Trends in age-at-recruitment and juvenile growth of cuttlefish, *Sepia officinalis*, from the English Channel

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The cuttlefish *Sepia officinalis* is an important fishery resource in the English Channel, and one of the largest stocks of cephalopods in the Northeast Atlantic. Cuttlefish live for approximately 2 years and catches consequently depend largely on recruitment. Early life stages were analysed for differences in juvenile growth and age-at-recruitment to the commercial fisheries. Recruits were sampled monthly between October 2000 and June 2003, and pre-recruits from the coastal waters of the UK and France in the summers of 2000 and 2002. Age (days) was determined from statoliths. Although most cuttlefish were recruited during autumn, there was some recruitment throughout the year. Age-at-recruitment varied significantly between season and cohort, but was consistently in the range 3–4 months, so although there was some hatching throughout the year, most cuttlefish hatched during summer. Fitted growth models indicated that the growth rates of pre-recruits (7–59 mm mantle length) were significantly higher in 2002 than in 2000. Spatial differences in growth rate were apparent in 2000, suggesting that pre-recruit growth may depend on local environmental conditions. Pre-recruits and recruits combined (7–106 mm mantle length) also showed significant variation in growth between hatching months and years. Hypotheses explaining the observed patterns of growth and recruitment are presented.

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Introduction

The common cuttlefish *Sepia officinalis* (Linnaeus, 1758) is widely distributed in eastern Atlantic Shelf waters (Boletzky, 1983). The English Channel (ICES Divisions VIId and VIIe) fishery is one of the largest fisheries for cephalopods in the eastern Atlantic. Reported annual landings more than tripled over the past decade, reaching approximately 15 000 t in 2002 (Anon., 2003). However, there are few regulations controlling fishing activity on the stock, and to date only preliminary stock assessments using depletion methods or cohort analysis (Dunn, 1999; Royer et al., 2002) to determine biomass trends and yields have been conducted.

Age studies are fundamental to understanding key aspects of stock dynamics such as growth, recruitment, and longevity (Begg *et al.*, 1999; Rodhouse, 2001). However, few data on age and growth are available for *S. officinalis* from the English Channel. These have been derived either from modal progression analysis using length frequency data (Medhioub, 1986; Dunn, 1999), or from preliminary studies using statoliths (Challier *et al.*, 2002). Even if clear length modes are apparent, the first method may be inaccurate if the length modes contain multiple cohorts, which could result from extended hatching periods (Jackson *et al.*, 1997, 2000). The use of statoliths to determine age is considered the most accurate method for determining age of cephalopods (Arkhipkin, 1991). The "one-day-one-ring" hypothesis has been validated for statoliths from several squid and sepioid species using chemical marking techniques or experimental rearing of animals of known age (Rodhouse and Hatfield, 1990;
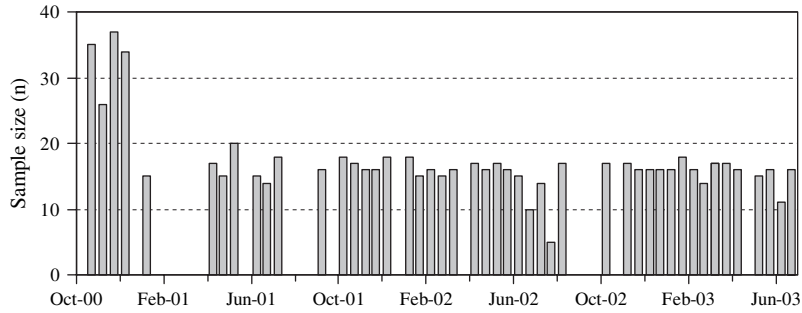
Figure 1. Distribution of samples of *S. officinalis* recruits from the English Channel (n = 820).

Jackson, 1994; Durholtz *et al.*, 2002). Experimental rearing has validated daily increments in the statoliths of *S. officinalis* up to an age of 240 days (Bettencourt and Guerra, 2001). Estimates of age and growth for wild populations in the English Channel have only been obtained from statoliths of juveniles (53−90 mm mantle length) caught between August and December 2000 (Challier *et al.*, 2002). A maximum age of 160 days was obtained from those specimens, and Challier *et al.* (2002) concluded that the peak hatching period for animals recruiting in autumn was between June and August. The results also indicated that early-hatched cuttlefish grew faster than those hatched later in summer.

S. officinalis spawn in the English Channel from spring to midsummer, and most eggs hatch in summer, along both the north and south coasts (Medhioub, 1986; Boucaud-Camou and Boismery, 1991; Dunn, 1999; Royer, 2002; Wang *et al.*, 2003). The main period of recruitment is autumn, but it is highly variable, annual estimates ranging from 31 to 74 million young cuttlefish over the period 1995−2002 (Royer, 2002). Temporal or geographic variation in growth during the juvenile phase could explain some of the variability in the rate at which *S. officinalis* recruit to the fishery, as found for the *Loligo forbesi* squid fishery in the English Channel (Challier *et al.*, in press). Such variation has been attributed to the effects of temperature and growth on survival during the early life phases (Waluda *et al.*, 1999, 2001).

This study provides new estimates of the age and growth of juvenile *S. officinalis* in the English Channel. Age-at-recruitment is examined for three cohorts, and we test the hypothesis that growth of early life stages varies between hatching grounds and years. Individual growth variability is also considered at a cohort and a micro-cohort scale, to assess temporal differences in growth during the juvenile phase.
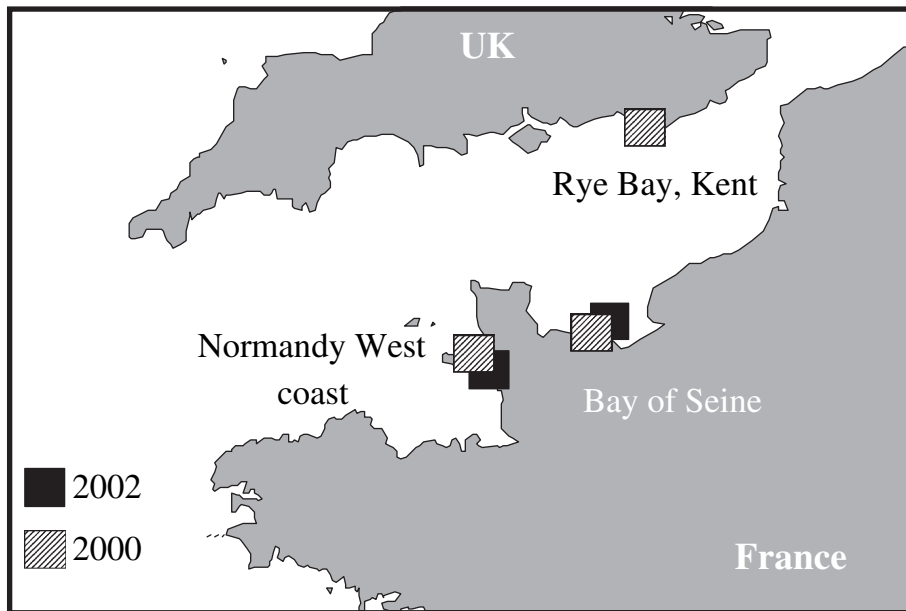

Figure 2. Map of the English Channel (Northeast Atlantic) showing sampling locations where early stages of *S. officinalis* were collected in 2000 and 2002.
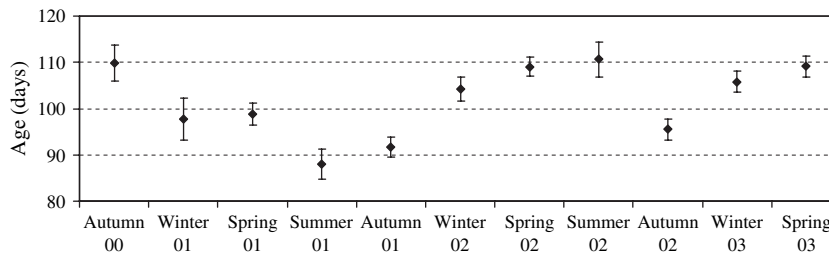
Figure 3. Seasonal change in the mean age of *S. officinalis* recruits caught in the English Channel, with 95% confidence intervals. Autumn, October–December; winter, January–March; spring, April–June; summer, July–September.

Material and methods

Sampling

Fishery statistics describing the commercial landings of recruiting cuttlefish at the port of Port-en-Bessin (Bay of Seine, France) were obtained from the Centre Administratif des Affaires Maritimes (CAAM). Recruits were defined as those animals in the smallest commercial category, with body weight <100 g. The weight of recruits as a percentage of the total catch ranged from 0.01% to 35%. Sampling was conducted following Challier *et al.* (2002). Recruits were sampled every 2 weeks between October 2000 and June 2003, from the fish market at Port-en-Bessin, approximately 17 animals being collected in each sampling interval (Figure 1). Pre-recruits were sampled during coastal research trawl surveys in three different areas: the Bay of Seine (113 animals), the Normandy west coast (62), and Rye Bay (31; Figure 2). Samples were collected at all three sites in summer 2000, and at the two southern (French) sites in 2002. In 2000, the samples from the Normandy west coast and Rye Bay just represent a snapshot, because they were taken during a 2-week period in September. Samples from the Normandy west coast in 2002 and the Bay of Seine were more representative, samples being taken weekly over summer (June to September). Surveys were carried out using fine-mesh trawls (20-mm stretched mesh) at depths between 1 and 8 m. The duration of each tow was approximately 10 min. Measurements of dorsal mantle length (DML, mm) and wet (live) body weight (g) were recorded for each animal, and the statoliths removed following Lipiński (1986) and preserved in 95% ethanol. Sex was not considered because the animals sampled were all immature. The length range of the pre-recruits varied between 7 and 59 mm DML, and that of recruits (animals <100 g) between 43 and 106 mm DML.

Statolith analysis

Statoliths were mounted and ground following Challier *et al.* (2002). Growth increments were examined using an image-analysis system comprising a video camera mounted on a light microscope (×40) and connected to a computerized image-capture system using advanced software (Aphelion, ADCIS and T.N.P.C©: Calcified Structure Digital Processing, Noesis). A series of images of the lateral dome of each statolith was recorded, lighting and contrast were optimized, and the images were automatically assembled into montages. Daily increments extending from the natal ring to the edge of the lateral dome were counted along a single straight transect using an extraction of grey-level peaks approach (T.N.P.C©). Poor preparation accounted for 25% of the total number of statoliths analysed, and in many cases (some 80% of the 1026 readable statoliths), increments were not visible at the edge of the dome. Where this was the case, the number of increments was extrapolated using the widths of the increments immediately adjacent. The average number of increments within a statolith estimated using this approach was ten (or 8% of the total number of increments), with a maximum of 18. Each statolith was read once by the same observer (Challier *et al.*, 2002).

Table 1. Two-way analysis of variance and Student Newman–Keuls test for age variations by period of recruitment for all cohorts. The term "Other seasons" refers to recruits caught in winter, spring, and summer. In statistical groups, homogeneous groups are sets of data with similar statistical characteristics, visualized by close X values in the table.

Factors	d.f.	SS	F-ratio	p
Season	1	6 229.9	36.7	***
Cohort	2	3 463.1	10.2	***
Cohort × season	2	27 446.3	80.9	***
Total	832	180 943.0		

SNK test	Count	Mean	Statistical groups		
Cohort					
2000	231	104.2			X
2001	338	99.2	X		
2002	264	101.4		X	
Season					
Autumn	356	98.7	X		
Other seasons	477	104.4			X

SS: Sum of Squares.
***p < 0.001.

Table 2. Multiple comparison test (Student Newman—Keuls) for age variation by periods of recruitment for all cohorts. The term "Other seasons" refers to recruits caught in winter, spring, and summer. In statistical groups, homogeneous groups are sets of data with similar statistical characteristics, visualized by close X values in the table.

Factors	Count	Mean	Statistical groups		
2000 Autumn	135	109.9			X
Other seasons	96	98.6		X	
2001 Autumn	141	90.9	X		
Other seasons	197	107.4			X
2002 Autumn	80	95.4	X		
Other seasons	184	107.3			X

Data analysis

Increments were similar in appearance to those in Figure 2 of Bettencourt and Guerra (2001), so counts were assumed to represent age in days. The mean age-at-recruitment was estimated for each season and for the three cohorts recruiting in autumn of 2000, 2001, and 2002. Differences were tested using two-way ANOVA, assuming homogeneous variance and normality for residuals. Where the tests were significant, Student Newman—Keuls multiple comparisons tests were used to test for significant differences between seasons within each cohort, and within seasons between the three cohorts.

Models of growth variation were initially tested on pre-recruiting cuttlefish (<59 mm DML) of the 2000 and 2002 cohorts. Exponential models were fitted by applying linear models to log-transformed length-at-age data. The linear model had the form

$$L_{i,f} = (\alpha_a + \delta_{a,f}) A_{i,f} + (\beta_0 + \gamma_f) \qquad (1)$$

where $L_{i,f}$ is the dorsal mantle length (DML, mm) of a cuttlefish in age class i among those that hatched in year/area f, and $A_{i,f}$ is the age of that cuttlefish (in days).

Estimated parameters are the growth rate ($\alpha_a + \delta_{a,f}$), which is the combination of α_a, reference growth rate, and $\delta_{a,f}$, the influence of year/area on growth rate, the theoretical hatchling length ($\beta_0 + \gamma_f$) (or the origin ordinate), which combines β_0 (reference hatch length) and γ_f (the influence of year/area on hatch length). The interpretation of the intercept as hatch size assumes exponential growth after hatching.

Growth variations were also investigated for juveniles of the 2000 and 2002 cohorts using pre-recruits and recruits combined ($7-106$ mm DML). Linear, exponential, and sigmoidal growth models were fitted, because the general pattern of juvenile growth is linear (Medhioub, 1986; Challier *et al.*, 2002) or sigmoidal (Richard, 1971; Boletzky, 1979; Forsythe and Van Heukelem, 1987). Residual plots were used to determine which model provided the best fit to the data (Quinn and Keough, 2002). Interannual differences in growth using the linear or exponential models were tested using Equation (1). Differences using the sigmoidal growth model were tested after fitting logistic curves of the form

$$L_i = \frac{L_\infty}{1 + \exp^{-k(A_i - A_{50})}} \qquad (2)$$

with $L_0 = \dfrac{L_\infty}{-1 + \exp^{(kA_{50})}}$

where L_i is the DML (mm) of a cuttlefish in age class i, A_i is the age of that cuttlefish (in days), and L_0 is the hatching length (in mm). Estimated parameters are the asymptotic length L_∞, the relative growth rate k, and the inflection point A_{50} (in days) of the curve (i.e. the age corresponding to the length at 50% of L_∞). The influence of the factor "year" on the regression coefficients (L_∞, k, and A_{50}) was then tested using a non-linear model with mixed effects. This is a non-linear regression model with a mixture of
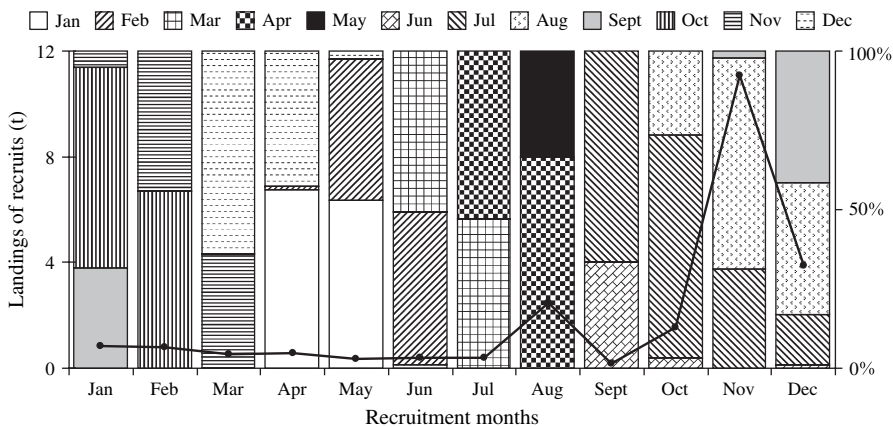

Figure 4. The hatch month for *S. officinalis* in the English Channel, plotted by recruitment month (n = 820). The solid line indicates the monthly landings of recruits (<100 g) at Port-en-Bessin. Data were averaged for the period 2000–2003.
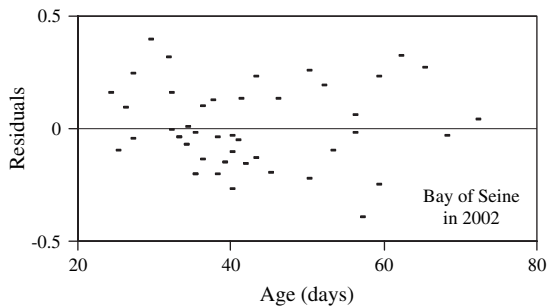
Figure 5. Example residual plot for the exponential growth model applied to *S. officinalis* of <59 mm DML.

fixed and random factors, but it is the fixed factor that is of interest. A factor is random if the effects associated with the levels of the factor are viewed as a random sample from a population of effects. Parameters can be in both sets, and in this case both fixed and random factors were set as "year".

Logistic growth models were used to examine the differences in growth of micro-cohorts, each micro-cohort being defined as cuttlefish hatched in the same month. Hatching month was back-calculated from the capture date using the age estimate obtained from statolith analysis (Challier *et al.*, 2002). Differences in micro-cohort growth were tested both within and between each cohort. A comparison of fitted logistic growth curves was evaluated globally using the residual sum of squares and mean square errors, through an F distribution according to the "extra sum of squares principle" described by Arkhipkin *et al.* (2000) and Markaida *et al.* (2004).

Linear and non-linear modelling techniques and analysis of variance were computed with the "lm" (linear modelling), "nls" (non-linear least squares), and "nlme"

(non-linear mixed effects model) procedures implemented in S-plus (MathSoft Inc.). The "lm" procedure, equivalent to the analysis of covariance, was used to test for significant differences between the fitted linear models, with comparisons between origin ordinates and between slopes.

Results

Age-at-recruitment

The mean age of recruits sampled between autumn (October) 2000 and spring (June) 2003 varied between 88 and 110 days (Figure 3). A decreasing trend in mean age-at-recruitment over the period autumn to summer was apparent in the 2000 cohort. In contrast, an increasing trend was apparent over the same period in the subsequent two cohorts. The age-at-recruitment was significantly different between cohorts and seasons (Table 1). Cuttlefish that recruited in autumn 2001 and 2002 were younger (90.9 and 95.4 days, respectively) than those recruited in other seasons (approximately 107 days), whereas those that recruited in autumn 2000 were older (109.9 days) than in other seasons (98.6 days; Table 2). The monthly catches revealed some recruitment throughout the year, but with a clear peak in autumn (Figure 4). Despite significant temporal differences in the age-at-recruitment, recruits were some 3−4 months old throughout the year.

Hatching period and variation in early growth

Hatching took place throughout the year, but most animals hatched in summer (July and August) and recruited to the fishery in the following autumn (Figure 4). Opportunistic samples taken during summer were removed from this analysis to avoid a seasonal bias in sample size.

Table 3. Spatial and interannual growth comparisons for *S. officinalis* using model (1), giving estimated linear regression coefficients and statistics for three areas of the English Channel in 2000 and 2002.

Year	Area	n	r^2	Growth rate (d^{-1})	p	Hatch length (mm)	p
Spatial growth variation							
2000	Bay of Seine	66	0.34	0.0188	*	2.065	*
	Normandy west coast	15	0.55	0.0295		1.417	
	Rye Bay	31	0.69	0.0337		1.431	
2002	Bay of Seine	47	0.82	0.0328	*	1.353	*
	Normandy west coast	62	0.55	0.0294		1.679	
Interannual growth variation							
2000	Bay of Seine	66	0.34	0.0188	***	2.065	***
2002		47	0.82	0.0328		1.353	
2000	Normandy west coast	15	0.55	0.0295	—	1.417	—
2002		62	0.55	0.0294		1.679	

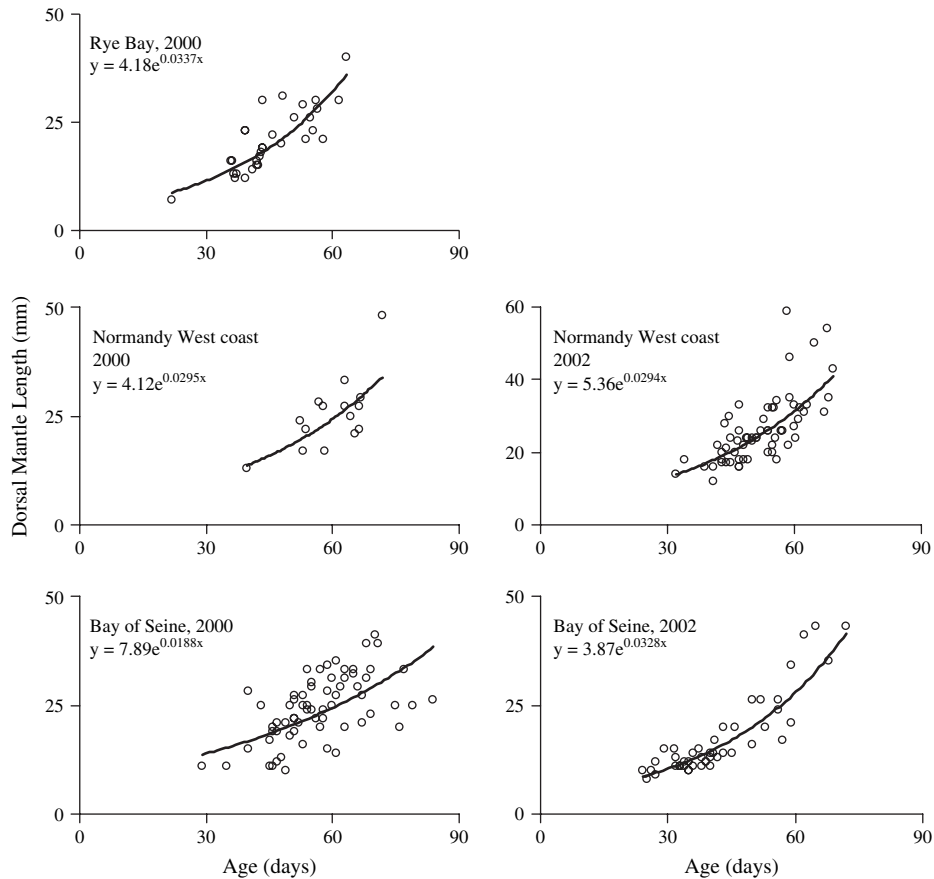***p < 0.001, *p < 0.05, — not significant.

Figure 6. Exponential models fitted to estimated age (days) and DML (mm) for *S. officinalis* from the English Channel, by area and year.

The exponential growth model was considered appropriate for small cuttlefish owing to the random scatter of residuals shown in Figure 5. Growth rates differed significantly between the Bay of Seine and the UK coast in 2000, and between the Bay of Seine and the Normandy west coast in 2002 (Table 3). Growth rates were also significantly different between years for the Bay of Seine, but not for the Normandy west coast (Table 3). Length-at-age for all years and areas (Figure 6) demonstrated that the instantaneous growth rate in 2000 was higher along the UK coast than along the French coast ($0.0337 \ d^{-1}$ in Rye Bay, $0.0295 \ d^{-1}$, and $0.0188 \ d^{-1}$ on the Normandy west coast and in the Bay of Seine, respectively).

Interannual growth

The UK samples were excluded from this analysis because of significant differences in early growth rates between the north and the south English Channel in 2000 (Table 3). Residuals from the exponential growth model for the 2002 cohort suggested that this model was appropriate for smaller cuttlefish, but the relatively limited dispersion and the decreasing variance indicated that the model was less

suitable for larger cuttlefish (Figure 7a). The pattern of residuals for the linear and logistic models suggested that these were more appropriate, but the length-at-age relationships were best described by the logistic growth function (Figure 7b, c), with r^2 highest for the logistic models (Table 4). There were significant differences between the fitted logistic growth models (Figure 8) between years (Table 4). The inflexion points were at about 67 days after hatching in both years, but the asymptotic lengths and relative growth rates differed significantly, indicating a slower growth of the 2000 cohort than that of 2002. Linear growth models (Table 4) also indicated a significant difference in growth rates between years, with faster growth in 2002 ($0.97 \ mm \ d^{-1}$).

Micro-cohort growth variation in juveniles

In order to study micro-cohort growth variations for juvenile cuttlefish, the pre-recruit samples from summer trawl surveys, and the recruit samples from commercial landings were combined. Although the hatching period extended throughout the year (Figure 4), samples of pre-recruits ($<59 \ mm$ DML) were only collected during
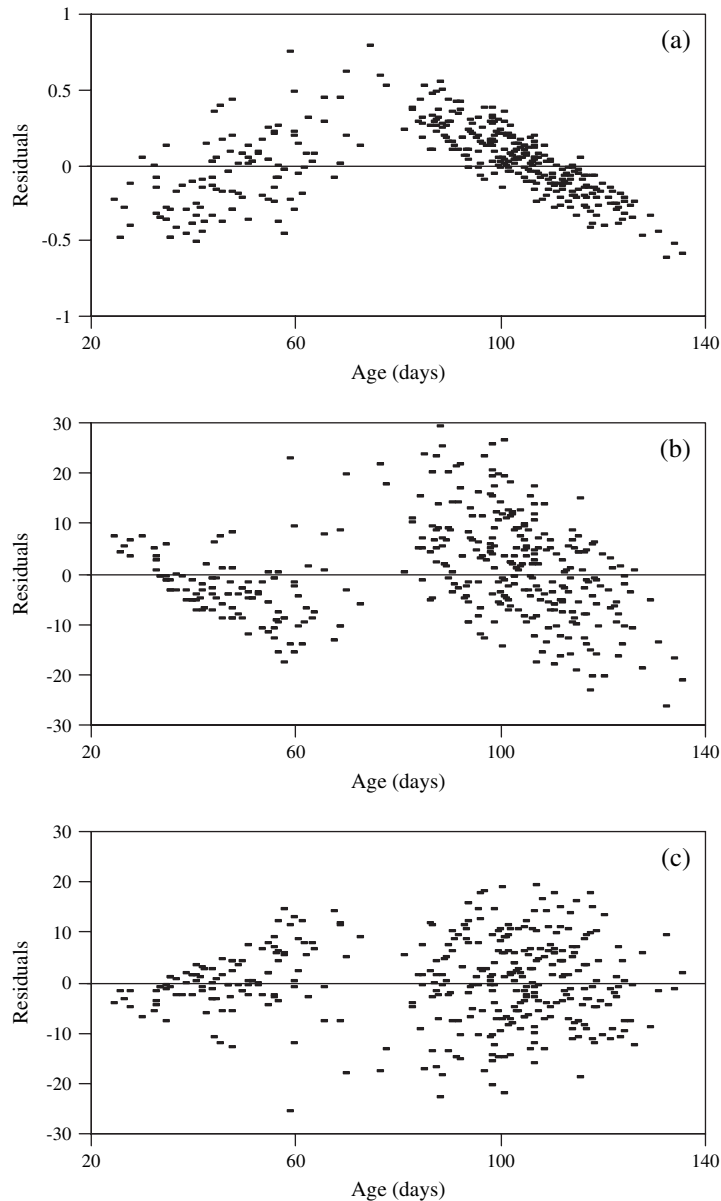
Figure 7. Example residual plots for (a) exponential, (b) linear, and (c) logistic growth models fitted to juvenile *S. officinalis*.

summer of 2000 and 2002. Growth comparisons between micro-cohorts from those years were only possible for months in which cuttlefish from all cohorts hatched, and for those months where the size range of cuttlefish was comparable. Therefore, comparisons were restricted to samples from June, July, and August. The logistic models (Figure 9) fitted to juvenile cuttlefish had similar trends in asymptotic length and relative growth rate over the 2 years, with the highest relative growth rate evident in August. The F-ratio indicated that the growth of cuttlefish in June, July, and August was significantly different between both years,

with consistently faster growth and greater asymptotic length in 2002 than in 2000 (Table 5). The timing of the reduction in growth rate (i.e. the inflexion point) differed by 6−9 days, and was at a smaller size in 2000 (June 2000, 45 mm DML; June 2002, 55 mm DML; July 2000, 40 mm DML; July 2002, 43 mm DML; August 2000, 37 mm DML; August 2002, 39 mm DML). The growth of micro-cohorts was also significantly different within each year, with an increasing relative growth rate and a decreasing asymptotic size from June to August (Table 6). In both years of the analysis, some juveniles reached the

Table 4. Interannual growth comparison for *S. officinalis* from 2000 and 2002 using models (1) and (2), giving estimated regression coefficients and statistics.

Logistic growth model

Year	n	r^2	L_∞	p	k	p	A_{50}	p	L_0
2000	326	0.85	82.05		0.086		66.95		0.3
2002	374	0.93	92.13	***	0.061	***	67.78	—	1.5

Linear growth model

Year	n	r^2	Growth rate $(mm\,d^{-1})$	p	Hatch length (mm)	p
2000	326	0.59	0.72		−3.3	
2002	374	0.88	0.97	***	−20.6	***

***p < 0.001.

asymptotic size before others. This may indicate that growth slows as an individual approaches the asymptotic size, whatever the time of year. However, it could also be an artefact caused by selectivity of the commercial category from which the samples were obtained.

Discussion

Sepia officinalis spend winter in the deeper water at the western end of the English Channel, then migrate inshore during spring, when the adults spawn and the juveniles undergo early maturation (Boucaud-Camou and Boismery, 1991; Dunn, 1999). Growth patterns are likely to be similar for animals while they are aggregated in the western English Channel during winter, but could vary when they are dispersed in coastal waters. Our results show that juvenile growth rates differed significantly in inshore waters, depending on location. As the trawl fisheries catching cuttlefish are size-selective, recruitment to the fisheries is largely dependent upon cuttlefish length. Therefore, such differences in juvenile growth rate are likely to influence age-at-recruitment, fast-growing cuttlefish recruiting earlier.

Although recruitment occurs mainly during autumn, seasonal differences of only 11−17 days in the age-at-recruitment and the back-calculated hatching dates for cuttlefish indicate that animals enter the fishery throughout the year. Recruitment was at 3−4 months, consistent with the findings of Challier *et al.* (2002) for English Channel cuttlefish sampled during autumn 2000. The time-series of data in the present study has revealed a complicated temporal pattern of recruitment in the English Channel. It had
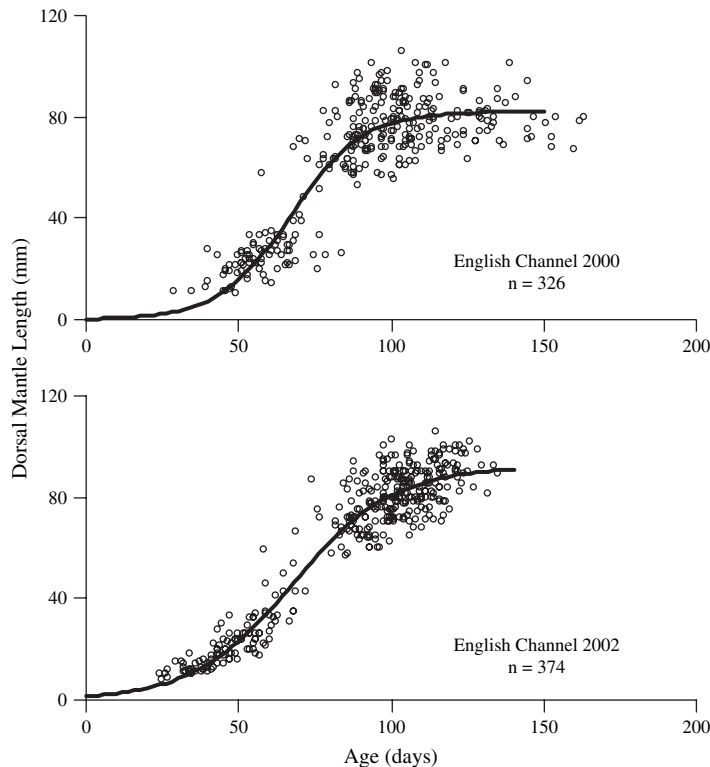

Figure 8. Monthly relationships between estimated age (days) and DML (mm) for juvenile *S. officinalis* from the English Channel by month and year.
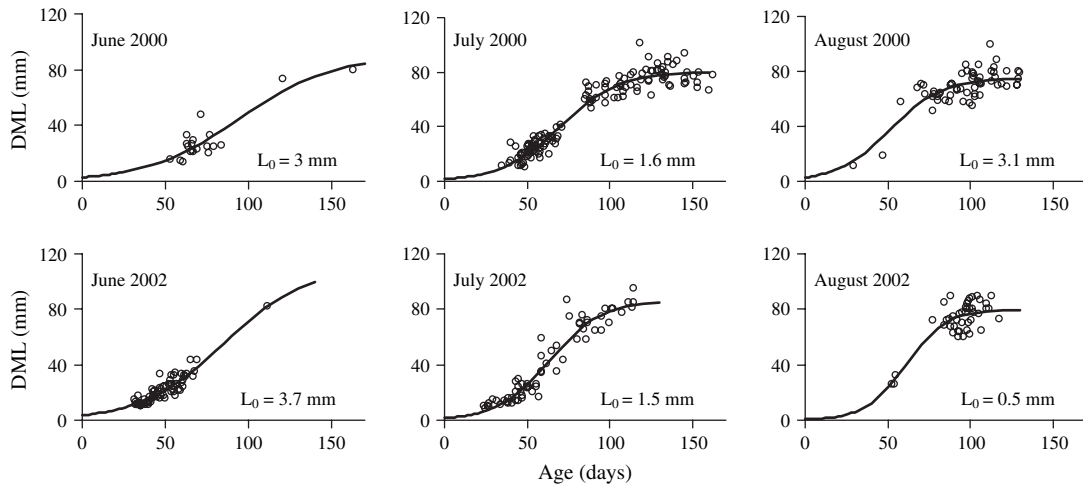
Figure 9. Logistic models fitted to estimated age (days) and DML (mm) of juvenile *S. officinalis* from the English Channel, 2000 and 2002.

previously been assumed that cuttlefish recruiting after the autumn peak were older than autumnal recruits, because it was thought that all cuttlefish hatched during summer (Medhioub, 1986; Boucaud-Camou and Boismery, 1991). The present study does not support this assumption, as although recruits after the autumn peak were indeed significantly older for the 2001 and 2002 cohorts, the opposite trend was found for the 2000 cohort. Despite significant differences between months and cohorts, recruits remained in the age range 3−4 months throughout the year. This range has previously been documented for cuttlefish in Galician waters (Guerra and Castro, 1988), and in the

Mediterranean Sea, where cuttlefish hatch throughout the year with hatching pulses in summer and autumn (Bettencourt, 2000). We propose two hypotheses to explain this pattern in the English Channel. First, spawning could take place throughout the year, although spawning cuttlefish are only found on the coastal shelf during spring (Boucaud-Camou and Boismery, 1991; Wang *et al.*, 2003). Dunn (1999), however, found that cuttlefish were caught commercially in the English Channel throughout the year, and that small numbers of mature male cuttlefish were present throughout the year, though this has yet to be demonstrated for females. Second, spawning could take place from spring

Table 5. Growth variations between micro-cohorts of *S. officinalis* using model (2), giving regression coefficients and statistics.

Month/year	n	r^2	L_∞	k	A_{50}	RSS	RMS	F-ratio	p
June									
2000	20	0.83	89.9	0.036	94.7	1 084	64		
2002	66	0.86	110.5	0.04	85.0	1 084	17	$F_{(3,80)} = 10.5$	***
Two cohorts	86	0.77	95.5	0.031	91.9	3 584	45		
July									
2000	131	0.95	80.4	0.056	69.9	5 508	43		
2002	63	0.93	86.3	0.064	63.5	3 875	65	$F_{(3,188)} = 14.5$	***
Two cohorts	194	0.93	79.9	0.062	65.9	12 218	65		
August									
2000	61	0.57	75.3	0.063	51.2	4 163	72		
2002	44	0.67	79.9	0.083	60.5	3 030	74	$F_{(3,99)} = 3.0$	*
Two cohorts	105	0.61	76.7	0.076	55.9	7 908	80		

RSS: residual sum of squares. RMS: residual mean square.
***$p < 0.001$, *$p < 0.05$.

Table 6. Growth variations among each micro-cohort of *S. officinalis* using model (2), giving regression coefficients and statistics.

Year and month	n	r^2	L_∞	k	A_{50}	RSS	RMS	F-ratio	p
June 2000	20	0.83	89.9	0.036	94.7	1 084	64	$F_{(6,203)} = 14$	***
July 2000	131	0.95	80.4	0.056	69.9	5 508	43		
August 2000	61	0.57	75.3	0.063	51.2	4 163	72		
3 months of 2000	212	0.88	80.0	0.060	69.2	18 322	90		
June 2002	66	0.86	110.5	0.04	85.0	1 084	17	$F_{(6,164)} = 4.1$	***
July 2002	63	0.93	86.3	0.064	63.5	3 875	65		
August 2002	44	0.67	79.9	0.083	60.5	3 030	74		
3 months of 2002	173	0.95	87.9	0.061	66.7	9 382	57		

RSS: residual sum of squares. RMS: residual mean square.
***$p < 0.001$.

through summer and, therefore, include periods when adults are both inshore and offshore. Eggs could therefore be laid in shallow, relatively warm coastal waters (< 40 m; Boletzky, 1983), as well as in some deeper and colder offshore waters. This hypothesis assumes that the rate (and thus the duration) of egg development is dependent on temperature. Delayed development of eggs deposited the previous year would therefore result in winter and spring hatching. Bouchaud and Daguzan (1989, 1990) showed that embryonic development of *S. officinalis* took approximately 5 months at 12°C, and ceased when the temperature dropped below 9°C, and also that eggs at lower temperature were able to restart embryogenesis when temperature increased. Winter sea surface temperatures may drop below 9°C throughout the English Channel (Dunn, 1999).

Sigmoidal growth curves have been applied to juvenile artificially reared *S. officinalis* (Richard, 1971; Boletzky, 1979), and were also the best descriptor of juvenile growth for the present samples. Forsythe and Van Heukelem (1987) described a similar two-phase growth curve, but with an exponential phase followed by a logarithmic phase. For the 2000 and 2002 cohorts, the fitted logistic curves indicated fast growth during summer, and slower growth during autumn and winter. Although the logistic curves gave a better fit to the data, the results of comparisons between years were similar for both the fitted logistic and linear models, both indicating that juvenile cuttlefish grew faster in 2002 than in 2000. Linear growth rates for the 2000 cohort ($1.4–1.9$ cm month^{-1}) were consistent with those previously estimated for the English Channel by Medhioub (1986; about 1.7 cm month^{-1}). Although growth was faster for the 2002 cohort, the within-cohort growth patterns were similar, growth rates increasing for cuttlefish hatched between June and August. The growth rate dropped between the end of September and the beginning of October for micro-cohorts in 2000, but in 2002 the drop extended from the beginning of September to mid-October. The reduction in growth rate may be related to a drop in temperature at around that time of year (Richard, 1971).

Growth differences between micro-cohorts have also been observed in *Loligo chinensis*, *Loligo gahi*, *Loliolus nocticula*, *Loligo pealeii*, and *S. officinalis* (Hatfield, 1991, 2000; Jackson, 1995; Jackson and Moltschaniwskyj, 2001; Macy and Brodziak, 2001; Challier *et al.*, 2002). Juvenile squid growth rate is influenced by feeding opportunities and environmental conditions, particularly temperature (Hatfield, 2000; Jackson and Moltschaniwskyj, 2002; Jackson and Domeier, 2003). Therefore, the differences in growth rates demonstrated here for the different hatching periods may be the direct result of environmental heterogeneity.

We identified a significantly slower instantaneous rate of growth in the Bay of Seine in 2000. In contrast to the other sampling sites, the Bay of Seine is strongly influenced by river input (Garnaud *et al.*, 2002). The rate of flow of the Seine was higher in 2000 than in 2002 (Delsinne, 2005), decreasing salinity and increasing turbidity in the areas frequented by juvenile cuttlefish. The euryhaline capacity of *S. officinalis* (Guerra and Castro, 1988) suggests that stress as a consequence of low salinity would be unlikely to slow growth directly, but it might decrease hatching success (Palmegiano and D'Apote, 1983) and influence the abundance of prey. As cuttlefish are visual predators, high turbidity and reduced visibility would likely negatively impact both prey attack frequency and/or capture success (Hanlon and Messenger, 1996). Differences in growth of pre-recruits between areas may also be caused by genetic variation. Allozymes, microsatellites, and mitochondrial DNA have shown stock structuring over small geographical scales (as small as 300 km) for the cuttlefish population around the Iberian Peninsula (Perez-Losada *et al.*, 1999, 2002; Shaw and Perez-Losada, 2000). However, no study has yet demonstrated genetic differences within the English Channel. A further alternative is that growth rate is density-dependent and that cuttlefish density varies significantly between areas. Density-dependence has been found to influence *Loligo gahi* in the Falkland Islands (Agnew *et al.*, 2000, 2002), the Indian squid *Loligo duvauceli* (Mohamed

and Rao, 1997), and the Japanese squid *Todarodes pacificus* (Okutani and Watanabe, 1983). Cuttlefish in the English Channel are fast-growing and active predators. Therefore, they are likely to be subject to food and/or space limitation through competition. However, no data were collected during this study to determine relative density.

Variability in annual recruitment is likely the most important process contributing to variability in catches from cuttlefish fisheries. In the English Channel, large interannual variations in cuttlefish recruitment have been estimated by Royer *et al.* (2002), which are typical of other cephalopod fisheries (*Loligo gahi*, Agnew *et al.*, 1998; *Illex argentinus*, Waluda *et al.*, 1999; *Loligo forbesi*, Royer *et al.*, 2002). The factors affecting recruitment are therefore key to understanding population dynamics for effective fisheries management. However, any relationship between growth rate and recruitment remains difficult to determine and will require the continued development of time-series of growth and recruitment estimates and a greater understanding of the relative contribution of nursery grounds to the observed recruitment.

Acknowledgements

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