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Growth and mating of southern African *Lycoteuthis lorigera* (Steenstrup, 1875) (Cephalopoda; Lycoteuthidae)

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Abstract *Lycoteuthis lorigera* is an oceanic squid that is abundant in the Benguela system. Little is known about the biology of this squid except that it is eaten in large numbers by numerous oceanic predators and that males grow to larger size than females, which is unique for oegopsid squid. The aim of this study was to better understand the biology of this species by investigating its age and growth, as well as its mating system. Toward this end, the age of 110 individuals, ranging from 35 to 110 mm, was estimated by counting statolith growth increments. Estimates of age ranged from 131 to 315 days and varied with mantle length. No significant differences were found in the size of males and females of equivalent ages. The relationship between ML and age for both sexes was best described by an exponential growth curve, probably because no early life stages were aged in this study. Only one mature male (ML 160 mm) was aged, and preliminary estimates suggest it was 386 days old. Instantaneous growth rates were low (0.54% ML/day and 1.4% BM/day) but consistent with enoploteuthid growth rates. When the growth rate of *L. lorigera* was corrected for temperature encountered during the animal's life, the growth rate was fast (0.47% BM/degree-days) and consistent with the hypothesis that small cephalopods grow fast and that large cephalopods grow older, rather than fast. Mature females were often mated and had spermatangia in a seminal receptacle on the dorsal pouch behind the nuchal cartilage. Males probably transfer spermatangia to the females using their long second and/or third arm pair since the paired terminal organs open far from the mantle opening.

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Introduction

Due to the full utilisation of neritic marine resources, the exploitation of deep-water ecosystems is increasing. The collection of basic biolog-

ical data on inhabitants of deep-water ecosystems is therefore important in designing management plans for sustainable exploitation of these systems. One of the most important inhabitants of these ecosystems are squid because they form a trophic link between epipelagic and bathypelagic ecosystems, as both active predators as well as important prey items (Clarke 1996). Currently, little is known about the life history (age, growth and reproduction) of most oceanic squid (Nesis 1995; Wood and O'Dor 2000; Arkhipkin 2004).

One particularly poorly understood oceanic family of squid is the Lycoteuthidae. This family consists of two subfamilies and four genera that comprise a total of five described species. One member of this family, *Lycoteuthis lorigera* (Steenstrup 1875), is an abundant squid in the Benguela ecosystem. This species dominates, in numbers the epibenthic cephalopod fauna on the continental slope of the South East Atlantic between 300 and 900 m depth (Roeleveld et al. 1992). Although no current fisheries exist, the high abundance and muscular appearance of *L. lorigera* suggests that this species might be a suitable resource for exploitation (Lipinski 1992).

L. lorigera is preyed upon by commercially important fish, such as deep-water Cape hake, *Merluccius paradoxus*, and Kingklip, *Genypterus capensis* (Lipinski et al. 1992), as well as several smaller cetacean species (Ross 1984), the Portuguese shark *Centroscymnus coelolepis* (Ebert et al. 1992), ribbonfish *Lepidopus caudatus* (Meyer and Smale 1991), the southern lantern-shark *Etmopterus granulosus* (Lipinski et al. 1992) and in New Zealand waters the species is preyed upon by petrels (Imber 1975). This species feeds on pelagic crustaceans and fishes, including myctophids (Voss 1962).

In spite of the abundance and the important role of *L. lorigera* in the South East Atlantic ecosystem, little is known about the biology of this species. Clearly, this needs to be improved, particularly as *L. lorigera* is a unique species amongst the oegopsids in having males that grow to a larger size than females. Another rare feature for squid is the presence of paired spermatophoric organs in males of *L. lorigera*. The aim of this study is to investigate the age, growth and mating system of *L. lorigera*.

The best method for estimating the age and growth of squid is counting statolith increments. Daily deposition of increments has been validated for numerous species of squid, including oegopsids (for review see Arkhipkin 2004). Although the daily deposition of increments has not yet been validated for *L. lorigera*, it has been in the paralarvae of the enoploteuthid *Abralia trigonura*, which belongs to a phylogenetic sistergroup of the Lycoteuthidae (Bigelow 1992; Young and Harman 1998).

The lifespan of oegopsid squid has been found to range from 3 months for the tropical Atlantic enoploteuthid *Pterygioteuthis gemmata*, which reaches an adult size of 3 cm (Arkhipkin 1997), to 2–3 years for the large sub-tropical mesopelagic octopoteuthid, *Taningia danae* (González et al. 2003). Most deepwater oegopsid squid, however, tend to live for a minimum of 1 year (Arkhipkin 2004). This is longer than the 1 year or less lifespan of myopsids (reviewed by Jackson 2004).

So far, no lycoteuthids have been aged. Given its unique biology, it would be interesting to determine where *L. lorigera* will fit on the oegopsid longevity scale. It is generally accepted that squid that inhabit colder waters (either polar or deeper waters) grow slower, and for longer (Arkhipkin 2004). To compensate for temperature differences, Wood and O'Dor (2000) introduced the *physiological timescale*; in which growth and longevity are corrected for temperature. Taking the animals' mean life time temperature of the environment into account, species that have a slow absolute growth rate can still grow relatively fast. This approach will be used in the interpretation of growth in *L. lorigera*.

In addition, information will be presented on the spermatophore production, morphology of the male reproductive apparatus and the mode of spermatophore transfer from male to female, to better understand the mating system of the species.

Materials and methods

An analysis of annual demersal surveys conducted by the Department of Environmental Affairs and Tourism (DEAT) of the Republic of

South Africa using the South African research vessel ''Africana'' and the Norwegian research vessel ''Dr. Fridtjof Nansen'' between 1986 and 2005 provided preliminary data on the distribution of *L. lorigera* around South Africa. This species was present in trawls between 192 and 1388 m deep, but was absent on the continental shelf (Fig. 1).

L. lorigera used for ageing purpose were collected during four research cruises in South African and Namibian waters (Table 1). The mantle length (ML) and body mass (BM) of animals were measured to the nearest mm and 0.1 g respectively. The stage of sexual maturity was determined using the method of Lipinski and Underhill (1995). Statolith nomenclature was after Clarke (1978). Statoliths were extracted and stored dry. The total statolith length (TSL) was measured to the nearest 0.01 mm.

Statoliths (Fig. 2) were sectioned frontally through the lateral dome using the method of Lipinski and Durholtz (1994) and polished using polishing cloth. Sectioned statolith images were recorded under phase contrast by an AxioCam MRc camera mounted on a Zeiss Axioscope 40 compound microscope. A TV2/3 ''C 0.63× camera mounted magnifying lens, together with a 10×/0.25 or a 40×/0.65 objective lens, were used to produce low and high resolution images, respectively. The images were recorded using AxioVision Ver. 4.2 software package supplied by Carl Zeiss Vision GmbH. A number of over-lapping high resolution images were taken of sectors with the highest ring clarity along transects from the nucleus, a distinct ring around the protostatolith, to the edge of the lateral dome (Fig. 3A). Increments were counted from images using the counting feature of the software. The rings in the outer part of the lateral dome (Fig. 3B) were often obscured, and extrapolation (based on the increment width of approximately 10 of the last countable rings) was then used to determine the number of rings in the periphery of the section. In order to increase accuracy, counting the increments on every axis was repeated five times. The mean of the separate counts was used for that particular axis.

The instantaneous relative growth rate (G) was calculated using the equation:

$G = (\ln W_2 - \ln W_1)/t$, where W_1 and W_2 are either ML (mm) or BM (g) at the beginning and end of time interval t (Forsythe and Van Heukelem 1987).

Wood and O'Dor (2000) introduced the physiological instantaneous relative growth rate (G/T). $G = (\ln W_2 - \ln W_1)/t_2 - t_1$, where W_1 is the hatchling mass (g) and W_2 is the mass of a mature female. $t_2 - t_1$ represents the age (days) at maturity. T is the average temperature encountered

Fig. 1 Distribution of *L. lorigera* around South Africa. Dots indicate presence of specimens in trawls and the dashed line indicates the 200 m depth contour
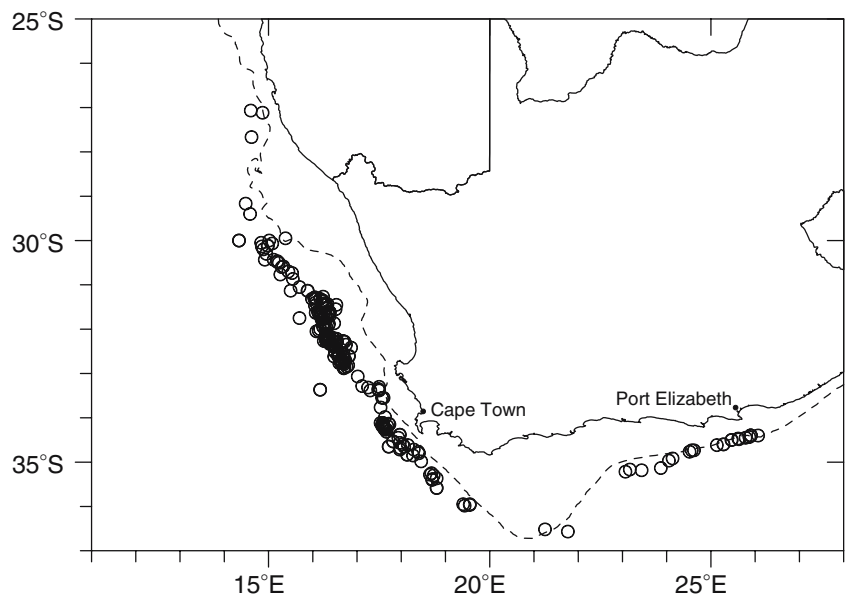
Table 1 Collection details and study purpose of *L. lorigera* specimens used in this study

Museum no./Station no.	*n*	Study purpose	Latitude	Longitude	Depth (m)	Collection dates	Vessel
NO 2 A7613	15	ML-BM/Ageing	27° 04′ S	14° 36′ E	280	16.08.1988	Africana
A24307–A24384	7	ML-BM/Ageing	30°–33° S	15°–17° E	314–448	21.01.2005–02.02.2005	Africana
NA 970-021–NA 1096-147	79	ML-BM/Ageing	28°–35° S	14°–18° E	392–582	10.02.2005–07.03.2005	Nansen
NA 1120, 1122, 1125	9	ML-BM/Ageing	28°–35° S	14°–18° E	529–605	01.10.2005–03.10.2005	Nansen
SAM-S3709	1	ML-BM/Testis mass	32° 43′ S	16° 43′ E	457	10.02.1988	Africana
SAM-S3481	1	ML-BM/Testis mass	35° 15′ S	18° 41′ E	Surface	08.02.1992	Africana
SAM-S2094	1	ML-BM/Testis mass	32° 29′ S	16° 35′ E	390	24.06.1987	Africana
SAM-S1793	1	ML-BM/Testis mass	34° 48′ S	18° 16′ E	510	06.07.1986	Africana
SAM-S1975	1	ML-BM/Testis mass	32° 15′ S	16° 24′ E	425	26.06.1987	Africana
SAM-S2046	3	ML-BM/Testis mass	33° 26′ S	17° 27′ E	680	05.03.1988	Africana
SAM-S2073	1	ML-BM/Testis mass	34° 40′ S	18° 12′ E	447	12.03.1988	Africana
SAM-S2078	3	ML-BM/Testis mass	34° 38′ S	18° 15′ E	482	14.03.1988	Africana
SAM-S3431	1	ML-BM/Testis mass	30° 12′ S	14° 53′ E	488	02.08.1990	Africana
SAM-S2047	2	ML-BM/Testis mass	33° 19′ S	17° 28′ E	451	06.03.1988	Africana
SAM-S789	2	ML-BM/Testis mass	35° 1′ S	18° E	600	24.05.1982	Africana
SAM-S3430	1	ML-BM/Testis mass	34° 39′ S	18° 04′ E	500	11.02.1992	Africana
SAM-S3436	1	ML-BM/Testis mass	32° 27′ S	16° 45′ E	357	15.02.1992	Africana
SAM-S4074	1	ML-BM/Testis mass	–	–	–	–	–
NA 892-036	2	ML-BM/Testis mass	29° 14′ S	14° 29′ E	451	9.05.2004	Nansen
NA-911-059	1	ML-BM/Testis mass	34° 23′ S	17° 48′ E	397	09.12.2004	Nansen
NA 631	1	ML-BM/Testis mass	32° 22′ S	16° 29′ E	450	02.06.2003	Nansen
NA 891	5	ML-BM/Testis mass	29° 21′ S	14° 29′ E	543	09.05.2004	Nansen

Fig. 2 Posterior (**A**) and anterior (**B**) view of respectively the left and right statolith of a mature female *L. lorigera* (ML = 91 mm)
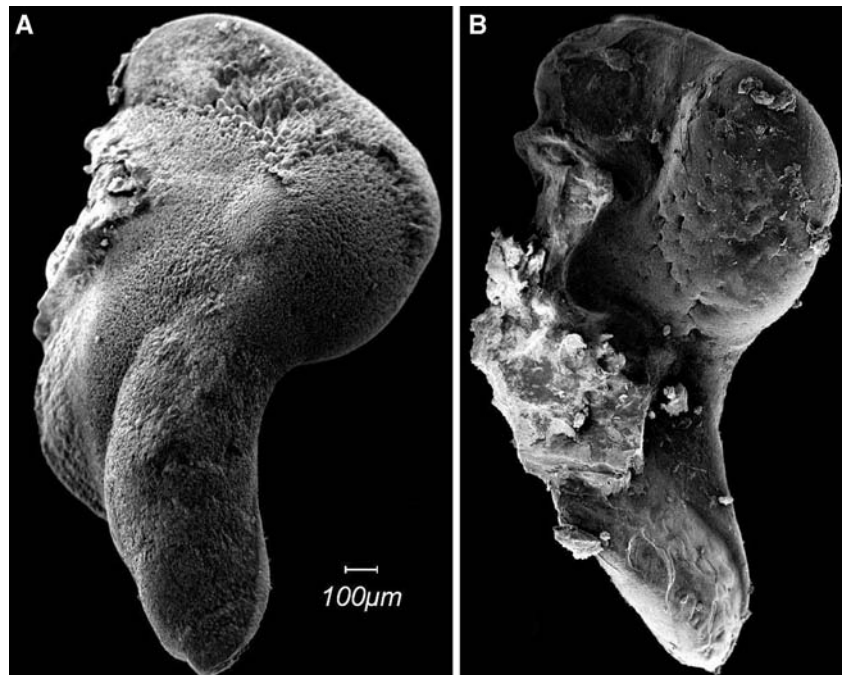
during the individual's lifetime. *G/T* is expressed in degree-days.

In order to estimate hatching mass for *L. lorigera*, a value of 80% of the egg mass was used.

The egg mass was calculated from the egg diameters (1.1 ± 0.1 mm) obtained from eggs from the oviduct. The eggs were assumed to be spherical (volume $4/3\pi r^3$), and to have a density

Fig. 3 A sectioned statolith of a mature female *L. lorigera* (ML 100 mm; 291 increments) (**A**) overview of a frontal section through the dorsal dome and the wing (**B**) Detail of the periphery of the dorsal dome showing narrow increments of approximately 1 μm
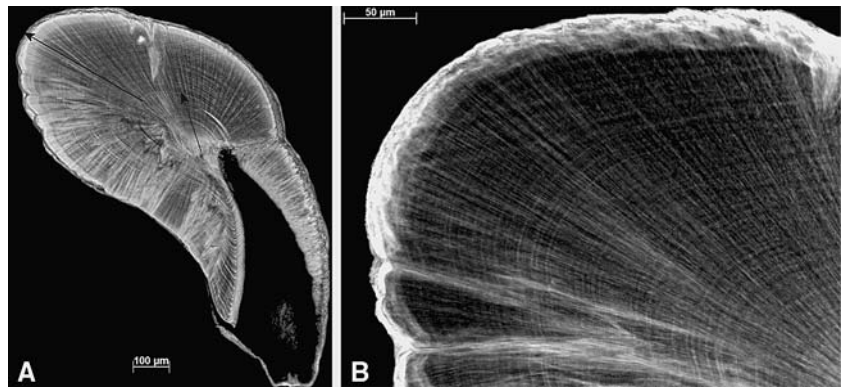
equal to the density of water (Wood and O'Dor 2000). The obtained value was compared to the mass of eggs preserved in 70% ethanol and was found to be realistic.

The mass of a mature female was estimated by using the mean mass of the mature females examined in this study (=45.1 g). The same was done to estimate the age at maturity for females (=299 days). Although both body mass and age varied, this was taken as a representative figure to estimate physiological growth rate. The average lifetime temperature (T) was estimated to be 8°C (Shannon 1985; depth 600 m at 24° S). To compare the obtained results with the results of Wood and O'Dor (2000), only the physiological growth rate of the female was estimated.

The body mass and testis mass of 29 mature males of *L. lorigera* (Table 1) were determined. The spermatophores of three males were counted and measured. The body mass obtained for males was used for the ML–BM relationship because of the absence of fresh mature males. The males were fixed in formalin and stored in 70% ethanol.

Results

Statoliths

TSL for females was 2.25 mm (ML = 99 mm) and 2.56 for males (ML = 174 mm). The relative size of the statoliths (% ML) decreased with increasing mantle length (TSLI = –0.0185 ML + 3.932; R^2 = 0.93).

There was no significant difference between the TSL of males and females of similar sizes (ML 54–82 mm; TSL 1.62–1.95 μm; Student *t*-test: $P > 0.05$: $n = 7$). The relationship between TSL and the number of increments (TSL = 0.08 age$^{0.57}$; R^2 = 0.94) indicates that the growth rate of the statoliths slows down with size (and age) by the deposition of smaller increments. This was confirmed in sectioned statoliths where the increments were widest in the first 100 days of the animal's life, with a maximum increment width of approximately 4 μm. Thereafter, the increment width decreased gradually to approximately 1 μm.

The nucleus was distinct in sectioned statoliths, with a mean maximum length of 22 μm (SD = 2.1; $n = 32$; range 18.25–26.42 μm). The increments that were closest to the nucleus had to be counted along an axis that runs towards the concave side of the statolith (Fig. 3A). At the point where increments were visible in the lateral dome, the counting axes were linked, and counting was completed along the second axis through the lateral dome. With the exception of one mature male in which 18% of the axis was extrapolated, extrapolation never exceeded 12%. For over 80% of the statoliths, a minimum of 93% of the total counting axis was readable. The agreement between counts of paired statoliths was good (mean difference = 2.7% ± 2.5%; $n = 13$), suggesting that our counts were accurate. Because of additional access to statoliths, another 9 statoliths of mature females were sectioned and growth increments were counted. Four of these statoliths could be completely counted and in the other five between 93 and 98% of all increments could be read.

Age and growth

Mature males were almost twice as large as mature females (Fig. 4). The allometric equations for the relationship between BM and ML was $BM = 0.0002ML^{2.72}$ for females and $BM = 0.0002ML^{2.67}$ for males.

The ML of mature females ranged from 88 to 110 mm, corresponding with an age of 290–315 days (Figs. 4, 5A). The ML of (formalin preserved) mature males ranged from 136 to 194 mm (Fig. 4). The smallest (unsexed) individual aged had a ML of 35 mm and was 131 days old. The smallest female measured had a ML of 46 mm ML and was 152 days old, while the youngest male measured 53 mm in ML and was 175 days old (Fig. 5A). The only mature male (ML = 160 mm) aged was estimated to have 386 growth increments. The size range of the seven immature males was 54–82 mm. Since the age of males and females of equivalent size did not differ significantly (Student *t*-test: $P > 0.05$; $n = 7$), it suggested that the growth of young males is comparable to that of females, but the males attain a bigger overall size because they grow for longer.

Exponential, linear and power growth curves were fitted to the ML- and BM-at-age data, for juveniles, females and males separately, as well as the pooled data (Table 2). Of these curves, both the ML-at-age and BM-at-age relationships were best described by an exponential growth curve (Fig. 5).

Using the exponential growth curve, the instantaneous growth rates for ML and BM were calculated to be 0.54% ML/day and 1.4% BM/day, respectively (Fig. 5).

To determine the physiological instantaneous growth (G/T), the hatching size of *L. lorigera* was estimated to be 0.00056 g while size at maturity was taken as the mean BM of the mature females for which age was determined (45.1 g). The mean age a mature female was 299 days. Assuming an average life time temperature of $T = 8°C$ (Shannon 1985; 600 m of depth), it was estimated that these females had an instantaneous relative growth rate (G) of 3.8% BM/day and a physiological instantaneous relative growth rate (G/T) of 0.47% BM/degrees-day. The G calculated here is different from the earlier fitted growth curve because it is based on only two data points: the size at hatching and the size at maturity.

Spermatophore transfer

The male reproductive system consists of a small testis and a small spermatophoric organ with a short terminal organ. Testis size varied between 19 and 55 mm in length and a maximum width of 2–9 mm. The largest testis mass of *L. lorigera* was 0.6 g (Fig. 6). There seemed to be a gradual increase in testis mass with mantle length, up to a

Fig. 4 Mantle length–body mass relationship for male, female and juvenile *L. lorigera*. Note that the values for mature males are based on formalin preserved specimens
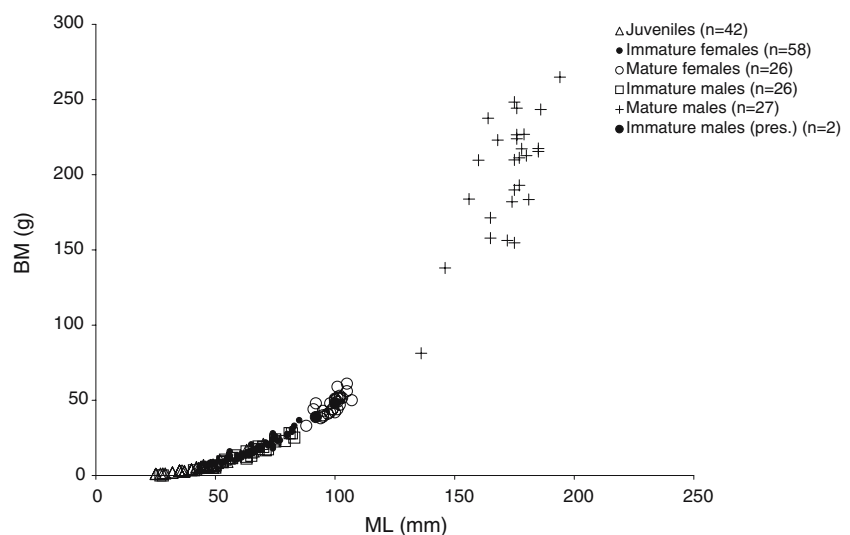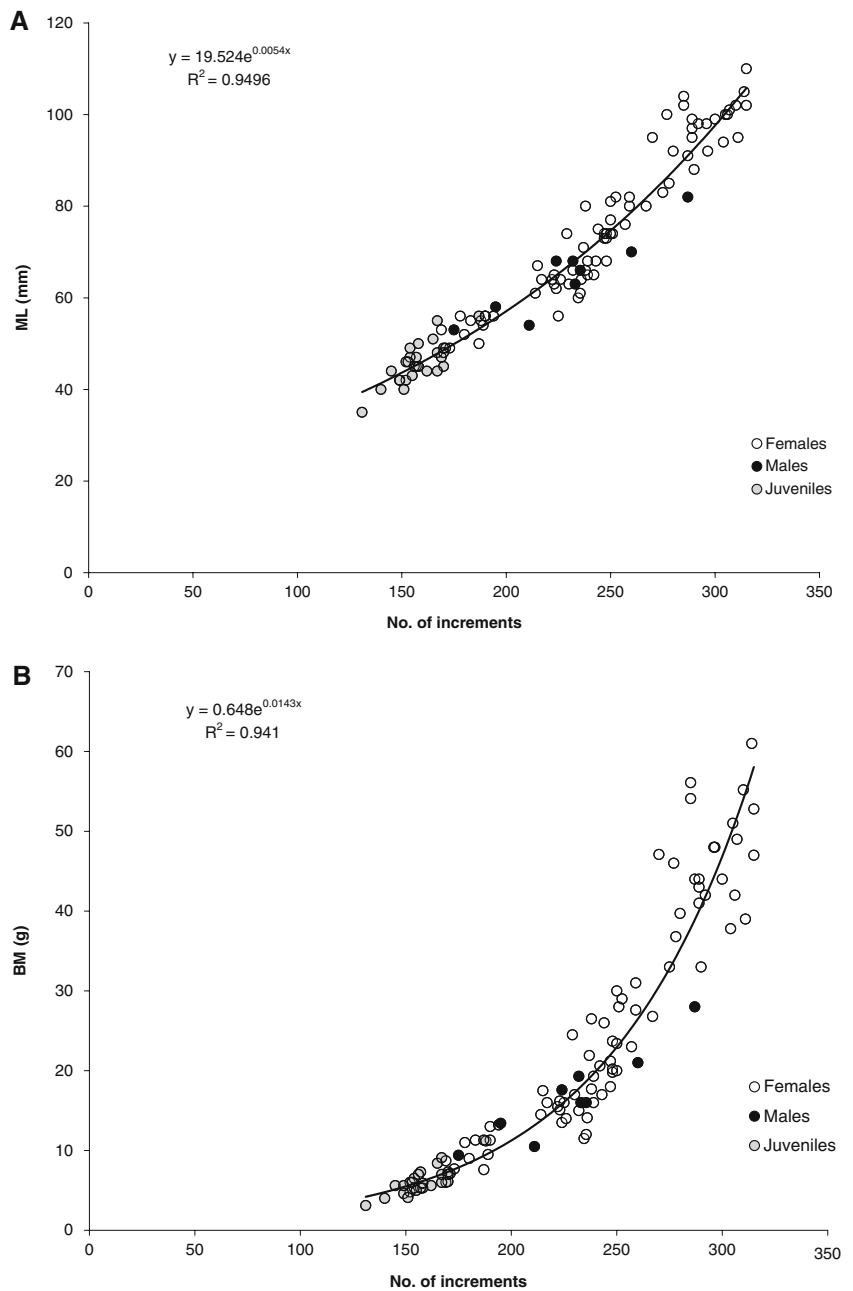
Fig. 5 Growth curve of pooled data (**A**) ML—no. of statolith increments (**B**) BM—no. of statolith increments

ML of 165 mm when testis mass decreased, most probably due to the production and transfer of spermatophores.

The terminal organ ranged from 28 to 37 mm in large mature males, with the exception of 17 mm in a mature male of 136 mm ML, and opened under the gill between 65 and 50 mm from the mantle margin. The lining of the terminal organ was transparent, with the spermatophores visible through the lining. The spermatophores were situated with their aboral end toward the opening of the terminal organ.

Spermatophores were typified by a short coiled sperm mass (10–28% TSL) and a cement body (32–57% TSL) that were attached laterally to the sperm reservoir. The length of the ejaculatory

Table 2 Values for growth curves fitted for pooled and separate data for *L. lorigera*

		ML— no. of increments			BM— no. of increments			
		a	*b*	R^2	*a*	*b*	R^2	*n*
Juveniles	Linear function	0.3125	–3.7393	0.6321	0.1187	–12.668	0.6557	27
	Power function	0.174	1.0997	0.6529	1.00E-06	3.043	0.6957	
	Exponential function	15.18	0.0069	0.6429	0.2777	0.0193	0.6939	
Males	Linear function	0.2515	7.3067	0.857	0.1594	–19.55	0.8696	9
	Power function	0.6041	0.8606	0.8378	2.00E-04	2.1335	0.8483	
	Exponential function	26.736	0.0038	0.8517	1.847	0.0095	0.8535	
Females	Linear function	0.3982	–22.599	0.9025	0.3276	–54.421	0.8235	74
	Power function	0.0754	1.2532	0.9041	6.00E-07	3.178	0.8845	
	Exponential function	19.752	0.0053	0.9226	0.8044	0.0135	0.8967	
All	Linear function	0.3605	–13.139	0.9285	0.2678	–39.16	0.8415	110
	Power function	0.1289	1.1557	0.9385	9.00E-07	3.0897	0.9393	
	Exponential function	19.524	0.0054	0.9496	0.648	0.0143	0.941	

Number of animals for which the no. of increments was determined is indicated as *n*. Linear function: $y = ax + b$; power function: $y = ax^b$; exponential function: $y = ae^{bx}$
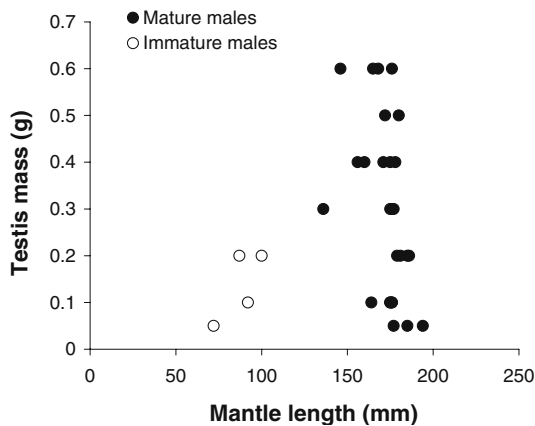
Fig. 6 Testis mass and ML relationship for immature and mature male *L. lorigera*

apparatus varied between 30 and 40% TSL. Spermatophore length was 8.0–12.6 mm in a male of 186 mm ML, and 9.0–11.0 mm in a small mature male of 136 mm ML.

An interesting feature of the reproductive system of male *L. lorigera* was the presence of paired spermatophoric and terminal organs. These paired organs were both functional, as spermatophores were found in both terminal organs. The number of spermatophores in the packed terminal organs of three males did not vary significantly within individuals (130 and 135; 54 and 55; 126 and 132 spermatophores in the right and left organ, respectively). However, in a small mature male (ML 136 mm) the left terminal organ contained 14 spermatophores, while the right spermatophoric organ and terminal organ were not fully developed. In addition, 25 spermatophores containing no sperm were found in the left terminal organ, while the right terminal organ was empty in a presumably spent male (ML 176 mm, BM 142 g).

Females possessed a specialised pouch for receiving the spermatangia, the seminal receptacle. The opening of the seminal receptacle was situated dorsally in the midline, where the mantle and the visceral sac fused, directly behind the posterior end of the nuchal cartilage (Fig. 7). The organ was only visible when the anterior 40 mm of the dorsal mantle, including gladius, were removed. The receptacle was approximately 10 mm long and had a maximum width of 4 mm at the opening, and had rugose walls. Inside the receptacle, a bundle of 10–15 spermatangia were found, adherent to each other, and the bundle occupied the whole lumen. Approximately 1–2 mm of the aboral ends of the spermatangia was protruding from the receptacle. The cement bodies of the spermatangia could be seen as reddish bodies at the oral end of the bundle, which was situated at the posterior end of the receptacle.

The paired oviducts of 10 mature females contained between 721 and 3798 ova. The maximum diameter of the ova measured 1.1 ± 0.1 mm (*n* = 10).
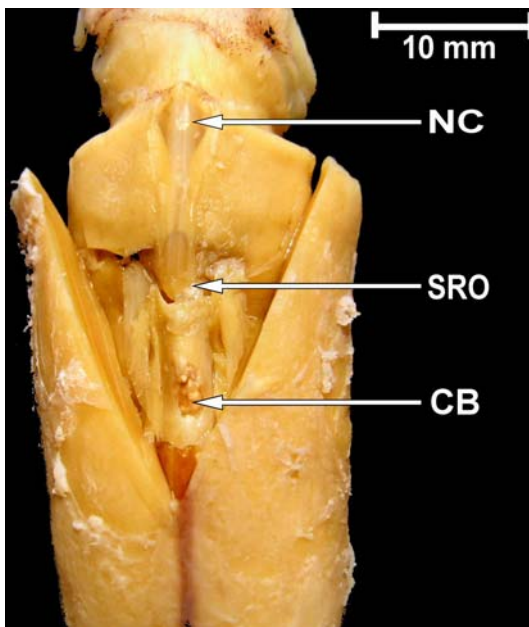
Fig. 7 Dorsal view of the mantle of a preserved mature female *L. lorigera* (ML = 100 mm) showing the opening of the seminal receptacle (SRO), the nuchal cartilage (NC) and the cement bodies (CB) of the spermatangia. A triangular part of the mantle has been removed to show the seminal receptacle

The nidamental gland length of 64 females increased with the onset of maturity. The glands of stage I females were 4.3 ± 1 mm ($n = 15$) in length, while those of stage II, III, IV and V were 8 ± 1.1 mm ($n = 21$), 18.5 ± 0.7 mm ($n = 2$), 20.7 ± 2.5 mm ($n = 6$) and 27.6 ± 4 mm ($n = 20$), respectively.

Discussion

Age and growth

A strong relationship was found between body mass and mantle length for both males and females. There was little variation in size at maturity for females, with the smallest mature female measuring 84% of the ML of the largest female. In comparison, the smallest mature male measured 70% of the ML of the largest male.

L. lorigera exhibits a strong sexual size dimorphism (SSD), with males attaining almost twice the size of females (ratio $ML_{max}\female/\male = 0.54$). Male biased sexual size dimorphism is common in the neritic squid family Loliginidae, but is unknown for oegopsids (Nesis 1987). This gives rise to the idea that there are common ecological or evolutionary forces acting on body size in males and females in both *L. lorigera* and loliginids. Male biased SSD generally occurs when there is strong male to male competition, female preference for large male size (sexual selection), or when there is trophic dimorphism (Fairbairn 1997).

Growth increments in the statoliths of *L. lorigera* were well resolved but extrapolation was often necessary to estimate final age. All the mature females aged in this study were 315 days old or younger, suggesting that their lifespan is one year or slightly less. In contrast, the one mature male we had access to was estimated to be more than a year old (386 days). This estimate, however, should be considered preliminary because 18% of its age was extrapolated. Nevertheless, it suggests that males of this species probably live longer than females.

The relationship between BM and age for squid between 35 and 105 mm ML was best described by an exponential growth curve. However, this curve is unlikely to adequately describe the growth of this species entire ontogenesis. A recent comparison of growth curves to describe cephalopod growth found that the exponential growth curve was the best fit for only the two smallest sample sizes (early life history stages were underrepresented) in a study of 12 species of squid. The overall best result was obtained when the Schnute curve was fitted, a 4 parameter sigmoid growth curve (Arkhipkin and Roa-Ureta 2005). It is likely that the lack of individuals <35 mm ML and greater than 110 mm ML is biasing our attempts to adequately describe growth. Unfortunately, squid of these sizes are proving extremely difficult to catch.

One objective in this study was to get an idea of the growth rate of *L. lorigera* and compare it with other squid species in the same ontogenetic stage and size class. For this reason, *G* was calculated from the fitted exponential growth curve to the obtained age at size data. Although the instantaneous growth rates of 0.54% ML/day and 1.4% BM/day were low, they were similar to those reported for the enoploteuthid squid

Abraliopsis pfefferi (Arkhipkin 1996) in their mature ontogenetic phase. Such similarities in growth rates might be explained by the fact that lycoteuthids and enoploteuthids are phylogenetic sistergroups (Young and Harman 1998).

Based on the instantaneous growth rate (*sensu* Wood and O'Dor (2000)) of 3.8% BM/day of *L. lorigera*, it is a slow growing squid. However, when this value is corrected for temperature, the physiological instantaneous growth rate (*G/T* = 0.47% BM/degree-days) of *L. lorigera* is higher than the growth rates presented for any of the teuthids examined by Wood and O'Dor (2000).

The physiological relative instantaneous growth rate and size at maturity found for *L. lorigera* correspond with the trend found by Wood and O'Dor (2000) for several other coleoids. There is a negative correlation between physiological relative instantaneous growth rate and size at maturity, implying that small cephalopods grow faster and that large cephalopods grow older, rather than faster. There seems to be a life history trade-off in squid between maturing early at a small size and maturing later at a large size, where fitness is increased by a short period between hatching and maturity for fast growing small squid. On the other hand, larger squid have a higher fecundity, which also increases fitness (Wood and O'Dor 2000). The low instantaneous growth rate for *L. lorigera*, and the contrasting high physiological instantaneous growth rate, show that life for some oceanic squid may appear slow, but when corrected for the low temperature these species encounter compared to neritic squid, life for oceanic squid is fast.

Mating system

Besides size, additional sexual dimorphic characters of the males are the extreme elongation of the second and third arm pair. Villanueva and Sanchez (1993) have studied these features in detail, stating that the first and fourth arm pairs do not show hectocotylisation in *L. lorigera*, but that the second and third arm pairs show extreme elongation and modification. The modification of the third arm pair accounts for one third of the total arm length. Although Forch and Uozumi

(1990) suggested modification of the fourth arm pair, they added that this might be due to sucker loss or regeneration. A general rule in the reproductive systems of squid seems to be that species that lack a hectocotylus have a long muscular terminal organ, which is used in the transfer of spermatophores (Nesis 1995). The terminal organs of *L. lorigera* are very short, and protrude from under the gills, about 50–65 mm from the mantle opening. Nesis (1995) mentioned that the short terminal organs in *L. lorigera* probably indicate functional immaturity, and the organs should grow much longer towards functional maturity. We do not agree with that, because spent males were found with empty spermatophores and short terminal organs. Without a long muscular terminal organ, a hectocotylus or specialised arm is necessary for the transfer of spermatophores to the female. The elongated and modified arm pairs two and three described by Villanueva and Sanchez (1993) are therefore very likely to play a role in spermatophore transfer. Additionally, the symmetry in both the elongation of arm pairs two and three and the terminal organs may be another clue that supports transfer of spermatophores using the long arms.

Males exhibit a strong decline in testis mass, and probably continuation of growth after reaching maturity. The reduction of testis mass is caused by the use of sperm for the production of spermatophores, which is generally an irreversible process. Such reduction in testis mass is also seen in spent males of the deepwater squid *Moroteuthis ingens*, a terminal spawner (Jackson and Mladenov 1994).

Paired spermatophoric complexes are rare in squid. The only other squid that share this development with *L. lorigera* are *Histioteuthis hoylei*, *Selenoteuthis scintillans* and *Lycoteuthis springeri* (Nesis 1982; from Arkhipkin 1992), the latter two being members of the same family as *L. lorigera*. Both male organs of *L. lorigera* contained spermatophores, indicating that they were both functional. Comparing the number of spermatophores in the terminal organ and the number of spermatangia in mated females indicates that males are capable of mating with several females.

The seminal receptacle is here described for the first time. The position of the organ is similar

to that of pyroteuthids (Young and Harman 1998). The organ has a small opening and it is plausible that the males use their modified long arm pairs two and/or three for the deposition of spermatangia into the seminal receptacle. Long, thin arms would be able to grasp the spermatophores from the opening of the terminal organ that is situated quite deep in the mantle cavity. Furthermore, the thin arms could be of use in depositing the spermatangia into the small opening of the seminal receptacle.

References

Arkhipkin AI (1992) Reproductive system structure, development and function in cephalopods with a new general scale for maturity stages. J Northw Atl Fish Sci 12:63–74

Arkhipkin AI (1996) Age and growth of the squid *Abraliopsis pfefferi* (Oegopsina: Enoploteuthidae) from the central-east Atlantic based on statolith microstructure. Sci Mar 60:325–330

Arkhipkin AI (1997) Age of the micronektonic squid *Pterygioteuthis gemmata* (Cephalopoda; Pyroteuthidae) from the central-east Atlantic based on statolith growth increments. J Moll Stud 63:287–290

Arkhipkin AI (2004) Diversity in growth and longevity in short-lived animals: squid of the suborder Oegopsina. Mar Freshwater Res 55(4):341–355

Arkhipkin AI, Roa-Ureta R (2005) Identification of ontogenetic growth models of squid. Mar Freshwater Res 56:371–386

Bigelow KA (1992) Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily increments in statoliths. Mar Ecol Prog Ser 82:31–40

Clarke MR (1996) Cephalopods as prey. III. Cetaceans. In: Clarke MR (ed) The role of cephalopods in the World's oceans. Philos Trans Roy Soc Lond, B. 351:1053–1065

Clarke MR (1978) The cephalopod statolith—an introduction to its form. J Mar Biol Ass UK 58:701–712

Ebert DA, Compagno LJV, Cowley PD (1992) A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) Benguela trophic functioning. S Afr J Mar Sci 12:601–609

Fairbairn DJ (1997) Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Ann Rev Ecol Syst 28:659–687

Forch EC, Uozumi Y (1990) Discovery of a specimen of *Lycoteuthis lorigera* (Steenstrup, 1875) (Cephalopooda: Teuthidae) from New Zealand and additional notes on its morphology. NZ J Mar Freshwater Res 24:251–258

Forsythe JW, Van Heukelem WF (1987) Growth. In: Boyle PR (ed) Cephalopod life cycles, volume II. Comparative reviews. Academic Press, London, UK, pp 135–156

González AF, Guerra A, Rocha F (2003) Recent advances in life history and ecology of the deep-sea hooked squid *Taningia danae*. Sarsia 88:297–301

Imber MJ (1975) Lycoteuthid squid as prey of petrels in New Zealand seas. NZ J Mar Freshwater Res 9(4):483–492

Jackson GD, Mladenov PhV (1994) Terminal spawning in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae). J Zool 234(2):189–201

Jackson GD (2004) Advances in defining life histories of myopsid squid. Mar Freshwater Res 55(4):357–365

Lipinski MR (1992) Cephalopods and the Benguela ecosystem: trophic relationships and impact. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) Benguela trophic functioning. S Afr J Mar Sci 12:791–802

Lipinski MR, Payne AIL, Rose B (1992) The importance of cephalopods as prey for hake and other groundfish in South African waters. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) Benguela trophic functioning. S Afr J Mar Sci 12:651–662

Lipinski MR, Durholtz MD (1994) Problems associated with ageing squid from their statoliths: towards a more structured approach. Ant Sci 6(2):215–222

Lipinski MR, Underhill LG (1995) Sexual maturation in squid: quantum or continuum? S Afr J Mar Sci 15:207–223

Meyer M, Smale MJ (1991) Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 1. Pelagic predators. S Afr J Mar Sci 10:173–191

Nesis KN (1982) Concise key for determination of cephalopod molluscs of the world Ocean. M., Liogkaya I pisch. promyslennost, 360 pp

Nesis KN (1987) Cephalopods of the world. T.F.H. Publications, Neptune City, NJ

Nesis KN (1995) Mating, spawning and death in oceanic cephalopods: a review. Ruthenica 6(1):23–64

Roeleveld MAC, Lipinski MR, Augustyn CJ, Stewart BA (1992) The distribution and abundance of cephalopods on the continental slope of the eastern south Atlantic. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds) Benguela trophic functioning. S Afr J Mar Sci 12:739–752

Ross GJB (1984) The smaller cetaceans of the south east coast of southern Africa. Ann Cape Prov Mus (Nat Hist) 15(2):173–410

Shannon LV (1985) The Benguela ecosystem Part I. Evolution of the Benguela, physical features and processes. Oceanogr Mar Biol Ann Rev 23:105–182

Villanueva R, Sanchez P (1993) Cephalopods of the Benguela Current off Namibia: new additions and considerations on the genus. Lycoteuthis J Nat Hist 27(1):15–46

Voss GL (1962) A monograph of the cephalopoda of the North Atlantic I. The family Lycoteuthidae. Bull Mar Sci Gulf Caribbean 12(2):264–305

Wood JB, O'Dor RK (2000) Do larger cephalopods live longer? Effects of temperature and phylogeny on interspecific comparisons of age size and maturity. Mar Biol 136:91–99

Young RE, Harman RF (1998) Phylogeny of the "Enoploteuthid" families. Smithsonian Contrib Zool 586:257–271