Stock structure of the English Channel common cuttlefish *Sepia officinalis* (Linnaeus, 1758) during the reproduction period

MICHAËL GRAS[1,2], GEORGES SAFI[1,2], HUGO LEBREDONCHEL[1,2], JÉRÔME QUINQUIS[3], ÉRIC FOUCHER[3], NOUSSITHÉ KOUETA[1,2] AND JEAN-PAUL ROBIN[1,2]

[1]BOREA, UMR CNRS 7208, IRD 207, UPMC, MNHN, UCBN, 14032 Caen, France, [2]Université de Caen Basse-Normandie, UMR BOREA: Biologie des ORganismes et des Ecosystèmes Aquatiques, Esplanade de la paix, CS 14032, 14032 Caen, France, [3]Ifremer, Laboratoire Ressources Halieutiques, Avenue du Général de Gaulle, BP 32, 14520 Port-en-Bessin, France

Within the English Channel, the common cuttlefish Sepia officinalis *is a semelparous species for which a 2-year life cycle was exclusively described in the 1980s. In the 1990s, new research indicated that whilst a 2-year life cycle was still evident for females and the large majority of males, a small proportion of males were actually maturing at only 1 year of age. Since 1980, the interest of French and UK fishers for this resource has increased and it is nowadays one of the most important demersal species of the area and is considered to be fully exploited. From the start of the 20th century, fishing effort and sea surface temperatures have increased in the English Channel and have probably impacted the life history traits of* S. officinalis. *A 2-year sampling programme was undertaken at French landing sites of the English Channel during the reproduction season in 2010 and 2011 to estimate if the proportion of 1-year-old mature animals has changed. Age determination was carried out by coupling polymodal decomposition and lipofuscin measurement. Size-at-maturity for each year and each sex was estimated by fitting a binomial error GLM. Results highlight that a variable percentage of males and females belonging to the first cohort are mature and that size-at-maturity was lower than that observed in the 1990s. Finally, different parameters, such as temperature and fishing pressure are explored to discuss changes in life history traits suggesting that cuttlefish could be an indicator of the temperature regime shift in the English Channel.*

INTRODUCTION

The common cuttlefish, *Sepia officinalis* (Linnaeus, 1758), is a short lived and semelparous cephalopod distributed from the West African coast (Senegal and Mauritania) to the English Channel and in the Mediterranean Sea (Mangold, 1987). It has a life cycle lasting between 1 and 2 years depending on the latitude at which it lives (Domingues *et al.*, 2006; Guerra, 2006). From West African to the Portuguese coasts, the entire population has a 1-year life cycle (Mangold-Wirz, 1963; Mangold, 1966; Guerra & Castro, 1988; Coelho & Martins, 1991). The Bay of Biscay is a transition zone where two different groups were identified; Group I Breeding (GIB), can breed at 1 year of age (45% of male specimens and 20% of female specimens), Group II Breeding (GIIB), breeds at 2 years of age (Le Goff & Daguzan, 1991; Gauvrit *et al.*, 1997). In the English Channel, the life cycle of *S. officinalis* was originally described as lasting exclusively 2 years (Boucaud-Camou & Boismery, 1991; Boucaud-Camou *et al.*, 1991). A decade later,

Dunn (1999a) found that the entire female population and 96% of male specimens had a 2-year life cycle (GIIB). The remaining males (4%) were found to be mature at the age of 1 year old, constituting a GIB.

The English Channel population of *S. officinalis* was mainly considered as a non-valuable by-catch before the 1980s (Dunn, 1999a). Since then, the increasing price of this species and the depletion of finfish stocks (Royer *et al.*, 2006; Molfese *et al.*, 2014) led French and UK fishers to exploit this stock. Landings increased from 4350 tonnes in 1992 to a maximum of 17,400 tonnes in 2004 (Gras *et al.*, 2014). During the 2000–2010 decade, an average of 11,000 tonnes was landed annually for an average turnover of €20 M (Pierce *et al.*, 2010; Portail CHARM III–Interreg IV, ©, 2012). The English Channel stock of *S. officinalis* was assessed in trials using a depletion model (Dunn, 1999b), a Virtual Population Analysis (Royer *et al.*, 2006) and a two-stage biomass model (Gras *et al.*, 2014). Whilst Dunn (1999b) does not give a clear indication of the stock status, Royer *et al.* (2006) and Gras *et al.* (2014) concluded that *Sepia officinalis* has been fully exploited since the beginning of the 1990s. Moreover, Gras *et al.* (2014) showed that *S. officinalis* abundance decreased during the period 2001–2008 and consequences of the fishing pressure on life history traits should be investigated.

Corresponding author:
M. Gras
Email: michael.gras@ymail.com

High fishing pressure directly and indirectly affects fish communities and populations. Among the direct effects of high fishing pressure on populations are increased mortality and size selectivity that tend to reduce the proportion of old and large specimens in the population (Smith, 1994). After several years of high exploitation, smaller specimens maturing faster are favoured, leading to decrease in mean size and length (or age) at maturity by favouring slow growth and early maturing specimens (Bianchi *et al.*, 2000; Shin *et al.*, 2005; Kantoussan *et al.*, 2009). Observations of such processes have been carried out in various stocks of the N-E Atlantic such as the North Sea herring (Shin & Rochet, 1998; Engelhard & Heino, 2004), the North Sea plaice (Grift *et al.*, 2003) and the northern cod (Olsen *et al.*, 2004). The English Channel has been trawled for over 200 years and from the beginning of the 20th century to date, the fishing pressure has increased considerably (Hawkins *et al.*, 2003). According to Guenette & Gascuel (2012), the French fishing effort displayed in the Celtic Sea and the Bay of Biscay (including western English Channel, ICES division VIIe where *S. officinalis* overwinters and is exploited by offshore trawlers) has been multiplied by 10 between 1950 and 2010. In the English Channel, the number of trawling vessels (coming from France and UK) who share the demersal resources has increased from 450 vessels in 2000 to almost 800 ten years later (Portail CHARM III–Interreg IV, ©, 2012). Finally, a compilation of French and UK data used to derive abundance indices (Gras, 2013; Gras *et al.*, 2014) shows an increase of the trawling effort from 572,000 h in 1992 to an average of 900,000 h for the period 2003–2007.

In addition to the fishing pressure, climate variations (including global warming which is made of natural and anthropogenic components) are also known to influence the abundance and spatial distribution of marine species (Beaugrand & Reid, 2003; Hawkins *et al.*, 2003; Beaugrand, 2009). According to the data collected by the Marine Biological Association of the United Kingdom (MBA), significant warming of the English Channel occurred throughout the 20th century (Southward & Roberts, 1987). Between 1986 and 2006, Saulquin & Gohin (2010) estimated this warming to be between 0.5 °C in the southern part of the Channel and 1.5 °C in its northern part. This warming has led to modifications in phytoplankton assemblages, fish larval abundances and pelagic fish abundances (Southward *et al.*, 1988). Moreover, a decline in community level, average length and length-at-maturity in demersal communities has been observed, suggesting that fish assemblages become dominated by species maturing faster and reproducing at a shorter length (Hawkins *et al.*, 2003). Due to their short life cycle and their high metabolic rate, cephalopods are assumed to be very sensitive to environmental warming (Pierce *et al.*, 2010).

In the context of high fishing pressure and global warming observed between the end of the 1980s and the end of the 2000s in the English Channel, this work aims to establish whether modifications in the life cycle of the *S. officinalis* exist. By focusing on the stock structure in the reproduction period, we would like to highlight whether the percentage of 1-year-old mature males observed by Dunn (1999a) has changed and whether a percentage of 1-year-old mature females exists or not. To achieve this goal, a 2-year sampling programme was carried out in spring at French landing sites within the English Channel. Length frequencies associated with measurement of lipofuscin were used to discriminate between the two cohorts and estimate the percentage of mature 1-year-olds. The size-at-maturity and the Gonado Somatic Index estimated are compared with results previously published (Dunn, 1999a). Results obtained are finally discussed in the framework of the environmental pressures exerted on the *S. officinalis* population inhabiting the English Channel.

MATERIALS AND METHODS

Study area: the English Channel

The English Channel is situated in the N-E Atlantic between the Celtic Sea and the North Sea. Following the International Council for the Exploration of the Sea (ICES), two subdivisions exist, VIId to the East and VIIe to the West. The western English Channel is characterized by a maximum depth of around 170 m and is strongly influenced by Atlantic waters. With a minimum temperature > 10 °C in winter, this area has favourable conditions for the overwintering of *Sepia officinalis* (Wang *et al.*, 2003). The eastern English Channel (ICES division VIId) is characterized by shallow waters, maximum depth of 50 m and a homogeneous water column. Winter sea temperature in this part of the Channel can reach as low as 5 °C, making it unsuitable for overwintering of *S. officinalis* (Pingree, 1980; Boletzky, 1983).

Previously described migration cycle of *S. officinalis* within the English Channel

In the English Channel, *S. officinalis* hatch inshore at the beginning of summer (Figure 1). After spending the entire summer feeding inshore, they migrate offshore to overwinter in the central western English Channel (Boucaud-Camou & Boismery, 1991; Dunn, 1999a; Royer *et al.*, 2006) where sea bottom temperature is favourable (Wang *et al.*, 2003). The following summer is also spent feeding inshore. At the end of this second summer, male specimens finish their maturation (in approximately September). In October, they perform their second offshore migration to the wintering grounds where female specimens complete their maturation. The final migration is performed at approximately 20 months old to reach the inshore spawning zones. Mass mortality of sexually mature adults occurs after the reproduction period (Boucaud-Camou & Boismery, 1991; Dunn, 1999a; Guerra, 2006; Royer *et al.*, 2006).

Sample collection

Samples of *S. officinalis* were collected from three French landing sites along the English Channel coastline in spring 2010 and 2011. Specimens were caught by trawlers or trap fishers in the Normano-Breton Gulf (ICES rectangles 26E8 and 27E8) and in the Bay of Seine (ICES rectangles 27E9 and 28E9). In 2010, from 12 April to 9 July, 734 specimens (395 males, 339 females) were collected in Erquy, Cherbourg and Port-en-Bessin landing sites. In 2011, from 5 April to 30 June, 655 specimens (444 males and 211 females) were collected in Port-en-Bessin and Cherbourg landing sites. The sex ratio was tested using a chi-square test.
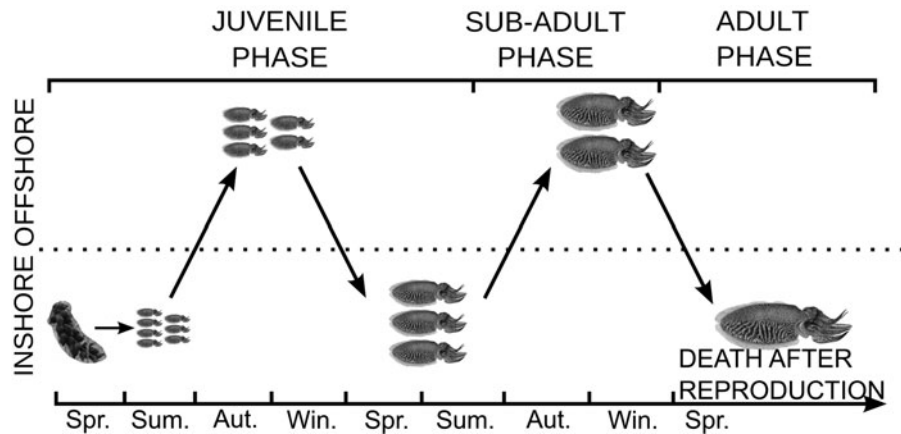
Fig. 1. Life cycle of the English Channel population of *S. officinalis* L. as described by Boucaud-Camou & Boismery (1991), Boucaud-Camou *et al.* (1991) and Dunn (1999a).

Biometry dissection and sex determination

The Dorsal Mantle Length (DML) of each specimen was measured to the lowest cm and length frequencies were represented on four histograms, one per sex and per year. Length classes are defined every cm, immature specimens are represented in white; mature animals are represented in grey. An attempt was made to fit two Gaussian models associated with a mixing effect to the two cohorts. If the model fitted the first cohort well, due to its shape, it was not possible to fit it to the second cohort. A truncation point between the first and second cohort is then defined by the least numerous length class after the first mode. However, due to the high inter-individual variability of the growth rate in *S. officinalis* (Challier *et al.*, 2002, 2005), this criteria cannot be used alone to determine which cohort a particular specimen belongs to. The measurement of lipofuscin (age pigment accumulated in tissues; Zielinski & Portner, 2000; Doubleday & Semmens, 2011) was used in this work to give a second indicator of age estimation. Fresh total Body Weight (BW) and Gonad Weight (GW) were also measured for each specimen.

The mantle of each specimen was opened by a ventral incision to determine the sex and maturity stage using the macroscopic scale developed in the framework of the international Workshop on Sexual Maturity Staging of Cephalopods (WKMSCEPH; ICES, 2010). Six maturity stages are described from undetermined to spent (post-reproduction) for each sex. In female specimens, maturity stages are mainly defined using oocyte size and development of the Nidamental Glands (NG). In male specimens, maturity stages are defined using testis size and spermatophore position in the Spermatophoric Complex (SC). This international scale is based on the same number of stages and the same criteria as the one developed by Dunn (1999a). Mantle tissue samples were collected from a subsample of specimens to measure lipofuscin concentrations. Tissue samples were kept frozen in liquid nitrogen to avoid tissue degradation and transported to the laboratory to be analysed.

Lipofuscin measurement

Experiments carried out in the past to study English Channel *S. officinalis* based age estimation only on polymodal decomposition of length frequencies (Boucaud-Camou & Boismery, 1991; Boucaud-Camou *et al.*, 1991; Dunn, 1999a). In cephalopods, growth rate is influenced by environmental conditions and presents a high inter-individual variability making this method inaccurate. Various hard structures have been tested for age determination in *S. officinalis* (Le Goff *et al.*, 1998; Neige, 2006) but the only consistent results were obtained from statolith daily rings during the juvenile phase (Challier *et al.*, 2002, 2006). However, statolith rings are very difficult to read in *S. officinalis* and are not usable after 240 days of age (Bettencourt & Guerra, 2001). Above this threshold, some studies proposed to use the concentration of lipofuscin as a proxy of age: lipofuscin is a pigment that accumulates in tissues through the lifetime of some invertebrates (Sheehy *et al.*, 1996; Ju *et al.*, 1999; Bluhm & Brey, 2001). This method has been successfully used in cephalopods to provide a rough estimation of *S. officinalis* age (Zielinski & Portner, 2000; Doubleday & Semmens, 2011).

Lipofuscin was measured according to Zielinski & Portner (2000). Mantles of *S. officinalis* were ground under liquid nitrogen and homogenized in a chloroform-methanol mixture (1:2, v/v). After centrifugation for 10 min at 2000 g, lipofuscin was found in the chloroform phase. In this phase an emission spectrum between 350 and 550 nm was obtained at an excitation wavelength of 350 nm using a Mithras LB940 fluorimeter (Berthold, Thoiry, France). The luminescence of the sample was determined at the maximum emission at 420 nm. Lipofuscin concentrations were expressed as relative fluorescence intensity according to Hill & Womersley (1991), using 0.1 µg quinine per mL 1N H_2SO_4 as a standard.

In a first step, we tested the applicability of lipofuscin concentrations to fish market samples of *S. officinalis* by measuring post-mortem variability over the 3 days following the death. A mantle was sampled on one living animal and lipofuscin was measured on the fresh tissue. The tissue was then kept on ice during the following 3 days. A large piece of mantle was taken every 24 h randomly on the mantle and used to perform replicated measures of lipofuscin. Differences were tested using an ANOVA. In a second step, lipofuscin concentrations were measured on two subsamples. A subsample of 11 immature specimens was taken from the first cohort (DML ranging 10–13 cm and assumed to be 1 year olds as they are short and immature) and a subsample of

17 mature specimens was taken from the group which length is highly over the boundary between the two cohorts (DML ranging 20–31 cm and therefore assumed to be 2-year-olds). This experiment describes inter-cohort differences in lipofuscin concentrations. Finally, results of lipofuscin concentration measured from the smallest mature specimens (two animals of 11 cm DML and one of 13 cm DML) were used in a Student *t*-test to estimate the probability of each small mature specimen to belong to each cohort.

Size-at-maturity estimation

The maturity stage of each specimen, observed in each length class, was used to fit a binomial error Generalized Linear Model (GLM) to estimate size-at-maturity. Specimens were considered as mature when they reached the 'Maturing stage' (2b), assuming that if they are maturing during the spring, they will become mature and able to breed and spawn before the end of the reproduction season in late summer.

Gonado-Somatic Index

An index of sexual development was computed with the Gonado-Somatic Index (GSI):

$$GSI = \frac{GW}{BW - GW}$$

GSI is a proxy of the energy allocated by the specimen to reproduction to the detriment of somatic growth. This index is a quantitative measure of sexual maturity and the relationship between GSI and DML complements the estimation of size-at-maturity. Student *t*-tests were performed to look for differences in GSI between the two sampled years, between mature and immature animals and between males and females. An F-test was used to highlight differences between GSI variances of mature males and females. Finally, a linear model was fitted to explore the correlation between mature male DML and GSI.

RESULTS

Length frequency of samples

Female specimens ranged from 6 to 27 cm DML in 2010 and from 7 to 26 cm DML in 2011. Male specimens ranged from 6 to 36 cm DML in 2010 and from 7 to 32 cm DML in 2011 (Figure 2). Length frequencies highlighted that a first cohort was identifiable and the maximum size of this first cohort could be determined at 16 cm for both sexes in 2010 and at 14 and 13 cm for females and males respectively in 2011. In 2010, the smallest mature females were 7 cm long while the smallest mature males were 8 cm long. In 2011, the smallest mature females were 11 cm long and the smallest mature males were 10 cm. In 2010, 17% of females and 30% of males assigned to the first cohort were found to be mature and in 2011, 3% of females and 13% of males of the first cohort were found to be mature. For both years, sex ratios were significantly different from 1:1 with males more numerous than females, particularly in 2011.

Size-at-maturity determined using a binomial error GLM

For both sexes, the size-at-maturity (Figure 3) was higher in 2010 than in 2011 and for both years, size-at-maturity in females was larger than in males. For male specimens, the smallest length class within which all individuals were found to be mature was 16 cm DML in 2010 and 14 cm DML in 2011; above these length classes all male specimens were found to be mature. In contrast, for female specimens, the smallest length within which all individuals were found to be mature was smaller at 14 cm in 2010 and 13 cm in 2011; however, above these length classes, immature individuals were still observed in larger length classes.

Variability in lipofuscin measurement and age estimation

Lipofuscin measurement from the first experiment (Figure 4) showed that, over a period of 3 days, no significant trend was observed in lipofuscin concentration; however, the standard deviation of the measure did increase with time. In the second experiment, lipofuscin accumulation measured in specimens belonging to the first and second cohorts were significantly different (Figure 5). Results of the lipofuscin measurement performed on the three small mature males (Figure 5, Table 1) showed that lipofuscin accumulation of these three specimens was not significantly different from that of the first cohort, but was significantly different from lipofuscin accumulation measured in GIIB. These three specimens could thus be considered as part of the GIB group.

Gonado-Somatic Index

The GSI (Figure 6) for each sex and each year, does not reveal any significant inter-annual differences. In both sexes, the GSI during the reproduction period was significantly higher for mature specimens than for immatures. Mature female specimens were characterized by a significantly higher GSI and a higher inter-individual variability than mature males. Finally, the GSI of mature male specimens was found to be significantly correlated with DML.

DISCUSSION

The life cycle of the *Sepia officinalis* population in the English Channel was described in the past as lasting 2 years for females and for the large majority of males (Boucaud-Camou *et al*., 1991; Dunn, 1999a). The present study highlights that, during the 2010 and 2011 reproduction seasons, a variable percentage of mature male and female *S. officinalis* belongs to the first cohort and could thus be considered as a GIB. Age determination was based on polymodal decomposition and adaption of lipofuscin measurement protocol (Zielinski & Portner, 2000; Doubleday & Semmens, 2011). The association of both methods is more accurate than the polymodal decomposition used alone and enabled to disentangle the two sampled cohorts. It has corroborated that the smallest mature animals observed are most likely 1-year-old *S. officinalis* and not small 2-year-old specimens. Finally, the GSI illustrates the amount of energy dedicated by each sex
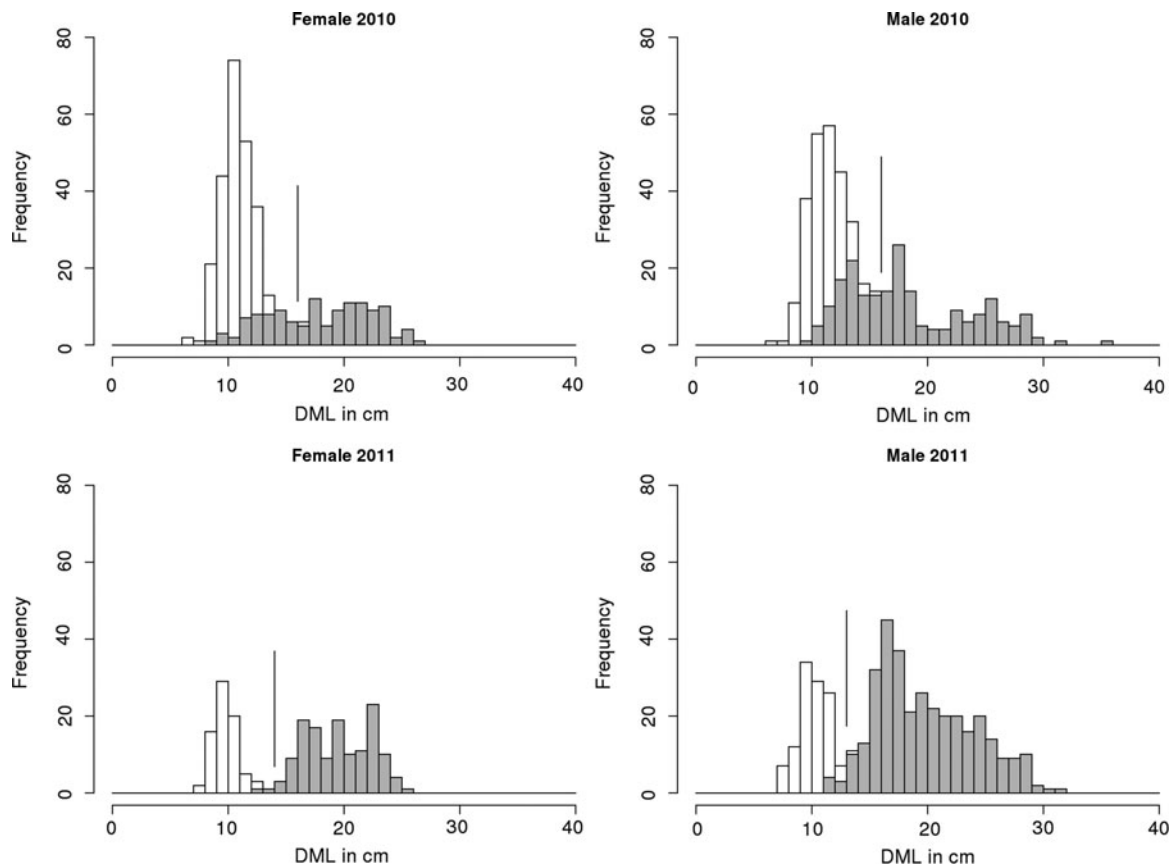
Fig. 2. Length frequencies of the female and male specimens collected during spring 2010 and 2011 in French English Channel landing sites. Immature specimens are displayed in white and mature specimens are displayed in grey. The vertical line drawn indicates the boundary between the first and the second cohorts.

to the development of the gonad to the detriment of the somatic growth.

Lipofuscin measurement has helped in determining the cohort to which each specimen belongs, but this method is not accurate enough for age estimation (Zielinski & Portner, 2000; Doubleday & Semmens, 2011). Moreover, accuracy decreases with increasing time between death and sampling; as the sampling process was based on commercial fishery landings, this parameter was not under control. Finally, lipofuscin measurement is expensive and time consuming and for this reason experiments cannot be carried out on a large number of specimens. An alternative method for rough age estimation could be set up using statoliths. Although statolith daily rings are not accurately readable in 1-year-old *S. officinalis* (Bettencourt & Guerra, 2001; Challier *et al.*, 2002, 2006), studies of several fish species have found that otolith length, thickness and weight continued to grow with age even when body growth rate was null (Reznick *et al.*, 1989; Campana, 1990; Newman, 2002). Age frequency distribution derived from otolith weights were found to be consistent with those derived from increment counts (Pilling *et al.*, 2003; Mc Dougall, 2004). Moreover, statolith diameter has also been successfully used as a proxy of age in the planktonic tunicate *Oikopleura vanhoeffeni* (Choe & Deibel, 2009). If *S. officinalis* statolith experiences daily increments throughout its life, measuring dome diameters could be another way to separate the two annual cohorts.

In cephalopod species, rearing experiments have shown that maturation is driven by different factors including photoperiod, food availability and temperature (Mangold, 1987). Cephalopods are known not to store ingested energy in their tissues and as such individuals, particularly females, need a regular food availability in order to reach maturity as observed for *Sepioteuthis australis* (Ho *et al.*, 2004) and *Loligo vulgaris* (Moreno *et al.*, 2005). Thus, the variability observed in the female GSI could be explained by food availability experienced by each specimen. In male specimens, the lower amount of energy dedicated to reproduction allows more energy for somatic growth and therefore explains both the low variability of the GSI and a larger DML than in females. It is also worth noting that, within this study, the size-at-maturity plots for males are quite homogeneous and do not reveal subgroups maturing at different sizes as previously described for other cephalopod species (Castro *et al.*, 1991; Coelho *et al.*, 1994; Moreno *et al.*, 1994; Boyle & Rodhouse, 2005). Finally, the English Channel warming (Hawkins *et al.*, 2003; Saulquin & Gohin, 2010) leads to the modification of species communities by increasing abundance of warm water species and decreasing abundance of cold water species. Such modifications could also influence the English Channel population of *S. officinalis* by modifying the competition and the predator-prey relationships.

Temperature is a key parameter influencing cephalopod life cycles, from egg development to reproduction (Rodhouse *et al.*, 1992; Boyle & Pierce, 1994; Robin *et al.*, 2014). An increase in environmental temperature generally accelerates the somatic growth of cephalopods, shortening the life cycle duration by accelerating maturation (Moreno
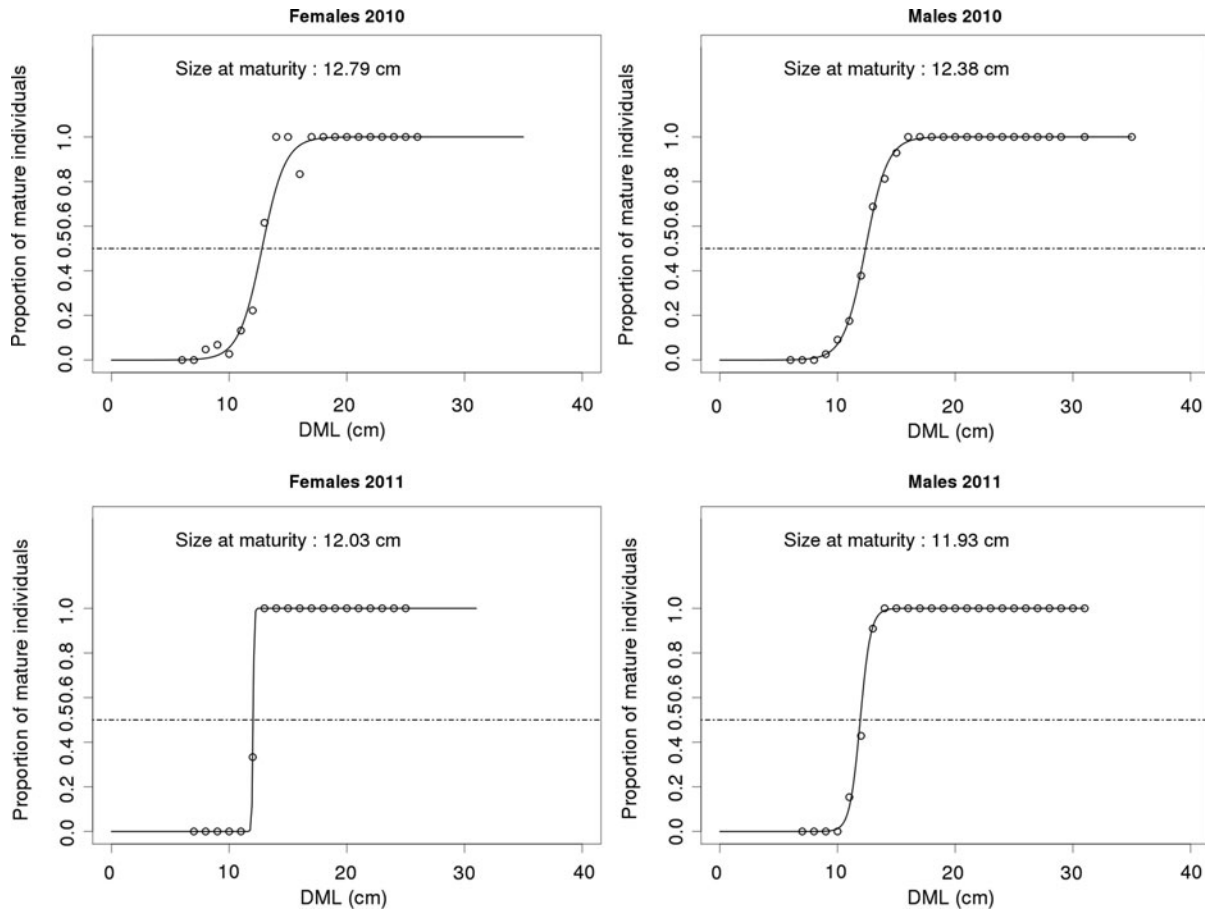
Fig. 3. Size-at-maturity determined using a binomial error GLM for female and male samples collected during spring 2010 and 2011 in French English Channel landing sites. Number of specimens measured per DML class is shown in Figure 2.

et al., 2007). This is a well-known feature in the life cycle of *S. officinalis* which shortens from the north of its distribution area (English Channel) to the south (West African coasts; Mangold-Wirz, 1963; Mangold, 1966; Guerra & Castro, 1988; Coelho & Martins, 1991). The warming of the English Channel (Hawkins *et al.*, 2003; Saulquin & Gohin, 2010) could be the cause of appearance of a GIB composed of

males and females and the observation of a lower size-at-maturity (on average 12.16 cm for males and 12.41 cm for females in 2010 and 2011 respectively) than that observed by Dunn (1999a) (14.6 cm for males and 16.4 cm for females). Further investigations are required to investigate if this size-at-maturity variability could be correlated with environmental indices (such as NAO index) and
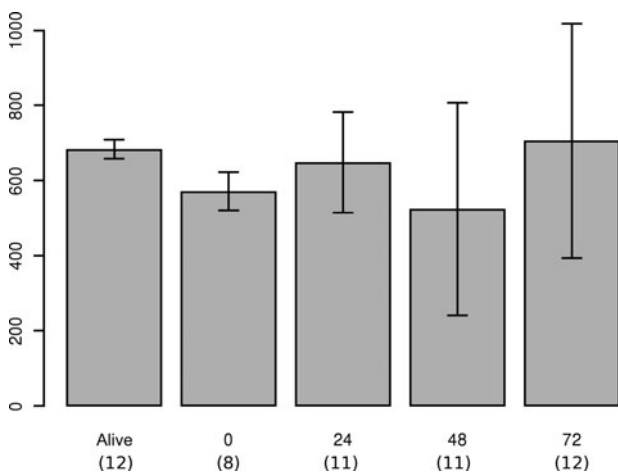

Fig. 4. Trend in lipofuscin concentration measured in the mantle sampled on one living *S. officinalis* from the death and every 24 h until 72 h after the death. Error bars are the standard deviations of each measure.
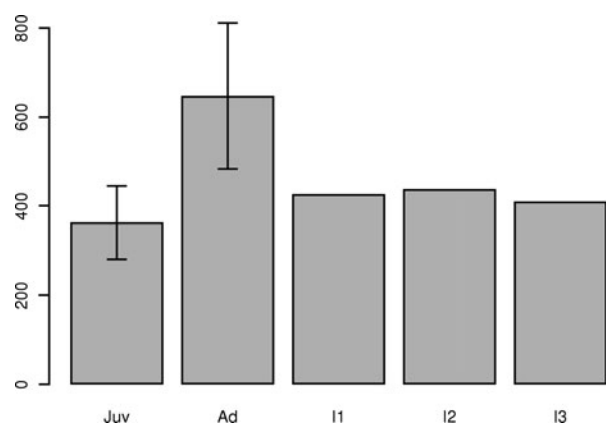

Fig. 5. Lipofuscin concentration measured in *S. officinalis* mantles for juveniles (Juv, 11 specimens, ranging 10–13 cm DML), adults (Ad, 17 specimens, ranging 20–31 cm DML) with the inter-individual standard deviation and lipofuscin concentration measured in three small mature specimens (I1, 11 cm DML; I2 11 cm DML; I3, 13 cm DML).

**Table 1.** Probabilities of three small male mature specimens to be different from the GIB and GIIB cohorts.

Specimens	Length (cm)	*P*, GIB	*P*, GIIB
First cohort (immature; 11 specimens)	10 < L < 13		
Second cohort (mature; 17 specimens)	20 < L < 31		
Individual 1	11	0.12	0.02
Individual 2	11	0.08	0.03
Individual 3	13	0.22	0.02

whether GIB is actually involved in reproduction by analysing the sperm reservoirs of females to understand whether cross-mating between generations exists (Gauvrit *et al.*, 1998). Warming of the English Channel could also lead to an extension of the reproduction season allowing the more precocious hatchlings sufficient time to mature prior to the following spring.

In the *S. officinalis* population of the English Channel, Challier *et al.* (2006) showed that recruitment in the trawling fishery occurs throughout the year at a constant age leading to the conclusion that *S. officinalis* hatches throughout the year. GIB observed in this study could thus be individuals which had hatched early in the reproduction season and which had had enough time before offshore migration to start maturation and finish it before the end of next spring.

The English Channel has long been exploited by both French and UK fishers. Trawling started 200 years ago and fishing pressure has regularly increased since the beginning of the 20th century (Hawkins *et al.*, 2003; Guenette & Gascuel, 2012; Gras, 2013). High fishing pressure greatly impacts demersal communities and can modify life history traits by favouring specimens which mature faster or reach maturity at a smaller size or lower age (Shin *et al.*, 2005; Kantoussan *et al.*, 2009). This phenomenon has been observed in a range of N-E Atlantic stocks (Shin & Rochet, 1998; Grift *et al.*, 2003; Engelhard & Heino, 2004; Olsen *et al.*, 2004) and could also have influenced the English Channel population of *S. officinalis*, which has been fully exploited since the beginning of the 1990s (Royer *et al.*, 2006; Gras *et al.*, 2014), leading to the appearance of a GIB and a potential decreasing trend in size-at-maturity. Modifications in demersal community assemblages caused by high fishing pressure could have modified the prey availability for *S. officinalis*. Maturation efficiency in cephalopods, which could be unable to store energy in their tissue (Mangold, 1987; Moreno *et al.*, 2005) could therefore be impacted.

Sepia officinalis is one of the top predators of the English Channel ecosystem (Araújo *et al.*, 2005). In contrast to other top predators, *S. officinalis* has a short lifespan and as such, the consequences of any regime shift can be easily observed in the short term and could thus provide a useful indicator of climate change. According to Jackson *et al.*
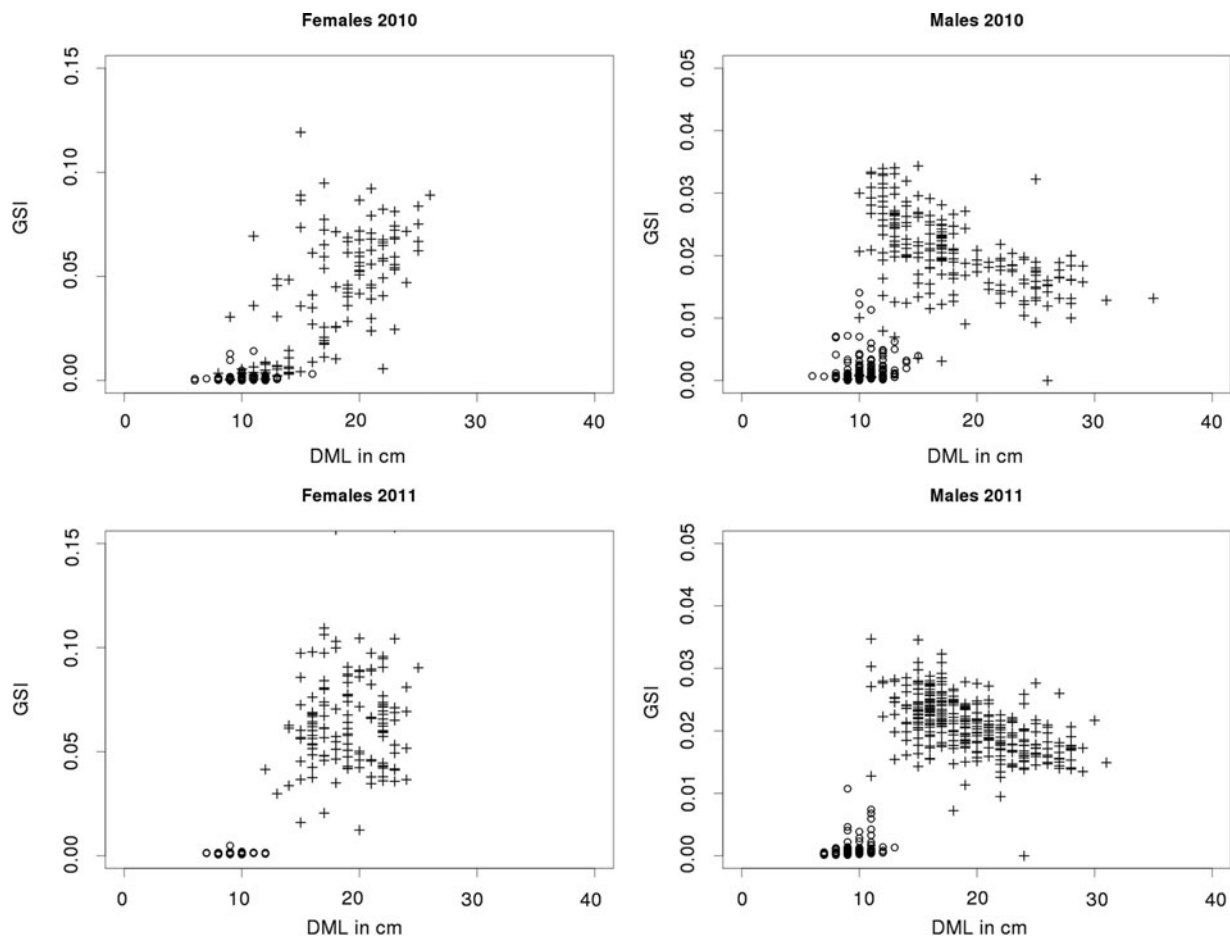
Fig. 6. Gonado Somatic Index (GSI) *vs* Dorsal Mantle Length (DML) for female and male samples collected during spring 2010 and 2011 in French English Channel landing sites. Immature specimens are displayed with circles while mature specimens are displayed with crosses.

(2000), an indicator of climate change must meet four criteria: (i) relevance to assessment and ecological functions, (ii) feasibility of data collection, (iii) response to variation and (iv) interpretation and utility of data to highlight the changing environment. Although *S. officinalis* is a non quota species (Pierce *et al.*, 2010), two scientific bottom trawl surveys sample it each year (Carpentier *et al.*, 2009; Gras *et al.*, 2014) and maturity stages can be easily determined using the international WKMSCEPH scale (ICES, 2010). This could be complemented by data collected at landing sites throughout the year according to the Data Collection Framework (DCF) programme. *Sepia officinalis* therefore meets the four criteria listed above and should be considered as an indicator for environmental shift.

REFERENCES

Araújo J.N., Mackinson S., Ellis J.R. and Hart P.J.B. (2005) An Ecopath model for the Western English Channel ecosystem with an exploration of its dynamic properties. *Science Series Technical Report*, CEFAS Lowestoft, no. 125, 45 pp.

Beaugrand G. (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. *Deep Sea Research Part II: Topical Studies in Oceanography* 56, 656–673.

Beaugrand G. and Reid P.C. (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology* 9, 801–817.

Bettencourt V. and Guerra A. (2001) Age studies based on daily growth increments in statoliths and growth lamellae in cuttlebone of cultured *Sepia officinalis*. *Marine Biology* 139, 327–334.

Bianchi G., Gislason H., Graham K., Hill L., Jin X., Koranteng K., Manickchand-Heileman S., Paya I., Sainsbury K., Sanchez F. and Zwanenburg K. (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science* 57, 558–571.

Bluhm B.A. and Brey T. (2001) Age determination in the Antarctic shrimp *Notocrangon antarcticus* (Crustacea: Decapoda), using the autofluorescent pigment lipofuscin. *Marine Biology* 138, 247–257.

Boletzky S. (1983) Sepia officinalis. In Boyle P.R. (ed.) *Cephalopod life cycles, Vol. 1. Species accounts*. London: Academic Press, pp. 31–52.

Boucaud-Camou E. and Boismery J. (1991) The migrations of the cuttlefish (*Sepia officinalis* L.) in the English Channel. In Boucaud-Camou E. (ed.) *La seiche/The cuttlefish*. Caen: Centre de publication de l'Université de Caen Basse-Normandie, pp. 179–189.

Boucaud-Camou E., Koueta N., Boismery J. and Medhioub A. (1991) The sexual maturity of *Sepia officinalis* L. from the Bay of Seine. In Boucaud-Camou E. (ed.) *La seiche/The cuttlefish*. Caen: Centre de publication de l'Université de Caen Basse-Normandie, pp. 141–151.

Boyle P.R. and Pierce G.J. (1994) Fishery biology of the Northeast Atlantic squid. *Fisheries Research* 21, 1–314.

Boyle P.R. and Rodhouse P.G. (2005) *Cephalopods: ecology and fisheries*. New York, NY: Wiley.

Campana S.E. (1990) How reliable are growth back-calculations based on otoliths? *Canadian Journal of Fisheries and Aquatic Sciences* 47, 2219–2227.

Carpentier A., Martin C.S. and Vaz S. (2009) *Channel habitat atlas for marine resource management, final report/Atlas des habitats des ressources marines de la Manche orientale CHARM II*. Boulogne-sur-Mer: Ifremer, 626 pp.

Castro B.G., Guerra A. and Jardón C.M.F. (1991) Variations in digestive gland weights of *Sepia officinalis* and *Sepia elegans* through their life cycles. In Boucaud-Camou E. (ed.) *La seiche/The cuttlefish*. Caen: Centre de publication de l'Université de Caen Basse-Normandie, pp. 99–104.

Challier L., Dunn M.R. and Robin J.-P. (2005) Trends in age-at-recruitment and juvenile growth of cuttlefish, *Sepia officinalis*, from the English Channel. *ICES Journal of Marine Science* 62, 1671–1682.

Challier L., Pierce G.J. and Robin J.-P. (2006) Spatial and temporal variation in age and growth in juvenile *Loligo forbesi* and relationships with recruitment in the English Channel and Scottish waters. *Journal of Sea Research* 55, 217–229.

Challier L., Royer J. and Robin J.-P. (2002) Variability in age-at-recruitment and early growth in English Channel *Sepia officinalis* described with statolith analysis. *Aquatic Living Resources* 15, 303–311.

Choe N. and Deibel D. (2009) Statolith diameter as an age indicator in the planktonic tunicate *Oikopleura vanhoeffeni*: variability in age-specific growth patterns in Conception Bay, Newfoundland. *Journal of Experimental Marine Biology and Ecology* 375, 89–98.

Coelho M.L. and Martins M.C. (1991) Preliminary observations on the biology of *Sepia officinalis* in Ria Formosa, Portugal. In Boucaud-Camou E. (ed.) *La seiche/The cuttlefish*. Caen, France: Centre de publication de l'Université de Caen Basse-Normandie, pp. 131–140.

Coelho M.L., Quintela J., Bettencourt V., Olavo G. and Villa H. (1994) Population structure, maturation patterns and fecundity of the squid *Loligo vulgaris* from southern Portugal. *Fisheries Research* 21, 87–102.

Domingues P.M., Bettencourt V. and Guerra A. (2006) Growth of *Sepia officinalis* in captivity and in nature. *Vie et Milieu – Life & Environment* 56, 109–120.

Doubleday Z.A. and Semmens J.M. (2011) Quantification of the age-pigment lipofuscin in known-age octopus (*Octopus pallidus*): a potential tool for age determination. *Journal of Experimental Marine Biology and Ecology* 397, 8–12.

Dunn M.R. (1999a) Aspects of the stock dynamics and exploitation of cuttlefish, *Sepia officinalis* (Linnaeus, 1758), in the English Channel. *Fisheries Research* 40, 277–293.

Dunn M.R. (1999b) *The exploitation of selected non–quota species in the English Channel*. PhD thesis. University of Portsmouth, UK.

Engelhard G. and Heino M. (2004) Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? *Marine Ecology Progress Series* 272, 245–256.

Gauvrit E., Le Goff R. and Daguzan J. (1997) Reproductive cycle of the cuttlefish, *Sepia officinalis* (L.) in the northern part of the Bay of Biscay. *Journal of Molluscan Studies* 63, 19–28.

Gauvrit E., Pinczon Du Sel G., Blanc A. and Daguzan J. (1998) Detection of cross-mating between two generations of the cuttlefish *Sepia officinalis* by sperm reservoir analysis. *Journal of Molluscan Studies* 64, 1–9.

Gras M. (2013) *Contribution des frayères côtières au recrutement du stock de seiche Sepia officinalis de Manche: lien entre le succès de la phase pré-recrutée et l'abondance de la ressource.* PhD thesis. Université de Caen Basse-Normandie, France.

Gras M., Roel B.A., Coppin F., Foucher E. and Robin J.-P. (2014) A two-stage biomass model to assess the English Channel cuttlefish (*Sepia officinalis* L.) stock. *ICES Journal of Marine Science* 71, 2457–2468.

Grift R.E., Rijnsdorp A.D., Barot S., Heino M. and Dieckmann U. (2003) Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Marine Ecology Progress Series* 257, 247–257.

Guenette S. and Gascuel D. (2012) Shifting baselines in European fisheries: the case of the Celtic Sea and Bay of Biscay. *Ocean and Coastal Management* 70, 10–21.

Guerra A. (2006) Ecology of *Sepia officinalis*. *Vie et Milieu – Life & Environment* 56, 97–107.

Guerra A. and Castro B.G. (1988) On the life-cycle of *Sepia officinalis* in the Ria de Vigo. *Cahiers de Biologie Marine* 29, 395–405.

Hawkins S.J., Southward A.J. and Genner M.J. (2003) Detection of environmental change in a marine ecosystem-evidence from the western English Channel. *Science of the Total Environment* 310, 245–256.

Hill K.T. and Womersley C. (1991) Critical aspects of fluorescent age-pigment methodologies: modification for accurate analysis and age assessments in aquatic organisms. *Marine Biology* 109, 1–11.

Ho J.D., Moltschaniwskyj N.A. and Carter C.G. (2004) The effect of variability in growth on somatic condition and reproductive status in the southern calamary *Sepioteuthis australis*. *Marine and Freshwater Research* 55, 423–428.

ICES (2010) Report of the Workshop on Sexual Maturity Staging of Cephalopods (WKMSCEPH). *ICES CM 2010/ACOM:49. Technical report*, ICES, Livorno, Italy.

Jackson L.E., Kurtz J.C. and Fisher W.S. (2000) Evaluation guidelines for ecological indicators. EPA/620/R-99/005. *U.S. Environmental Protection Agency, Office of Research and Development Technical Report May*, Research Triangle Park, NC.

Ju S.J., Secor D.H. and Harvey H.R. (1999) Use of extractable lipofuscin for age determination of blue crab *Callinectes sapidus*. *Marine Ecology Progress Series* 185, 171–179.

Kantoussan J., Ecoutin J.-M., Fontenelle G., Thiaw O.T., Tito de Morais L. and Laë R. (2009) The relevance of size parameters as indicators of fishery exploitation in two West African reservoirs. *Aquatic Ecology* 43, 1167–1178.

Le Goff R. and Daguzan J. (1991) Growth and life cycles of the cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) in South Brittany (France). *Bulletin of Marine Science* 49, 341–348.

Le Goff R., Gauvrit E., Pinczon Du Sel G. and Daguzan J. (1998) Age group determination by analysis of the cuttlebone of the cuttlefish *Sepia officinalis* L. in reproduction in the Bay of Biscay. *Journal of Molluscan Studies* 64, 183–193.

Mangold K. (1966) *Sepia officinalis* de la mer Catalane. *Vie et Milieu – Life & Environment* 17, 961–1012.

Mangold K. (1987) Reproduction. In Boyle P.R. (ed.) *Cephalopod life cycles, Vol. 1. Species accounts.* London: Academic Press, pp. 157–200.

Mangold-Wirz K. (1963) Biologie des céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie et Milieu – Life & Environment* 13, 1–285.

Mc Dougall A. (2004) Assessing the use of sectioned otoliths and other methods to determine the age of the centropomid fish, barramundi (*Lates calcarifer*) (Bloch), using known-age fish. *Fisheries Research* 67, 129–141.

Molfese C., Beare D. and Hall-Spencer J.M. (2014) Overfishing and the replacement of demersal finfish by shellfish: an example from the English Channel. *PLoS ONE*, 9, 1–10. doi: 10.1371/journal.pone.0101506.

Moreno A., Azevedo M., Pereira J.A. and Pierce G.J. (2007) Growth strategies in the squid *Loligo vulgaris* from Portuguese waters. *Marine Biology Research* 3, 49–59.

Moreno A., Morais da Cunha M.M. and Pereira J.M.F. (1994) Population biology of veined squid (*Loligo forbesi*) and European squid (*Loligo vulgaris*) from the Portuguese coast. *Fisheries Research* 21, 71–86.

Moreno A., Pereira J.A. and Morais da Cunha M. (2005) Environmental influences on age and size at maturity of *Loligo vulgaris*. *Aquatic Living Resources* 18, 377–384.

Neige P. (2006) Morphometrics of hard structures in cuttlefish. *Vie et Milieu – Life & Environment* 56, 121–127.

Newman S.J. (2002) Growth rate, age determination, natural mortality and production potential of the scarlet seaperch, *Lutjanus malabaricus* Schneider 1801, off the Pilbara coast of north-western Australia. *Fisheries Research* 58, 215–225.

Olsen E.M., Heino M., Lilly G.R., Morgan M.J., Brattey J., Ernande B. and Dieckmann U. (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428, 932–935.

Pierce G.J., Allcock L., Bruno I., Bustamante P., Gonzalez A.F., Guerra A., Jereb P., Lefkaditou E., Malham S., Moreno A., Pereira J.A., Piatkowski U., Rasero M., Sanchez P., Santos M.B.N., Santurtun M., Seixas S., Sobrino I. and Villanueva R. (2010) Cephalopod biology and fisheries in Europe. *ICES Cooperative Research Report no. 303*, Copenhagen, Denmark.

Pilling G., Grandcourt E.M. and Kirkwood G.P. (2003) The utility of otolith weight as a predictor of age in the emperor *Lethrinus mahsena* and other tropical fish species. *Fisheries Research* 60, 493–506.

Pingree R.D. (1980) Physical oceanography of the Celtic Sea and English Channel. In Banner F.T., Collins M.B. and Massie K.S. (eds) *The North-West European shelf seas: the sea bed and the sea in motion 2. Physical and chemical oceanography, and physical resources*, Vol. 24, Part B. Amsterdam: Elsevier, pp. 415–465.

Portail CHARM III – Interreg IV, © (2012) Atlas des pêcheries de Manche, Channel fisheries atlas. Engelhard G., Vignot C., Leblond E., Lesueur M., Guitton J. (eds) http://charm-project.org/fr/outils/atlas-des-pecheries/atlas-des-pecheries-outils.

Reznick D., Lindbeck E. and Bryga H. (1989) Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* 46, 108–112.

Robin J.-P., Roberts M., Zeidberg L., Bloor I., Rodriguez A., Briceño F., Downey N., Mascaró M., Navarro M., Guerra A., Hofmeister J., Barcellos D.D., Lourenço S.A.P., Roper C.F.E., Moltschaniwskyj N.A., Green C.P. and Mather J. (2014) Transitions during cephalopod life history: the role of habitat, environment, functional morphology and behaviour. *Advances in Marine Biology* 67, 361–437.

Rodhouse P.G., Symon C. and Hatfield E.M.C. (1992) Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Marine Ecology Progress Series* 89, 183–195.

Royer J., Pierce G.J., Foucher E. and Robin J.-P. (2006) The English Channel stock of *Sepia officinalis*: modelling variability in abundance and impact of the fishery. *Fisheries Research* 78, 96–106.

Saulquin B. and Gohin F. (2010) Mean seasonal cycle and evolution of the sea surface temperature from satellite and in situ data in the English Channel for the period 1986–2006. *International Journal of Remote Sensing* 31, 4069–4093.

Sheehy M.R.J., Shelton P.M.J., Wickins J.F., Belchier M. and Gaten E. (1996) Ageing the European lobster *Homarus gammarus* by the lipofuscin in its eyestalk ganglia. *Marine Ecology Progress Series* 143, 99–111.

Shin Y.-J. and Rochet M.-J. (1998) A model for the phenotypic plasticity of North Sea herring growth in relation to trophic conditions. *Aquatic Living Resources* 11, 315–324.

Shin Y.-J., Rochet M.-J., Jennings S., Field J.G. and Gislason H. (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science* 62, 384–396.

Smith P.J. (1994) Genetic diversity of marine fisheries resources. Possible impacts of fishing. *FAO Fisheries Technical Paper no. 344*, Rome, Italy.

Southward A.J., Boalch G.T. and Maddock L. (1988) Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *Journal of the Marine Biological Association of the United Kingdom* 68, 423–445.

Southward A.J. and Roberts E.K. (1987) One hundred years of marine research at Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 67, 465–506.

Wang J., Pierce G.J., Boyle P.R., Denis V., Robin J.-P. and Bellido J.M. (2003) Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences – a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters. *ICES Journal of Marine Science* 60, 1149–1158.

and

Zielinski S. and Portner H.-O. (2000) Oxidative stress and antioxidative defence in cephalopods: a function of metabolic rate or age? *Comparative Biochemistry and Physiology Part B* 125, 147–160.

Correspondence should be addressed to:
M. Gras
BOREA, UMR CNRS 7208, IRD 207, UPMC, MNHN, UCBN, 14032 Caen, France and Université de Caen Basse-Normandie, UMR BOREA: Biologie des ORganismes et des Ecosystèmes Aquatiques, Esplanade de la paix, CS 14032, 14032 Caen, France
email: michael.gras@ymail.com