass post-2002 could be a consequence of either or both adverse environmental conditions or heavy fishing pressure. Concerning reference points for management, a SSB value of 11 000 t would seem to be appropriate because below that threshold, recruitment levels are unknown. In order to better monitor stock dynamics, in-season surveys would be needed to assist managers and decision-makers in deciding real-time management measures if the stock is seen to be endangered. Moreover, the results of the BTS and CGFS surveys could be used as indicators of stock status before the fishing season starts (because both abundance indices positively correlate to French and UK lpue (p-value <5%) and to total landings (p-value <1‰)). An R package with lpue standardization, model-fitting procedure, and estimating model output has been developed and is freely available to provide the basis for annual stock assessments and subsequent scientific advice (Gras and Robin, 2013).

In order to manage the West Africa octopus (*Octopus vulgaris*) stock, two fishing closures have been established to protect the stock during the spawning and recruitment periods. These closures have worked well and, coupled with the overall reduction of fishing effort, seem to be having a positive long-term effect on the resource (Boumaaz and Dridi, 2002; Jouffre *et al.*, 2002). In France, an equivalent measure could be taken by not allowing exemptions from the rules banning spring and summer trawling inshore (within the 3-mile zone). In spring, the objective would be to protect cuttlefish spawning habitats, assuming that natural substrata suitable for egg laying (seaweeds, seagrass beds, and peacock worms; Bloor, 2012) are less damaged by trap fishing than by trawl. As shown above, the early life stages are critical in the cuttlefish life cycle, so any reduction in trawling activity during summer would protect juveniles and favour recruitment.

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