

Age and growth of two sympatric squid *Loligo vulgaris* and *Loligo forbesi*, in Galician waters (north-west Spain)

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Age and growth of *Loligo vulgaris* and *L. forbesi* were studied by the examination of growth increments in 96 and 135 selected (white zone <10%) statoliths, respectively. Squid were obtained by monthly sampling from the catches of commercial trawling and hand-jigs in Galician waters (north-west Spain) between February 1991 and October 1993. Mantle length (ML) of *L. vulgaris* ranged from 70 to 480 mm and varied between 70 and 685 mm in *L. forbesi*. A negative allometry between statolith length and ML or body weight (BW) was found in both species. Sexual dimorphism was apparent in both species, males grew faster and longer than females. The statolith analysis suggests that growth patterns of *L. vulgaris* and *L. forbesi* in Galician waters are different. The exploited population of *L. vulgaris* was composed of two groups: one formed by individuals hatched in winter–spring and another by specimens hatched in summer–autumn. Squid hatched in winter–spring reached larger sizes at the same age than those hatched in summer–autumn. These two groups were also observed in *L. forbesi*. However, squid of this species hatched in winter–spring were smaller than those hatched in summer–autumn at the same age. Reasons for this discrepancy are discussed. The life span of *L. vulgaris* was about one year whereas the life span of *L. forbesi* extended to 18 months.

INTRODUCTION

The loliginid squid *Loligo vulgaris* Lamarck, 1798 and *Loligo forbesi* Steenstrup, 1856 constitute one of the most important cephalopod fishery resources of Europe and West Africa. A total of 15,000 tonnes and 3,000 tonnes of both species, respectively, were caught during 1995 in these areas (FAO, 1997). Knowledge of the demographic structure of populations permits the evaluation of population biomass changes caused by natural or fishing mortality. This information implies a precise study of the age and growth of individuals. Furthermore, it is important to study the age and growth of cephalopods since knowledge of these parameters makes it possible to compare different maturation, feeding and ecological patterns of a species during its life cycle (Bettencourt et al., 1996).

Cephalopod statoliths show growth increments and their use in age estimations is becoming established. It has been validated that growth increments are deposited daily in several species (for a review see Jackson, 1994). This opens up the possibility of using age-based assessment even if age cannot be reliably estimated from length as in the case of cephalopods (Pierce & Guerra, 1994).

Published information on the age and growth of *L. vulgaris* using statoliths are based on specimens from the north-west Mediterranean (Natsukari & Komine, 1992), north-west Spain (Guerra & Rocha, 1994), the West Saharan Shelf (Arkhipkin, 1995) and the south of Portugal (Bettencourt et al., 1996). These studies have shown that growth rates varied considerably among individuals. Double exponential, Gompertz and Power functions, were used to describe growth of the species. And finally, all these studies concluded that the life span of *L. vulgaris* is about one year.

Statolith studies of *L. forbesi* are basically restricted to investigation by Collins et al. (1995a) in Irish waters. Preliminary results by Martins (1982) examining only 40 statoliths of specimens from the Azores showed ages of 7–8 months for 310 mm of mantle length (ML) in females and 15 months for 740 mm ML in males. Collins et al. (1995a) provided indirect evidence of the daily deposition of growth increments in the statolith of this species. Growth data were fitted to a logarithmic function and it was shown that males grew faster and attained larger sizes than females. Collins et al. (1995a) also indicated a one year life span for this species whilst Guerra & Rocha (1994) estimated a life span of 16 months.

Studies by Natsukari & Komine (1992), Arkhipkin (1995), Collins et al. (1995a) and Bettencourt et al. (1996) found a great growth and age variability between specimens of the same size. Thus, squid of the same size showed that the increments counted in prepared statoliths ranged between 80 and 150 and from 60 to 200 in *L. vulgaris* and *L. forbesi*, respectively.

Moreover, comparisons between ageing results of these studies are difficult because they are based on specimens from different fishing grounds and they were carried out by different authors using different methodologies. It is well known that cephalopod growth is influenced markedly by biotic and abiotic factors (Forsythe & Van Heukelem, 1987; Forsythe, 1993), and that errors between readers and due to differences in methodologies are considerable when counting increments (González, et al., 1998). To date, ageing studies based on both species from the same fishing ground, except for some preliminary observations by Guerra & Rocha (1994), have not been achieved.

The aim of the present study was to evaluate age and growth of both species from the same fishery area, and to

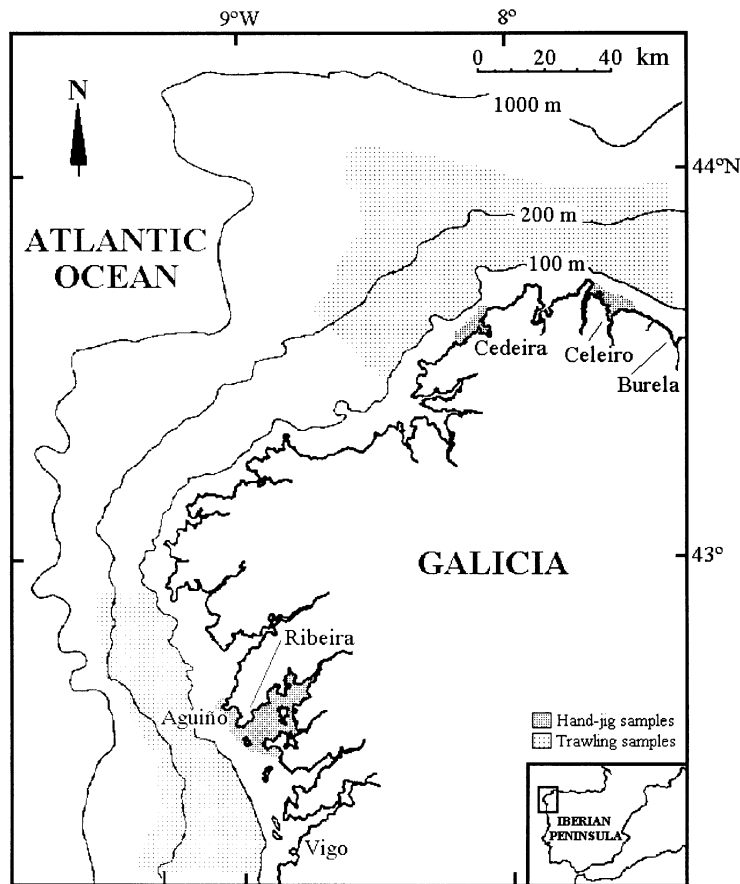


Figure 1. *Loligo vulgaris* and *L. forbesi*. Map of the Galician coast (north-west Spain) showing the sampling ports and the fishing grounds where trawl and hand-jig samples were collected.

compare estimates obtained by the same researcher using the same methodology.

MATERIAL AND METHODS

Statolith sampling

From February 1991 to October 1993 samples of commercially caught squid *Loligo vulgaris* and *L. forbesi* were collected at fish markets from the Galician (north-west Spain) fishing ports of Cedeira, Celeiro, Burela, Aguiño and Ribeira (Figure 1). Monthly samples were obtained from both trawling and hand jig fisheries. These squid species are caught as a by-catch in the multi-species trawler fishery. Depths where trawlers operate range from 100 to 400 m. Trawl mesh size is 60 mm in the codend. Both species are caught by a direct small-scale hand-jig fishery at depths of between 4 and 40 m. This artisanal fishery was described by Simón et al., (1996). Allozyme electrophoretic analysis has shown that animals caught in both fisheries belong to the same populations (Pérez-Losada, 1998). After sorting according to species a random representative sample was taken of the total landing.

A total of 1828 *L. vulgaris* (41 unsexed, 862 males and 925 females) and 792 *L. forbesi* (31 unsexed, 399 males and 356 females) were sampled. An average number of 55 specimens of *L. vulgaris* and 24 specimens of *L. forbesi*

were obtained in each sample, and taken to the laboratory in 0°C ice-boxes and then frozen at -30°C. The dorsal mantle length (ML in mm) and wet body weight (BW in g) of each thawed specimen was noted after defrosting at room temperature, sex was determined and a maturity stage assigned (Boyle & Ngoile, 1993). Sizes of the individuals sampled ranged from 70–480 mm ML and 67–685 mm ML, respectively.

A total of 269 *L. vulgaris* statoliths (2 unsexed, 127 males and 140 females) and 278 *L. forbesi* statoliths (18 unsexed, 144 males and 116 females) were taken from squid with ML ranging from 70–480 mm and 67–685 mm, respectively. Statoliths were removed (Arkhipkin, 1991) and stored in 99.5% ethyl alcohol.

Statolith preparation and increment counts

All statoliths were measured (to 0.01 mm) from the end of the dorsal dome to the rostrum tip (statolith length, SL), using a dissecting microscope (×15) fitted with an eyepiece micrometer. Statoliths were prepared as described by Arkhipkin (1991) and Villanueva (1992). The statoliths were mounted in Pro-texx resin, ground and polished on both sides using 3M commercial waterproof sandpaper, coarse (30 µm) and fine grain (1 µm), respectively. Statolith terminology follows that of Clarke (1978).

Growth increments were counted using an Image Analysis System comprised of a light microscope

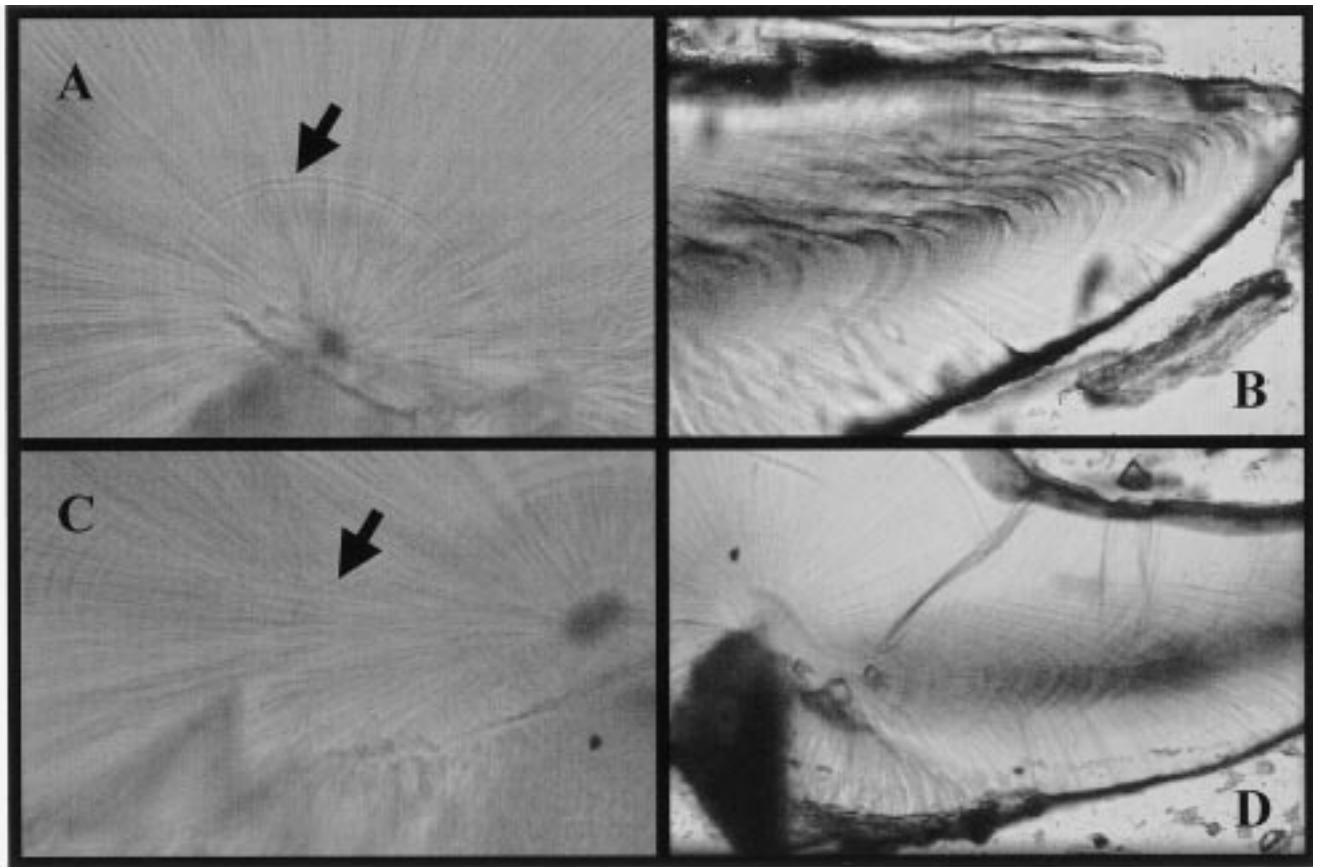


Figure 2. *Loligo vulgaris* and *L. forbesi*. Photomicrograph of ground statoliths and increments: (A) *L. vulgaris*, nucleus and natal ring; (B) *L. vulgaris*, tip of the rostrum; (C) *L. forbesi*, nucleus and natal ring; (D) *L. forbesi*, rostrum.

OPTIPHOT-2 (40 objective) with a video output to a high resolution colour monitor connected to a computer and photographic printer. The software package used was VIDS (Video Image Digital Software). Increments were counted by hand on the TV monitor screen ($\times 700$ dpi). An increment was defined as the bipartite structure within the statolith composed of a dark and light ring (Lipinski et al., 1991; Jackson, 1994). Growth increments were counted from the natal ring to the end of the rostrum (Natsukari et al., 1988). The total number of increments (NI) in each statolith was counted, and the distance along the statolith where the increments were not visible (white zone or obliterate zone, whose location varies) was measured. Statoliths with more than 10% of white zone were rejected. Increments in the white zone were estimated by interpolation. The consistency of statolith-increment counting was tested by obtaining two replicate counts by the same reader for 17 statoliths of each species which yielded coefficients of variations of 0.7–2.2%. Therefore, accumulative effects of counting error by the same reader were judged to be negligible. The validity of the ageing technique used in this work and semi-automatic increment counts were demonstrated by González et al. (1988) re-analysing a set of previously analysed known-age *Sepioteuthis lessoniana* statoliths.

Growth increments were validated to be daily in *L. forbesi* by Hanlon et al., (1989), assuming that increments were also deposited daily in *L. vulgaris*. The hatching date of each specimen was estimated by back-calculation from date of capture and increment counts.

The relationships between mantle length (ML), body weight (BW) and statolith length (SL) were estimated considering sexes separately. Gompertz, exponential, power and logarithmic curve growths were tested. Differences of slopes and elevations in the relationships SL–ML and SL–BW between sexes were compared using Student's test (Zar, 1984) with variables logarithmically transformed.

Growth rate estimations

Daily growth rates (DGR mm d^{-1}) and instantaneous daily growth rate, G , were calculated using the equations given by Forsythe & Van Heukelem (1987):

$$\text{DGR} = \frac{(W_2 - W_1)}{(T_2 - T_1)} \quad (1)$$

$$G = \left(\frac{(\ln W_2 - \ln W_1)}{(T_2 - T_1)} \right) \times 100 \quad (2)$$

where W_1 and W_2 are ML (mm) at the beginning and the end of the time interval $T_2 - T_1$.

Growth equations obtained were logarithmically transformed and their slopes and elevations compared using Student's test (Zar, 1984).

Table 1. *Loligo vulgaris* and *L. forbesi* relationships between statolith length (SL); mantle length in mm (ML) and body weight in g (BW).

Relationship	Sex	a	b	r^2	N
<i>Loligo vulgaris</i>					
SL–ML	Males	0.3358	0.3045	0.75	127
	Females	0.3242	0.3174	0.68	140
SL–BW	Males	0.8582	0.1280	0.76	123
	Females	0.8423	0.1346	0.71	133
<i>Loligo forbesi</i>					
SL–ML	Males	0.4892	0.2692	0.89	132
	Females	0.4257	0.2996	0.83	105
SL–MW	Males	1.1275	0.1100	0.88	130
	Females	1.1078	0.1164	0.84	103

Intercept (a), slope (b), coefficient of determination (r^2) and number of statoliths (N) are indicated for the power equation ($SL = a(ML)^b$).

RESULTS

Statolith microstructure

Each growth increment in the statolith of both species comprises two components, one optically translucent (light) layer and another opaque (dark) layer (Figure 2). This opaque layer will be called a 'ring'. The nucleus appears as an opaque droplet-like area in both species. Several tiny primordia appear as small, dark concretions, which are more densely distributed inwards. Careful observations showed that faint increments were partially visible in the nucleus. Those increments were probably formed during the embryonic development.

The natal ring, which is formed at hatching, was observed as an especially prominent opaque dark layer. This was the starting point for counting increments to estimate age in days after hatching in both loliginid species.

In the present study increments were observed in two ways: from the natal ring to the rostrum and from the natal ring to the dorsal dome. However, the increments were more clearly visible in the first case. This was the reason why the increments were counted from the natal ring to the rostrum in both species. Moreover, two types of rings were recognized in prepared statoliths: fine, relatively light, uniformly spaced rings, and thick, dark rings.

Table 2. *Loligo vulgaris* and *L. forbesi* comparisons between males and females of the equations (slope and intercept) given in Table 1 for relationships SL vs ML and SL vs BW using Student's *t* test.

Comparison	Slope				Intercept			
	<i>t</i>	<i>v</i>	<i>P</i>	Prob.	<i>t</i>	<i>v</i>	<i>P</i>	Prob.
<i>Loligo vulgaris</i>								
SL–ML	0.2308	15	$P > 0.05$	ns	0.2324	16	$P > 0.05$	ns
SL–BW	1.1944	12	$P > 0.05$	ns	1.1190	13	$P > 0.05$	ns
<i>Loligo forbesi</i>								
SL–ML	0.8126	22	$P > 0.05$	ns	0.7579	23	$P > 0.05$	ns
SL–BW	2.1321	22	$P < 0.05$	*	1.8548	23	$P > 0.05$	ns

Prob., level of probability; *, significant differences; ns, no significant differences.

Growth of the statolith

The relationship between statolith length (SL) and mantle length (ML) and body weight (BW) in both species (excluding unsexed animals) was best described by a power equation (Table 1). In both species and sexes, power (allometric) slope was < 1 , revealing negative allometry between statolith growth and ML or BW. No significant differences ($P > 0.05$) were found in SL–ML and SL–BW relationships between *L. vulgaris* males and females (Table 2). The power equations fitted for the SL–ML relationship showed no significant differences ($P > 0.05$) between *L. forbesi* males and females. However, differences between the slope of the male and female SL–BW equations were statistically significant ($P < 0.05$) in *L. forbesi* (Table 2).

Age and growth of squid

The youngest squid had a total of 167 increments (female of 92 mm ML) and 119 increments (unsexed of 67 mm ML) in *L. vulgaris* and *L. forbesi*, respectively. The maximum number of increments for females was 361 increments (255 mm ML) and 382 increments (383 mm ML) for males of *L. vulgaris*. In the case of *L. forbesi*, the maximum number of increments for females was 514 increments (322 mm ML) and 480 increments (400 mm ML) for males.

Assuming that increments were deposited daily, hatching dates were back calculated from date of capture and increment counts (Figure 3). The distributions of hatching dates by sex between September 1990 and October 1991 are illustrated in Figure 4. Hatching occurred throughout the year in both species, although most hatching occurred in winter, spring and summer.

Loligo vulgaris

The 64% of the prepared statoliths were rejected because they had more than 10% of white zone. A total of 96 statoliths (43 males and 53 females) were used for age estimations.

Figure 5 shows the relationship between the statolith length (SL) and the number of increments (NI) in males and females.

Figure 6 illustrates the relationship between NI and ML of males and females hatched between December 1990–July 1991.

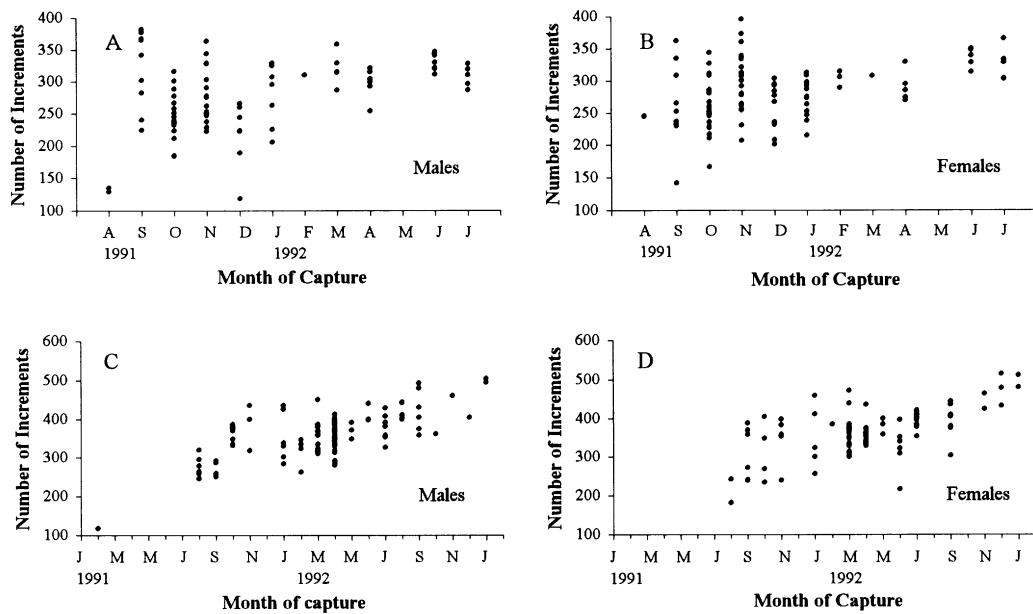


Figure 3. *Loligo vulgaris* and *L. forbesi*. Relationship between number of increments counts and date of capture. (A) *Loligo vulgaris* males; (B) *Loligo vulgaris* females; (C) *L. forbesi* males; (D) *L. forbesi* females.

Data analysis showed that statolith increment values for males and females can be separated into two groups, according to hatching dates: summer–autumn and winter–spring groups (Figure 6). The best growth curve that fitted the data for both sexes and groups was an exponential function. Parameters of these exponential functions as well as daily growth rate (DGR) and instantaneous daily growth rate (G) values for males and females of both groups are shown in Table 3.

The post-hatch life span of males and females of the species should be about one year or less because it would be possible to reach the maximal ML recorded (480 mm for males and 350 mm for females) within one year with the estimated growth rates.

Males and females of this species showed a significantly different growth rate (Table 4), males grew faster than females. However, no significant differences ($P > 0.05$) were found in the growth rate of specimens of the same sex hatched in summer–autumn or winter–spring (Table 4).

Loligo forbesi

The 51% of the prepared statoliths were rejected because they had more than 10% of white zone. A total of 135 statoliths (78 males and 57 females) were used for age estimations.

A relatively high individual variation in statolith length (SL) vs number of increments (NI) in males and females is apparent from Figure 7.

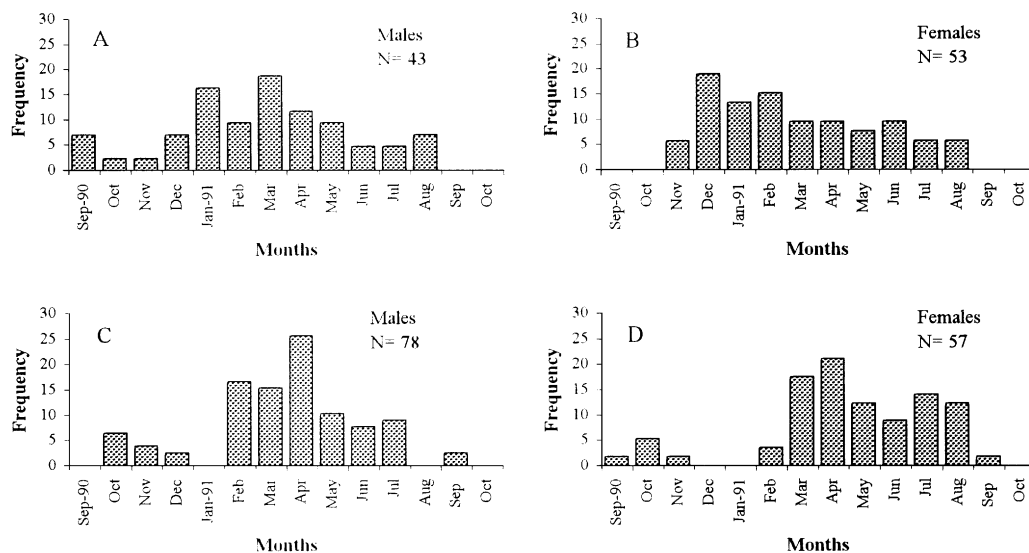


Figure 4. *L. oligo vulgaris* and *L. forbesi*. Distribution of hatching dates; (A) *L. vulgaris* males; (B) *L. vulgaris* females; (C) *L. forbesi* males; (D) *L. forbesi* females. Data were back-calculated from statolith increment counts and month of capture for both species and sexes.

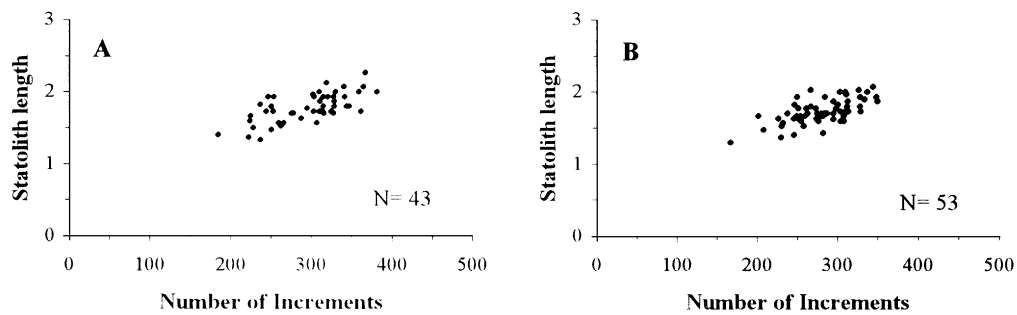


Figure 5. *Loligo vulgaris*: relationship between statolith length and number of increments of males (A) and females (B).

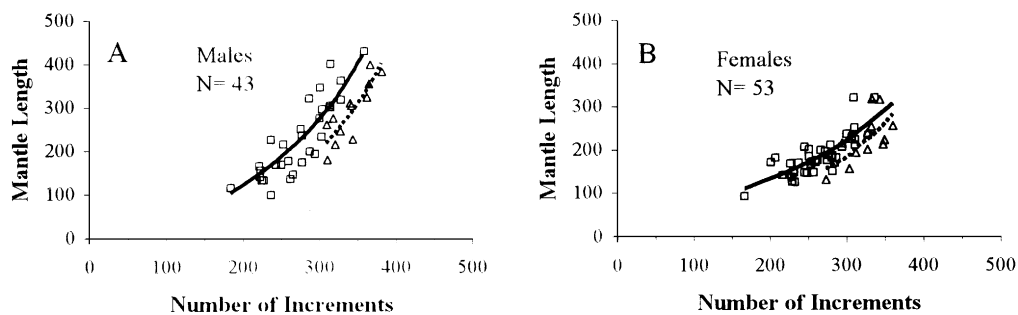


Figure 6. *Loligo vulgaris*: relationship between number of increments and mantle length in males (A) and females (B). Proposed growth curves for specimens hatched in summer–autumn (Δ) and winter–spring (\square) seasons are illustrated.

Figure 8 shows the relationship between NI and ML in males and females hatched between December 1990–July 1991. It can be observed that a considerable ML variation among individuals of same age was found.

According to their hatching date, males of *L. forbesi* can be separated into three groups: summer, autumn and winter/spring. In females, however, only two groups can be defined: summer–autumn and winter–spring groups (Figure 8). The growth functions that best fitted the data of both sexes were of three types: exponential in the case of males hatched in summer and winter–spring, linear for males hatched in autumn, and, finally, logarithmic in the case of both female groups. The parameters of these functions, DGR and G values are shown in Table 5.

Considering the number of increments counted (Figure 8), the post-hatch life span of *L. forbesi* males and females should be about 18 months.

Significant sexual difference in growth was observed when comparing males and females of this species in all hatching seasons (Table 6). Significant differences were found between the growth of specimens hatched

at different seasons for the same sex of this species (Table 6).

Loligo vulgaris and Loligo forbesi growth comparison

A comparison between sexes of both species (Table 7) showed that growth of *L. forbesi* males hatched in autumn was significantly faster than growth of *L. vulgaris* males hatched at any season of the year. However, no significant differences ($P > 0.05$) were found when comparing growth of *L. vulgaris* males with growth of *L. forbesi* males hatched in summer. Growth of males and females of both species hatched in other seasons was significantly different (Table 7). Growth functions parameters (Tables 3 and 5) suggest that small (< 200 mm ML) *L. forbesi* females grew faster than small (< 200 mm ML) *L. vulgaris* females, whilst the contrary seems to occur in larger females of both species.

The statolith analysis showed that two groups composed the exploited population of *L. vulgaris* in Galician waters: one formed by individuals hatched in winter–spring and

Table 3. Growth estimations using the exponential equation ($ML = a(e^{bNI})$) of *Loligo vulgaris* hatched in different seasons.

Growth estimation		a	b	r^2	N	NI range	DGR	G
Males	summer–autumn	16.176	0.0084	0.68	12	300–382	0.54–3.04	0.84
	winter–spring	21.14	0.0084	0.74	31	185–380	0.71–3.98	0.84
Females	summer–autumn	24.278	0.0068	0.52	14	260–361	0.51–2.05	0.68
	winter–spring	43.88	0.0053	0.67	39	167–350	0.56–1.65	0.53

NI, number of increments; ML, mantle length (mm); a, intercept; b, slope; r^2 , coefficient of determination; N, number of statoliths; NI range, range of increments used to estimate the equation; DGR, daily growth rate (mm d^{-1}); G, instantaneous daily growth rate.

Table 4. Comparisons between growth equations of *Loligo vulgaris* (slope and intercept) given in Table 3 using Student's test.

Comparison	Slope				Intercept			
	<i>t</i>	<i>v</i>	<i>P</i>	Prob.	<i>t</i>	<i>v</i>	<i>P</i>	Prob.
Males								
summer–autumn vs winter–spring	0.0508	38	<i>P</i> >0.05	ns	0.2268	39	<i>P</i> >0.05	ns
Females								
summer–autumn vs winter–spring	0.3653	49	<i>P</i> >0.05	ns	0.3560	50	<i>P</i> >0.05	ns
Males vs Females								
summer–autumn vs summer–autumn	2.7893	22	<i>P</i> <0.02	*	2.3954	23	<i>P</i> <0.05	*
summer–autumn vs winter–spring	3.9031	47	<i>P</i> <0.001	**	3.3001	48	<i>P</i> <0.002	**
winter–spring vs winter–spring	3.4190	65	<i>P</i> <0.002	**	2.7692	66	<i>P</i> <0.01	*
winter–spring vs summer–autumn	2.5579	40	<i>P</i> <0.02	*	2.1414	41	<i>P</i> <0.05	*

Prob., level of probability; *, significant differences; ns, no significant differences.

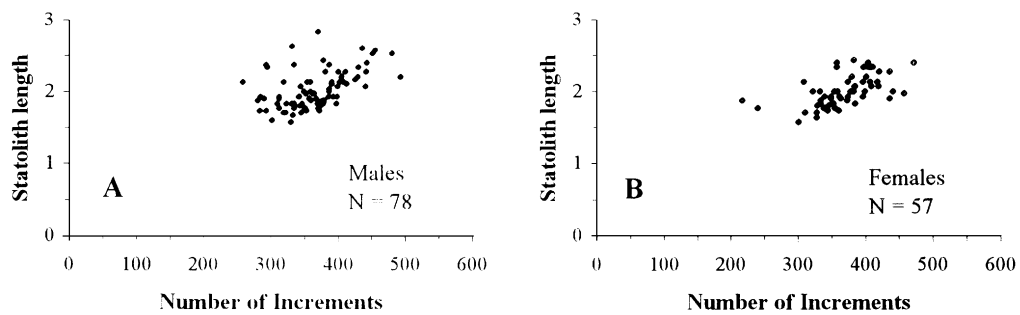


Figure 7. *Loligo forbesi*: relationship between statolith length and number of increments of males (A) and females (B).

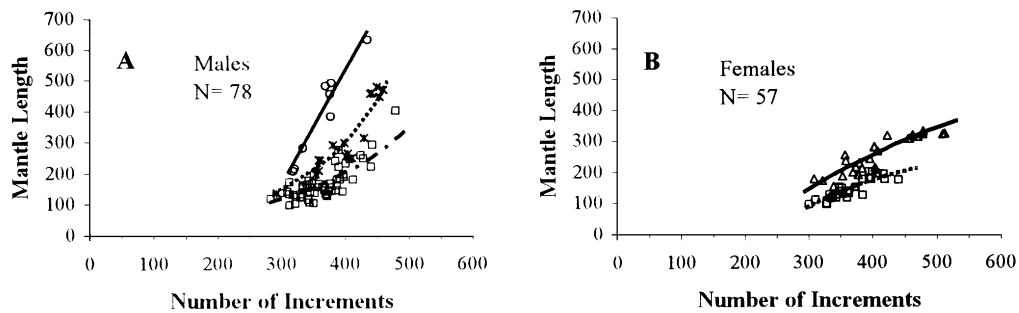


Figure 8. *Loligo forbesi*: relationship between number of increments and mantle length in males (A) and females (B). Proposed growth curves for males hatched in summer (×), autumn (○) and winter–spring (□) and for females hatched in summer–autumn (△) and winter–spring (□) seasons are shown.

Table 5. Growth estimations using the exponential ($ML = a(e^{b \cdot NI})$), logarithmic ($ML = a + b \ln(NI)$) and linear ($ML = a + b \cdot NI$) equations for *Loligo forbesi* hatched at different seasons of the year.

Growth estimation		Equation	a	b	<i>r</i> ²	N	NI range	DGR	G
Males	summer	exponential	14.92	0.0056	0.89	16	280–480	0.41–1.13	0.56
	autumn	linear	−959.57	3.7079	0.92	8	310–450	3.71	0.49–4.34
	winter–spring	exponential	20.503	0.0056	0.61	54	284–480	0.57–1.55	0.56
Females	summer–autumn	logarithmic	−1977.9	371.43	0.81	27	305–514	0.75–1.30	0.23–1.09
	winter–spring	logarithmic	−1656.9	305.18	0.76	30	301–440	0.62–1.07	0.26–1.61

NI, number of increments; ML, mantle length (mm); a, intercept; b, slope; *r*², coefficient of determination; N, number of statoliths; NI range, range of increments used to estimate the equation; DGR, daily growth rate (mm d^{−1}); G, instantaneous daily growth rate.

Table 6. Comparisons between growth equations of *Loligo forbesi* (slope and intercept) given in Table 5 using Student's test.

Comparison	Slope				Intercept			
	<i>t</i>	<i>v</i>	<i>P</i>	Prob.	<i>t</i>	<i>v</i>	<i>P</i>	Prob.
Males								
summer vs winter–spring	8.4835	66	<i>P</i> <0.001	**	5.6689	67	<i>P</i> <0.001	**
summer vs autumn	2.7853	20	<i>P</i> <0.01	*	2.3533	21	<i>P</i> <0.05	*
autumn vs winter–spring	10.9925	58	<i>P</i> <0.001	**	6.0975	58	<i>P</i> <0.001	**
Females								
summer–autumn vs winter–spring	12.6618	53	<i>P</i> <0.001	**	6.2500	54	<i>P</i> <0.001	**
Males vs Females								
summer vs summer–autumn	4.0649	39	<i>P</i> <0.001	**	3.1888	40	<i>P</i> <0.005	**
summer vs winter–spring	9.9331	42	<i>P</i> <0.001	**	5.2545	43	<i>P</i> <0.001	**
summer vs summer–autumn	7.5540	31	<i>P</i> <0.001	**	4.3314	32	<i>P</i> <0.001	**
autumn vs winter–spring	12.0885	34	<i>P</i> <0.001	**	5.1374	35	<i>P</i> <0.001	**
winter–spring vs summer–autumn	6.6803	77	<i>P</i> <0.001	**	5.3330	78	<i>P</i> <0.001	**
winter–spring vs winter–spring	3.2271	80	<i>P</i> <0.002	**	2.8968	81	<i>P</i> <0.005	**

Prob., level of probability; *, significant differences; ns, no significant differences.

Table 7. Comparisons of growth equations between *Loligo vulgaris* and *Loligo forbesi* (slope and intercept) given in Tables 3 & 5 using Student's test.

Comparison	Slope				Intercept			
	<i>t</i>	<i>v</i>	<i>P</i>	Prob.	<i>t</i>	<i>v</i>	<i>P</i>	Prob.
<i>Loligo vulgaris</i> vs <i>Loligo forbesi</i>								
Males								
summer–autumn vs summer	0.7732	24	<i>P</i> >0.05	ns	0.9375	25	<i>P</i> >0.05	ns
summer–autumn vs autumn	2.2594	16	<i>P</i> <0.05	*	1.8549	17	<i>P</i> >0.05	ns
summer–autumn vs winter–spring	9.3731	62	<i>P</i> <0.001	**	6.0657	63	<i>P</i> <0.001	**
winter–spring vs summer	0.8598	42	<i>P</i> >0.05	ns	0.8656	43	<i>P</i> >0.05	ns
winter–spring vs autumn	2.7699	34	<i>P</i> <0.01	*	2.3844	35	<i>P</i> <0.05	*
winter–spring vs winter–spring	9.9083	80	<i>P</i> <0.001	**	6.3114	81	<i>P</i> <0.001	**
Females								
summer–autumn vs summer–autumn	2.0422	37	<i>P</i> <0.05	*	1.9896	38	<i>P</i> >0.05	ns
summer–autumn vs winter–spring	10.0132	40	<i>P</i> <0.001	**	5.3766	41	<i>P</i> <0.001	**
winter–spring vs summer–autumn	3.5347	62	<i>P</i> <0.001	**	3.1500	63	<i>P</i> <0.005	**
winter–spring vs winter–spring	14.5383	65	<i>P</i> <0.001	**	6.8709	66	<i>P</i> <0.001	**

Prob., level of probability; *, significant differences; ns, no significant differences.

another by specimens hatched in summer–autumn. Those hatched in the first period attained larger sizes at the same age than those hatched in the second period.

These two groups were also observed in the exploited population of *L. forbesi*. However, *L. forbesi* born in winter–spring were smaller than those hatched in summer–autumn at the same age. Moreover, males hatched in autumn showed the largest sizes at any age in the fishery.

DISCUSSION

Growth increments within the statolith microstructure of *Loligo vulgaris* and *L. forbesi* are similar to the increments in *L. vulgaris* from the West Saharan Shelf (Arkhipkin, 1995) and in *L. forbesi* from Irish waters (Collins et al., 1995a). It seems that the growth increment pattern observed is quite constant in loliginid species.

Thus, similar increments were found in *L. opalescens* (Hixon & Villoch, 1983); *Photololigo edulis* (Natsukari et al., 1988), *L. bleekeri* (Kinoshita, 1989) and *Septoteuthis lessoniana* (Jackson, 1990). The nucleus of both species studied in this paper showed a droplet-like form and was constituted by several tiny primordia as observed by Arkhipkin (1995) in *L. vulgaris* from west African waters. The natal ring of *L. vulgaris* and *L. forbesi* from north-west Spain was identified as described in *L. vulgaris* from the western Mediterranean (Natsukari & Komine, 1992). As pointed out by Natsukari et al. (1993), it was considered that estimating age from only the number of thick, dark rings observed was very risky. Accordingly we counted both types of increments found in our prepared statoliths: those formed by a fine ring and a translucent layer and the increments constituted by a dark ring and a translucent layer.

The statoliths of *L. forbesi* are larger than the statoliths of *L. vulgaris*. Statoliths length of *L. forbesi* varying from 2.2% ML in juveniles of 70 mm ML to 0.41% ML in mature males of 685 mm ML, and from 1.7% ML in juveniles 70 mm ML to 0.45% ML in mature *L. vulgaris* males of 480 mm ML. Arkhipkin (1995) found a similar statolith length range in *L. vulgaris* from the Saharan shelf. The growth in length of the statolith decreases gradually with individual growth in both species. This pattern was also found in other loliginid species as *Alloteuthis subulata* and *A. africana* (Arkhipkin & Nekludova, 1993), but in *L. vulgaris* and *L. forbesi* the allometric coefficient (b) was approximately 2.5 times larger than that of both *Alloteuthis* spp., reflecting faster allometric growth of *L. vulgaris* and *L. forbesi* statoliths. Bettencourt et al. (1996) also found that the statolith of *L. vulgaris* from the south coast of Portugal decreased gradually with individual growth. These authors indicated that this result might be related to the onset of sexual maturation as described in other cephalopods.

A hatching period occurring throughout the year in both species was also observed in other geographical areas (Natsukari & Komine, 1992; Arkhipkin, 1995; Collins et al., 1995a,b; Bettencourt et al., 1996). Although main and secondary peaks of hatching were observed in both species, the method of using the statolith data to evaluate hatching date is not without its problems. Most notably the seasonal variation of squid abundance at the time of capture is not taken into account (Collins et al., 1997). The fact that our results indicate some sex specific peaks in hatching could be caused by different migration patterns, causing only one of the sexes to be sampled. Segregation of sexes at different depths and asynchronic migration of sexes were deduced from observation by Mangold-Wirz (1963) and Worms (1983) in *L. vulgaris* from the western Mediterranean. However, further research is necessary in order to clarify that migratory pattern.

The great variation in individual growth rates in *L. vulgaris* and *L. forbesi* found in the present study agrees with that observed in wild populations of these species by other authors. Thus, Natsukari & Komine (1992), Arkhipkin, (1995) and Bettencourt et al. (1996) found that *L. vulgaris* specimens of the same length could have variations of 150 increments. Collins et al. (1995a) observed variations of 200 increments for *L. forbesi* individuals of the same length. Such variability has also been reported in laboratory cultured *L. vulgaris* and *L. forbesi* (Turk et al., 1986; Hanlon et al., 1989). Considerable variations in individual growth rates were also observed in other loliginid squid, e.g. *Alloteuthis subulata*, *Photololigo edulis*, *Heterololigo bleekeri* and *Loligo gahi* (Lipinski, 1986; Natsukari et al., 1988; Kinoshita, 1989; Hatfield, 1991). Considerable variation in individual growth rate is probably a common character in all loliginids as shown by these previous findings along with the results in this study. This high variability in individual growth rates could be associated with temperature, food availability and the individual size at maturation (Forsythe & Van Heukelen, 1987; Rodhouse & Hatfield, 1990; Bettencourt et al., 1996).

Sexual dimorphism observed in both species, with males growing faster and attaining larger sizes than females, is common amongst loliginid squid (see reviews

in Boyle, 1983; Natsukari & Komine, 1992; Arkhipkin, 1995; Collins et al., 1995a).

The results obtained from statolith analysis in both species suggest the existence of two different lifestyles. *L. vulgaris* seems to be a species closely related with coastal waters throughout its life cycle. The individuals of this species hatched in winter–spring in shallow waters (Guerra & Rocha, 1994) should have high growth rates during early stages of development in summer and autumn when environmental conditions are more favourable. This is mainly due to the presence of a coastal summer–autumn upwelling that notably increases the productivity of Galician waters (Fraga, 1981; Blanton et al., 1984; Rocha et al., 1999). On the contrary, squid hatched in summer–autumn would find unfavourable environmental conditions when pre-recruit, which should account for lower growth rates than those hatched in winter–spring. Moreover, *L. forbesi* seems to be a more oceanic species than *L. vulgaris*, carrying out relatively long offshore displacements throughout its life cycle. The individuals of this species hatched inshore in winter–spring are found offshore in summer–autumn. Therefore, they would not benefit from the favourable conditions prevailing in coastal waters during upwelling. This would account for their relatively low growth rates. An inshore displacement of these individuals seems to occur when they start to mature. The small maturing animals would reach coastal waters in winter–spring. On the other hand, the specimens hatched inshore in summer would arrive at offshore areas, larger than the individuals hatched in winter–spring. This can be induced by the high food availability during upwelling. These squid would return to coastal waters in summer when upwelling is strongest but when fish populations, that constitute their main prey (Rocha et al., 1994), are still not very abundant. However, individuals hatched in autumn would return to coastal waters later than those hatched in summer, when fish populations are abundant in coastal waters. This increase in food availability might account for their high growth rates. Therefore, squid hatched in autumn would have larger sizes than the summer ones at the same age. The difference in size at the same age observed between males and females hatched in autumn could be explained because females diverted more energy from somatic growth to gonad production than males (Collins et al., 1995a).

Daily growth rate (DGR) and instantaneous growth rate (G) of *L. vulgaris* obtained in the present paper agree with those estimated from the wild (Natsukari & Komine, 1992; Arkhipkin, 1995; Bettencourt et al., 1996), and from laboratory reared specimens (Turk et al., 1986). Moreover, instantaneous growth rate differences observed between *L. forbesi* males and females hatched in autumn agree with those reported by Collins et al. (1995a). It can also be observed that G values estimated by these authors agree with those obtained in the present study for males and females hatched in other seasons.

No evidence was found that either male or female *L. vulgaris* live longer than one year. This agrees with the results obtained using statolith analysis in other regions (Natsukari & Komine, 1992; Arkhipkin, 1995; Bettencourt et al., 1996). Large *L. forbesi* males and females live 18 months in Galician waters. This disagrees with the

observations of Collins et al. (1995a) in Irish waters, where a one-year life cycle was postulated. However, this could agree with Martins' observations (1982) in specimens from the Azores. The discrepancy between Collins et al. (1995a) and our findings could be due to the fact that the maximum size of *L. forbesi* never surpassed 505 mm ML in Irish waters, whereas larger animals are relatively common in Galicia and the Azores (Guerra & Rocha, 1994; Porteiro & Martins, 1994). Nevertheless, these differences might also reflect the different methods and zones employed in statolith increment reading, to the natal ring toward the dorsal dome by Collins et al. (1995a) and toward the rostrum in the present study. Thus, it would be possible that in the larger males the increments become highly compressed in the dorsal dome but more easily resolved in the rostrum.

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