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

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Abstract :

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.

Keywords : Sepia officinalis, English Channel, life history traits, maturity, warming, fishing pressure

INTRODUCTION

The common cuttlefish, *Sepia officinalis* (Linnaeus, 1758), is a short lived and is a semelparous cephalopod (Mangold, 1987) distributed from the West African coast (Senegal and Mauritania) to the English Channel and in the Mediterranean Sea. It has a life cycle

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lasting between 1 and 2 years depending on the latitude at which it lives. From West African to the Portuguese coasts, the entire population has a 1 year life cycle (Mangold, 1966; Guerra and Castro, 1988; Coelho and Marthins, 1991). The Bay of Biscay is a transition zone where two different groups were identified; Group I Breeding (GIB), can breed at one year of age (45% of male specimens and 20% of female specimens), Group II Breeding (GIIB), breeds at two years of age (Le Goff and Daguzan, 1991; Gauvrit et al., 1997). In the English Channel, life cycle of *S. officinalis* was first described as lasting exclusively two years (Boucaud-Camou and Boismery, 1991; Boucaud-Camou et al., 1991). A decade later, Dunn (1999a) found that the entire female population and 96% of male specimens have a 2 year life cycle (GIIB). The remaining males (4%) were found to be mature at the age of one year old, constituting a GIB.

However, all these studies based age estimation only on polymodal decomposition of length frequencies. In cephalopods, growth rate is influenced by environmental conditions and presents a high inter-individual variability making this method unaccurate. Various hard structures have been tested for age determination in *S. officinalis* (Le Goff et al., 1998) 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 and 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 and Brey, 2001). This method has been successfully used in cephalopods to provide a rough estimation of *S. officinalis* age (Zielinski and Pörtner, 2000; Doubleday and Semmens, 2011).

English Channel population of *Sepia officinalis* was 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) lead French and UK fishers to exploit this stock. Landings increased from 4350 tonnes in 1992 to a maximum of 17400 tonnes in 2004 (Gras et al., 2014). During the 2000-2010 decade, an average of 11000 tonnes was landed annually for an average turnover of €20M (Pierce et al., 2010; Portail CHARM III - Interreg IV, 2012). The English Channel *Sepia officinalis* was assessed in trial using a depletion model (Dunn, 1999b), a Virtual Population Analysis (Royer et al., 2006) and a two-stage biomass model (Gras et al., 2014). If 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 beginnning 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.

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 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 and Rochet, 1998; Engelhard and 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 twentieth century to date, the fishing pressure has increased considerably (Hawkins et al., 2003). According to Guenette and 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 hours 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 and Reid, 2003; Hawkins et al., 2003; Beaugrand, 2009). According to the data collected by the Marine Biological Association of the United Kingdom (MBA), warming of the English Channel has been highlighted throughout the twentieth century (Southward and Roberts, 1987). Between 1986 and 2006, Saulquin and Gohin (2010) estimated this warming between 0.5C in the southern part of the Channel and 1.5C in its northern part. This warming has lead 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 wether 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 if the percentage of one-year old mature males observed by Dunn (1999a) has changed and if a percentage of one-year old mature females exists. To achieve this goal, a two-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 disentangle the two cohorts and estimate the percentage of mature one-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.

MATERIAL AND METHODS

Study area: the English Channel

The English Channel is situated between the N-E Atlantic and the North Sea. Following the International Council for the Exploration of the Sea (ICES) two divisions exist, VIId to the East and VIIe to the West. The western English Channel is characterised by a maximum depth of around 170 m and is strongly influenced by Atlantic waters. With a minimum temperature >10C in winter, this area has favourable conditions for the overwintering of *S. officinalis* (Wang et al., 2003). The eastern English Channel (ICES division VIId) is characterised 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 5C, 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 (Fig. **Erreur ! Source du renvoi introuvable.**). After spending the entire summer feeding inshore, they migrate offshore to overwinter in the central western English Channel (Boucaud-Camou and 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 and Boismery, 1991; Dunn, 1999a; Royer et al., 2006).

Figure **Erreur ! Source du renvoi introuvable.**

Sample collection

Samples of *S. officinalis* were collected from 3 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 April 12 to July 9, 734 specimens (395 males, 339 females) were collected in Erquy, Cherbourg and Port-en-Bessin landing sites. In 2011, from April 5 to June 30, 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.

Biometry dissection and sex determination

The Dorsal Mantle Length (DML) of each specimen was measured to the smallest whole cm and length frequencies were represented on 4 histograms, one per sex and per year. Breaks 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 well the first cohort, due to its shape, it was not possible to fit it to the second cohort. A rough threshold between the first and second cohort is thus 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 on its own to determine which cohort a particular specimen belongs to. The measurement of Lipofuscin (age pigment accumulated in tissues; Zielinski and Pörtner, 2000; Doubleday and 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 until analysis to avoid tissue degradation and transported to the laboratory to be analysed.

Lipofuscin measurement

Lipofuscin was measured according to Zielinski and Pörtner (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 2000g, 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 and Womersley (1991), using 0.1 µg quinine per ml 1N HSO 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 2 subsamples. A subsample of 11 immature specimens was taken from the first cohort (DML ranging 10-13 cm and assumed to be one-year olds as they are immature) and a subsample of 17 mature specimens was taken from group which length is highly over the boundary between the two cohorts (DML ranging 20-31 cm and therefore assumed to be two-year olds). This experiment describes inter-cohort differences in lipofuscin concentrations. Finally, results of lipofuscin concentration measured from the smallest mature specimens (2 of 11 cm DML and 1 of 13 cm DML) were used in a Student 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. A Student test was used to show if GSI varies from one year to another, if differences exist between immature and mature animals and between mature males and females. A F-test was used to highlight differences between GSI variances of mature males and females. Finally, a linear model was used to explore the correlation between mature males 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 (Fig. **Erreur ! Source du renvoi introuvable.**). 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 cm 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.

Figure **Erreur ! Source du renvoi introuvable.**

Size-at-maturity determined using a binomial error GLM

For both sexes, the size-at-maturity (Fig. **Erreur ! Source du renvoi introuvable.**) 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 found to occur.

Figure **Erreur ! Source du renvoi introuvable.**

Variability in lipofuscin measurement and age estimation

Lipofuscin measurement from the first experiment (Fig. **Erreur ! Source du renvoi introuvable.**) showed that, over a period of three 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 (Fig. **Erreur ! Source du renvoi introuvable.**). Results of the lipofuscin measurement performed on the 3 small mature males (Fig. **Erreur ! Source du renvoi introuvable.**, Table 1) highlighted that lipofuscin accumulation of these 3 specimens was not significantly different from the first cohort, but was significantly different from lipofuscin accumulation measured in GIIB. These 3 specimens could thus be considered as part of the GIB group.

Figure **Erreur ! Source du renvoi introuvable.**

Figure **Erreur ! Source du renvoi introuvable.**

Table 1

Gonado-Somatic Index

The GSI (Fig. **Erreur ! Source du renvoi introuvable.**) for each sex and each year, does not reveal inter-annual significant differences. For both sexes, the GSI during the reproduction period was significantly higher for mature specimens than for immatures. Mature female specimens were characterised 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.

Figure **Erreur ! Source du renvoi introuvable.**

DISCUSSION

The life cycle of *S. officinalis* population in the English Channel was described in the past as lasting two years for females and the large majority of males (Boucaud-Camou et al., 1991; Dunn, 1999a). The present study highlights that, during 2010 and 2011 reproduction seasons, a variable percentage of mature male and female *S. officinalis* belongs to the first cohort and could be considered as a GIB. Age determination was based on polymodal decomposition and adaption of lipofuscin measurement protocol (Zielinski and Pörtner, 2000; Doubleday and Semmens, 2011). Both associated methods give more accurate than the polymodal decomposition used alone in previous studies and enabled to disentangle the two sampled cohorts. It has corroborated that the smallest mature animals observed are most likely one year old *S. officinalis* and not small two years olds. Finally, the GSI illustrates the amount of energy dedicated by each sex 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 and Pörtner, 2000; Doubleday and Semmens, 2011). Moreover, accuracy decreases with increasing time between death and sampling; as the sampling process was based on commercial fishery landings, this parameter is 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 one year old *S. officinalis*

(Bettencourt and 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 and 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 and the sporadic presence of immature females belonging to the second cohort could be explained by food availability experienced by each specimen. In male specimens, the lower amount of energy dedicated to the reproduction lets more energy to 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 (Coelho et al., 1994; Moreno et al., 1994; Boyle and Rodhouse, 2005). Finally, the English Channel warming (Hawkins et al., 2003; Saulquin and 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 and Pierce, 1994). An increase in environmental temperature generally accelerates the somatic growth of cephalopod, shortening the life cycle duration by accelerating maturation (Moreno 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, 1966; Guerra and Castro, 1988; Coelho and Marthins, 1991). The warming of the English Channel (Hawkins et al., 2003; Saulquin and Gohin, 2010) could be the cause of appearance of a GIB made 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 wether GIB is actually involved in reproduction by analysing the sperm reservoirs of female to understand wether 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 *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 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 twentieth century (Hawkins et al., 2003; Guenette and 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 and Rochet, 1998; Grift et al., 2003; Engelhard and Heino, 2004; Olsen et al., 2004) and could also have influenced the English Channel population of *S. officinalis*, which is fully exploited since the beginning 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 modify the prey availability for cuttlefish. Maturation efficiency in cephalopods, which are unable to store energy in their tissue (Mangold, 1987; Moreno et al., 2005) could therefore be impacted.

S. officinalis is one of the top predators of the English Channel ecosystem. 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. (2000), an indicator of climate change must meet 4 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), 2 scientific bottom trawl surveys sample it each year (Carpentier et al., 2009) 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 under the framework of the Data Collection Framework (DCF) programme. *S. officinalis* therefore meets the 4 criteria listed above and should be considered as an indicator for environmental shift.

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Table 1: Probabilities of 3 small male mature specimens to be different from the GIB and GIIB cohorts.

Specimens	Length (cm)	P-value, GIB	P-value, 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

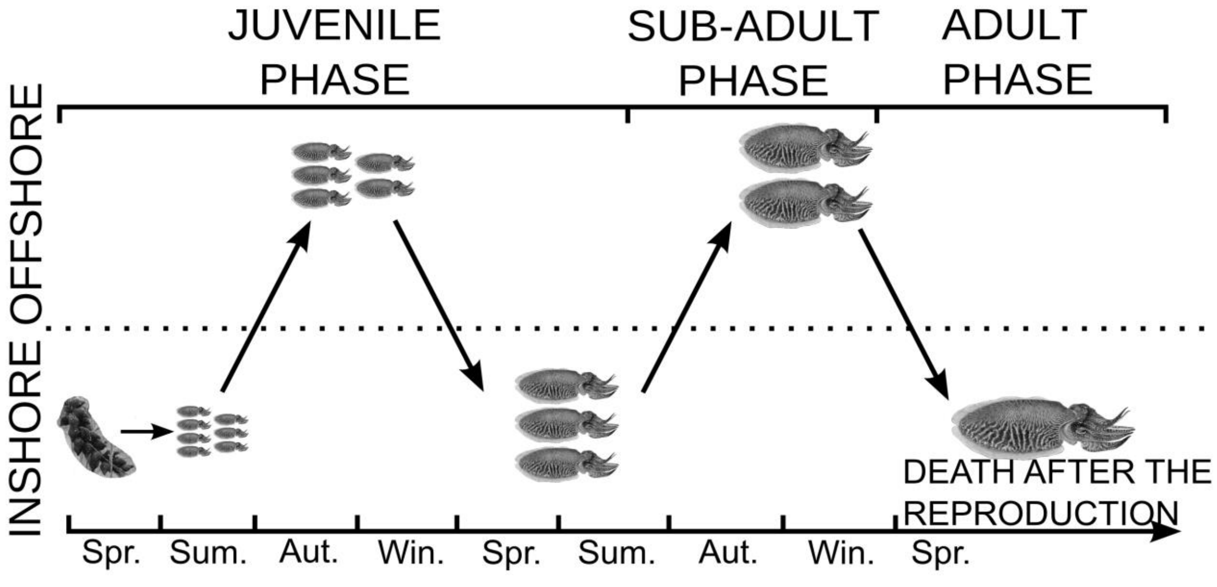

Figure 1: Life cycle of the English Channel population of *S. officinalis S. officinalis* L. as described by Boucaud-Camou and Boismery (1991), Boucaud-Camou et al. (1991) and Dunn (1999a).

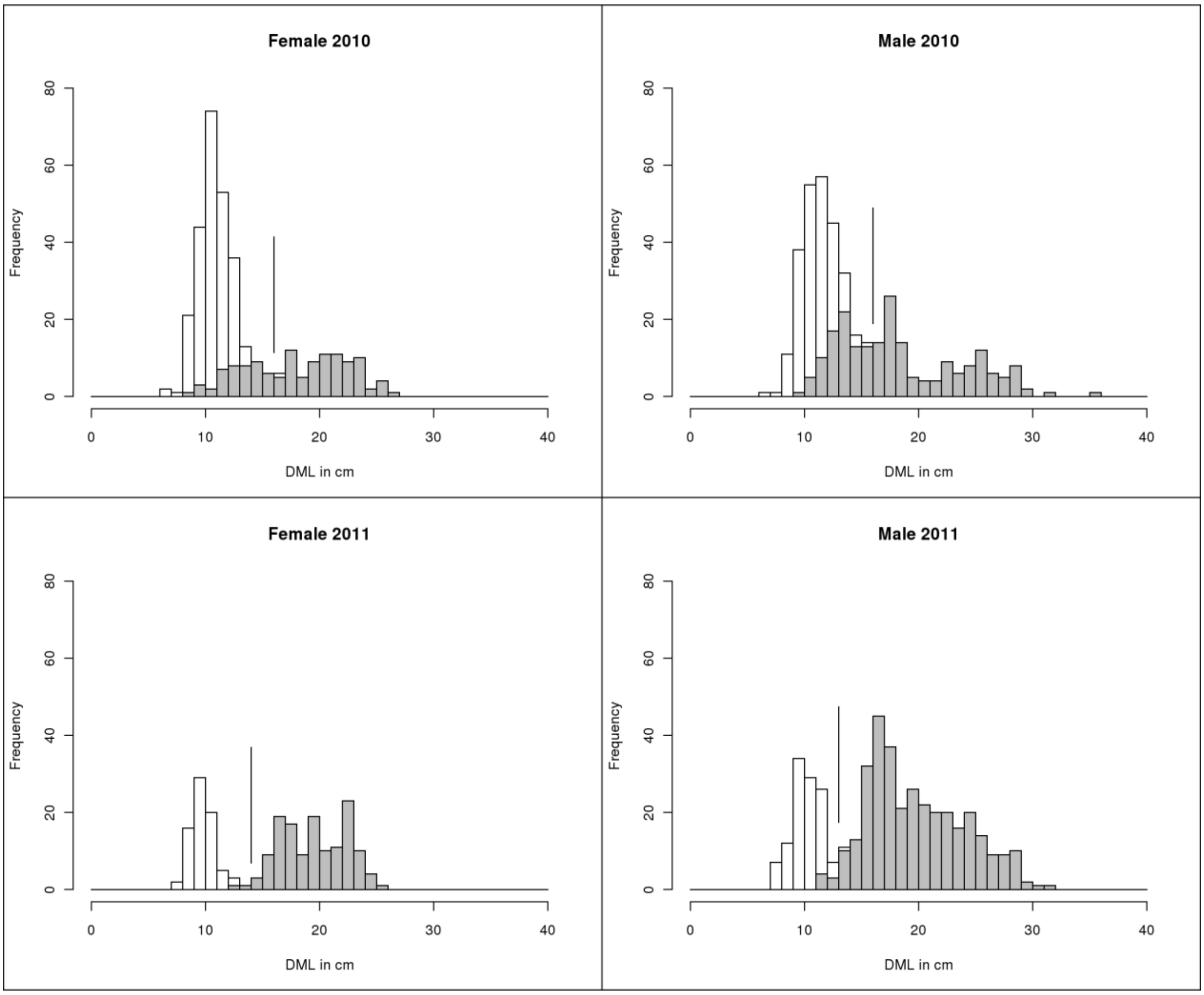

Figure 2: Length frequencies of the female and male samples collected during springs 2010 and 2011 in French English Channel landing sites. Immature specimens are displayed in white and mature specimens are displayed in grey. The vertical line drawn

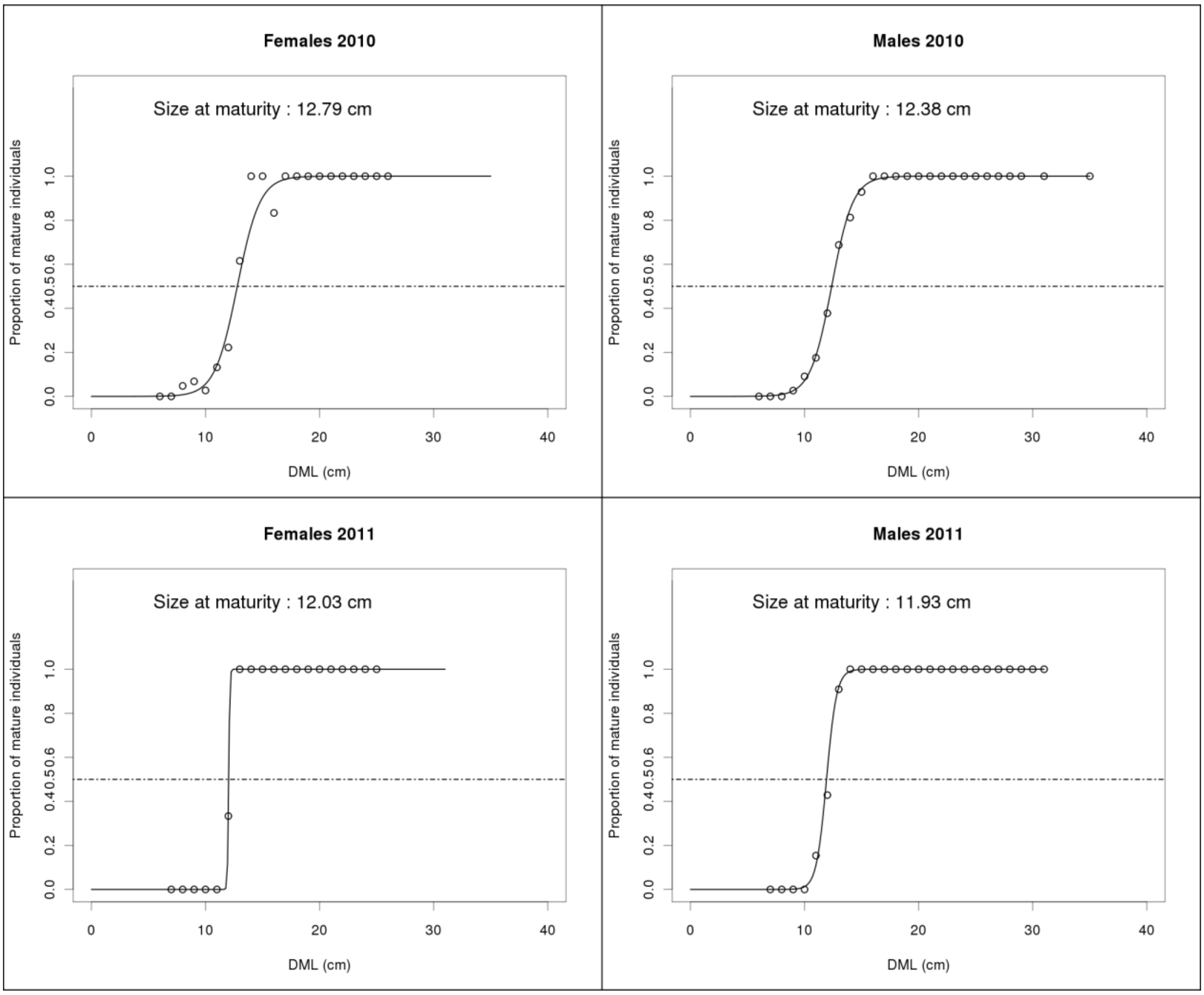

Figure 3: Size-at-maturity determined using a binomial error GLM for female and male samples collected during springs 2010 and 2011 in French English Channel landing sites. The 95% confidence interval of the fitted binomial error GLM is displayed with dashed lines. Number of specimens measured per DML class is pointed out in the figure **Erreur ! Source du renvoi introuvable.**

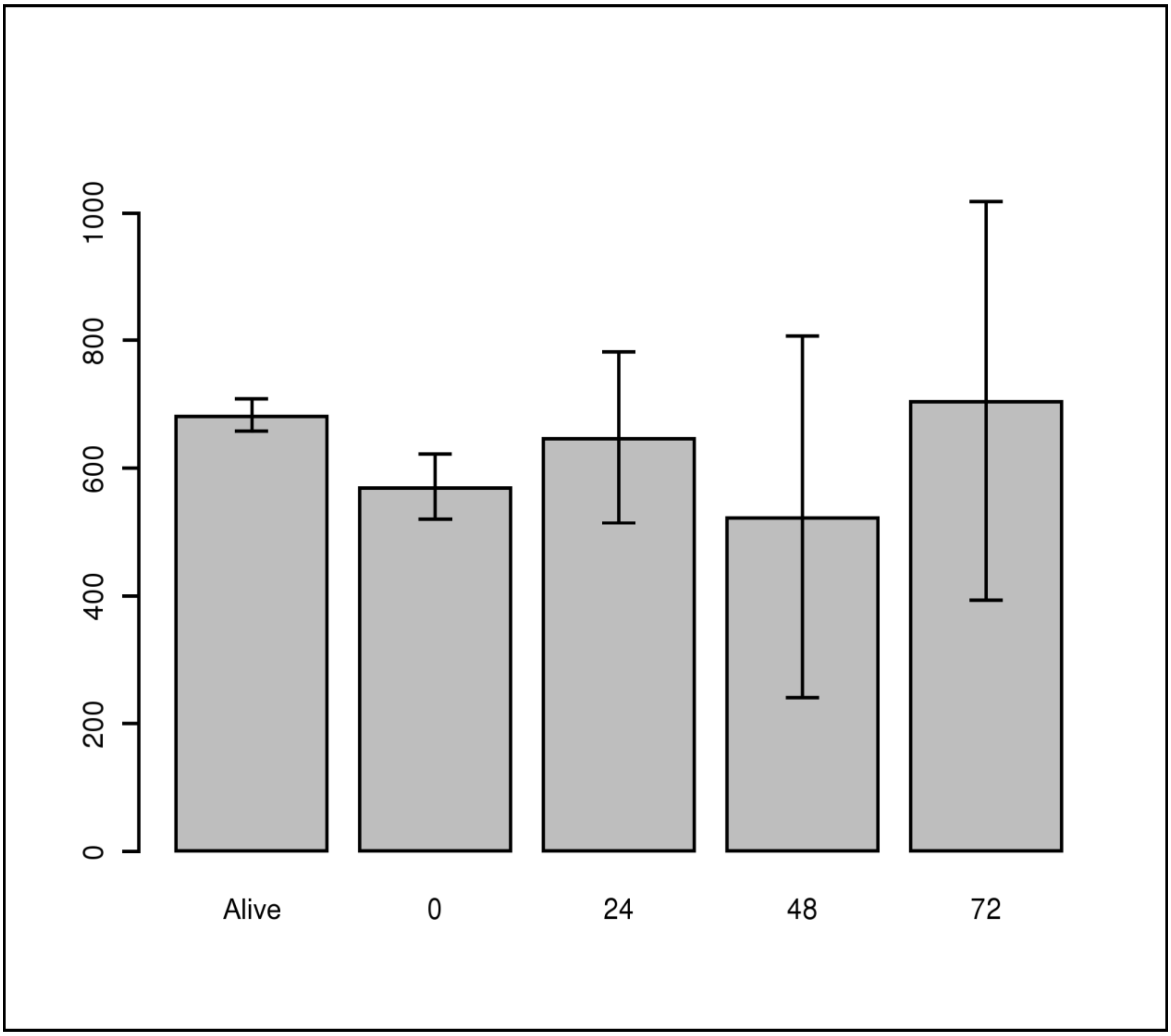

Figure 4: Trend in lipofuscin concentration measured in the mantle sampled on one living *S. officinalis* from the death and every 24 hours until 72 hours after the death. Error bars are the standard deviations of each measure. Number of measures performed at each time step is mentioned between brackets.

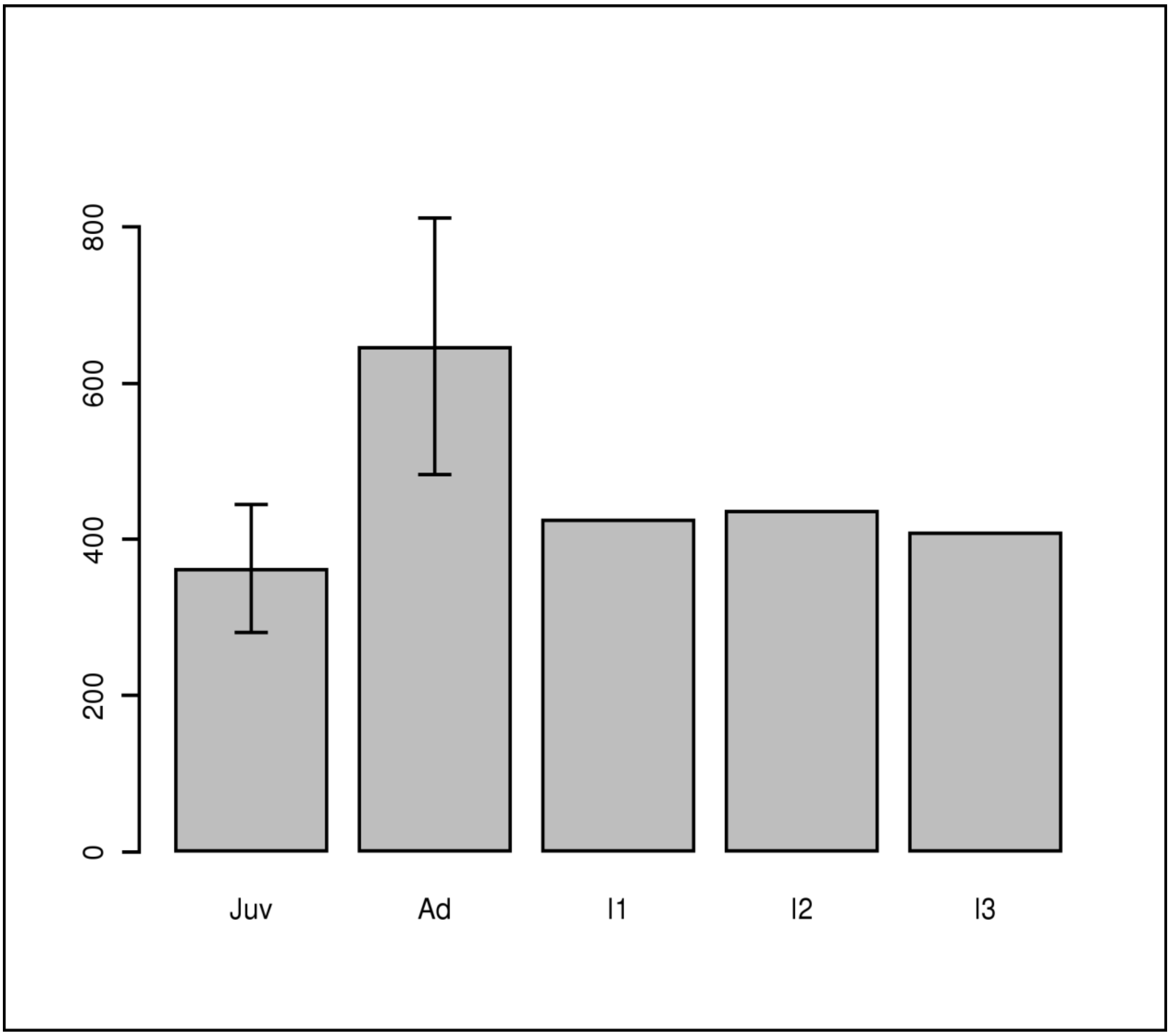

Figure 5: Lipofuscin concentration measured in *S. officinalis* mantles for juveniles (Juv, 11 specimens, ranging 10-13 cm DML), Adults (Ad, 17 specimens, ranging 20-31 cm DML) with the inter-individual standard deviation and lipofuscin concentration measured in 3 small mature specimens (I1, 11 cm DML; I2 11 cm DML; I3, 13 cm DML).

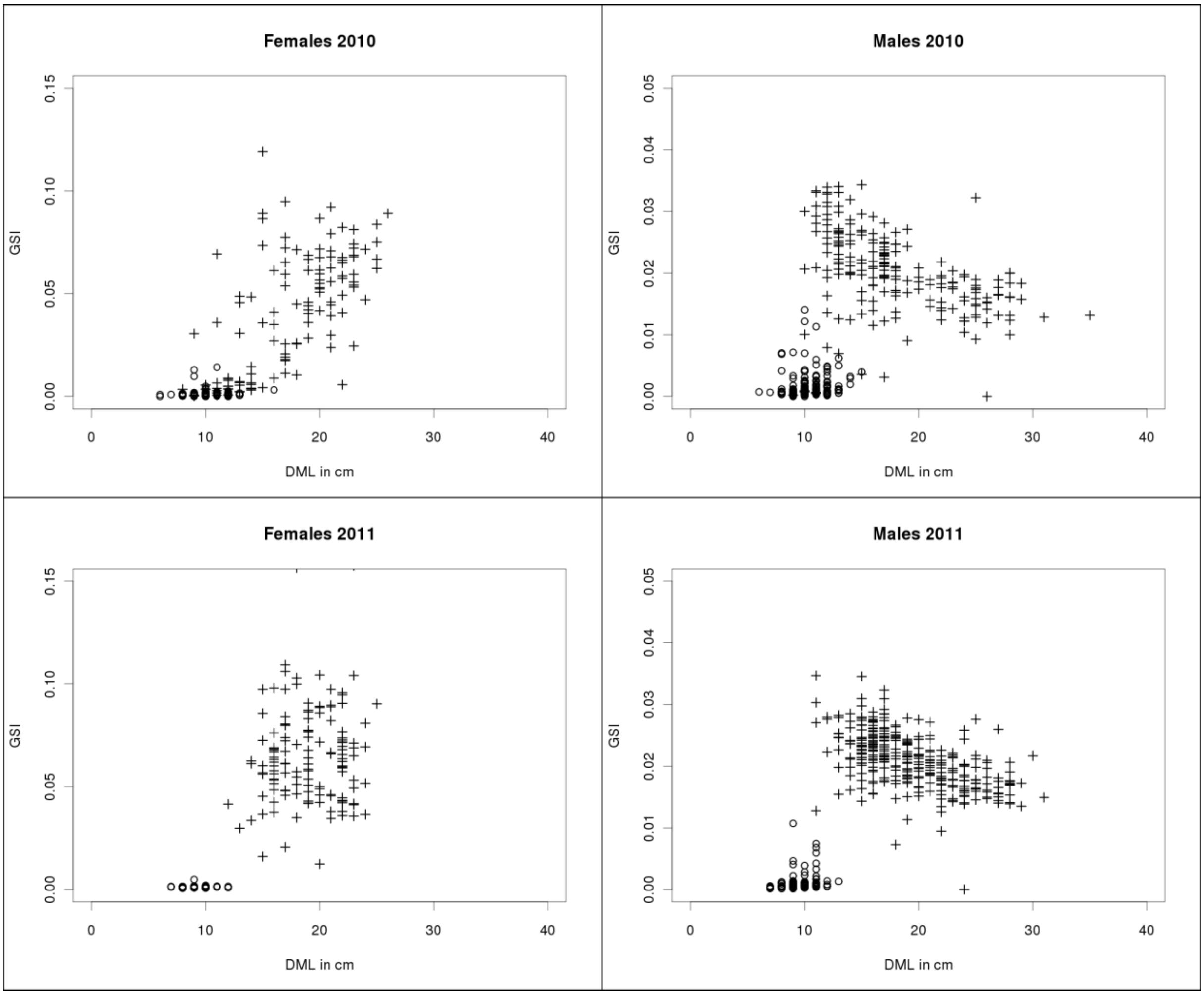

Figure 6: Gonado Somatic Index (GSI) vs Dorsal Mantle Length (DML) for female and male samples collected during springs 2010 and 2011 in French English Channel landing sites. Immature specimens are displayed with circles while mature specimens are displayed with crosses.