Growth of *Sthenoteuthis oualaniensis*, using a new method based on gladius microstructure

Vyatcheslav A. Bizikov


A study of individual and group growth rates based on a method of growth determination using the gladius was carried out in two populations of the purple-back flying squid (*Sthenoteuthis oualaniensis*) in the Arabian Sea. The duration of the life cycle in all populations and size groups examined was approximately one year. The growth pattern of linear increase was either slightly S-shaped or almost linear, while growth in weight followed a power-type pattern. Generally, females grew faster than males. Use of the gladius as a recording structure makes it possible to study the real growth of a specimen, rather than the statistical correlation of length/weight versus age, as in the commonly used statolith method. Analysis of individual growth rates in large-sized spawning females revealed a growth rhythm with roughly a one-month periodicity in which phases of rapid growth (17–21 days; 1.6–3.6 mm per day) alternate with phases of slow growth (12–14 days; 0.4–1.2 mm per day). This new method is simple to use and may be applied even on board a vessel during research cruises.

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Introduction

Cephalopod age and growth investigations have been developing over the past two decades, with the most advanced aging method based on the daily growth marks on the statoliths. The statolith method enables estimation of the absolute age of a squid in days and calculation, more or less, of the parameters of the pooled growth curve. However, it cannot be accurately applied in the analysis of individual growth rates. Determination of individual growth gives better information about the real growth of a species than does pooled growth rates.

A method of determining growth in individual squid using time-recording structures has not existed until now. One of the most promising squid structures for this purpose is the gladius (pen), a chitinous supporting structure within the muscle along the dorsal midline of the mantle. While the shape of the gladius varies greatly, its morphological structure seems common to all oegopsid and myopsid squid (Naef, 1921; Toll, 1982). Typically, the gladius of recent squid as well as the shell of fossil Coleoidea consists of three morphological parts – the proostracum, conus, and rostrum – and has three shell layers – the ostracum (middle layer), hypostracum (inner layer), and periostracum (outer layer) (Fig. 1) (Bizikov, 1987, 1991). The conus consists of the conus *sensu stricto* and cone flags. The proostracum is always present in the gladius, while the rostrum and conus are absent in some species.

Naef (1921) was apparently the first scientist to describe the growth lines on the gladius proostracum (Naef, 1922). Much later, La Roe (1971) and Spratt (1978) briefly mentioned the growth increments in the gladii of two loliginid squid: *Sepioteuthis sepioidea* and *Loligo opalescens*, respectively. However, they were unable to interpret the periodicity of the formation of the striae.

Recently, growth increments have been found along the dorsal surface of the proostracum of the purple-backed squid (*Sthenoteuthis oualaniensis* (Leeson, 1830)) from the Arabian Sea (Arkhipkin and Bizikov, 1991). As the gladius length correlates well with the mantle length, it is possible to calculate individual size-specific growth rates with a degree of resolution previously impossible. In the study mentioned above, growth rates calculated from the gladii showed a high correlation with those calculated using statoliths, supporting the hypothesis of daily periodicity in the gladius increments. They concluded that the gladius and statolith provide quite different information for growth and
age studies: the increments in the statolith provide an estimate of the absolute age of a specimen but it cannot be used to back calculate daily growth rates because variation in the orientation of the statolith during preparation affects the results. In contrast, the increase in the gladius can be used to estimate daily growth of an individual but cannot be used to estimate absolute age because the increments become progressively difficult to distinguish as the origin is approached.

Thus, we suggest the gladius is a valuable tool for squid life history reconstruction. However, more research into gladius increment analysis is needed. The aim of this article is to give an account of results from a study of individual as well as group growth in different populations of *S. oualaniensis* in the Arabian Sea using the method based on the growth increments in the gladius.
Materials and methods

Squid (*S. oualaniensis*) were caught by jigs and pelagic trawls during the winter cruises of RV “Hydrobiolog” (1987) and RV “Professor Vodyanotsky” (1990) in the Red Sea, the Gulf of Aden, and the northwestern Arabian Sea: 15°00′N–21°30′N and 59°15′E–65°30′E. Biological analysis was performed on 7900 specimens. From this large sample 44 squid were dissected and their gladii were analysed on board the ships. Among these specimens were six squid (three males and three females) from the tropical population and 38 squid from the Arabian population, including 26 large-sized females, 5 medium-sized females, and 7 males (population structure of this species is discussed below).

Gladii were extracted from fresh squid and were preserved in a 4% formalin solution. Growth was analysed using the middle plate (rachis) of the gladius proostracum which is formed by the medium shell layer, namely the ostracum (Fig. 1A, C). No special treatment is necessary prior to counting. The gladius was simply washed in warm soapy water and the increments counted on intact gladii under zoom magnification (14–56×) with either incident or reflected light.

Periodic growth lines (increments) were observed on the dorsal surface of the middle plate of the gladii as a series of microstructural ridges (Fig. 2). The shape of increments corresponds to the form of the gladius anterior edge. The increments are best expressed in the anterior third of the gladius; in the posterior direction they become progressively fainter and can hardly be recognized in the posterior third of the gladius near the stem.

Prior to counting, each gladius was marked with India ink at 1-cm intervals starting from the posterior end (cone apex). Increments were counted and measured in each 1-cm interval from the anterior end until the increments became unreadable in the region near the stem. As the gladius length in Ommastrephidae is almost equal to the dorsal mantle length, it was possible to reconstruct size-specific growth rates by dividing the length of the interval (10 mm) by the number of increments counted in that interval. Average growth rates for each 1-cm interval were then calculated by taking the mean growth rates (in mm day⁻¹) of all gladii in a particular group. To avoid mixing specimens with different growth parameters, growth rates were calculated separately for males and females as well as for squid from different populations and size groups. Cumulative growth curves were made by integrating the average growth rates for each 1-cm interval, from the smallest to the largest mantle length (Table 1). The curves
Table 1. Growth and age data generated from cumulative growth curve of female S. oualaniensis from a tropical population.

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<td>No. of increments</td>
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<td>SQ No. 1</td>
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<td>Mean number of increments</td>
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<td>8.3</td>
<td>11.7</td>
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<td>Growth rates (mm/day)</td>
<td>1.11</td>
<td>1.46</td>
<td>1.20</td>
<td>0.86</td>
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<td>1.15</td>
<td>1.50</td>
<td>1.25</td>
<td>1.15</td>
<td>1.50</td>
<td>1.36</td>
<td>1.30</td>
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<td>1.33</td>
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<td>Cumulative average growth (average total number of increments)</td>
<td>0</td>
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<td>16</td>
<td>24.3</td>
<td>36</td>
<td>44.3</td>
<td>53</td>
<td>59.7</td>
<td>67.7</td>
<td>76.4</td>
<td>83.1</td>
<td>90.4</td>
<td>98.1</td>
<td>106.1</td>
<td>113.6</td>
<td>120.1</td>
<td>127.6</td>
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<td>Age (days)</td>
<td>95</td>
<td>108.0</td>
<td>111.0</td>
<td>119.3</td>
<td>131.0</td>
<td>139.3</td>
<td>148.0</td>
<td>154.7</td>
<td>162.7</td>
<td>171.4</td>
<td>178.1</td>
<td>185.4</td>
<td>193.1</td>
<td>201.1</td>
<td>208.6</td>
<td>215.1</td>
<td>222.6</td>
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</table>

SQ Nos. 1–3 = three individual females.
Growth rate = the length of the interval (mm) divided by the mean number of increments in the interval.
Age = estimate of age (in days) assuming that one gladius increment corresponds to one day. The “initial age” at a length of 8 cm is estimated to be 95 days based on statolith data (Arkhipkin and Bizikov, 1991). Age values were calculated by adding the growth values (total number of increments) to the initial age of 95 days.
obtained in this way were fixed upon the mantle length scale. To fix them upon the time-scale it was necessary to estimate the initial age at the starting point of the curve on the basis of the statolith method.

In a case of a simple pattern of growth in length, growth was approximated by the linear regression:

$$DML = A + B \cdot T \quad (1)$$

where $DML =$ mantle length (mm), $T =$ age in days; $A$ and $B =$ coefficients to be estimated by the least squares method.

When the growth in length follows a non-linear pattern, it is simply described without fitting any equation.

The growth in weight was reconstructed by transformation of growth in length (Ricker, 1975; Ursin, 1979) on the assumption that:

$$W = A \cdot L^B \quad (2)$$

The curves of growth in weight were also well described by the power regression:

$$W = A_1 \cdot T^{B_1} \quad (3)$$

where $W =$ squid weight (g); $T =$ age (days); $A_1$, $B_1 =$ coefficients.

To estimate the coefficients $A$ and $B$ or $A_1$ and $B_1$, Equations (2) and (3) were transformed into logarithmic (linear) form:

$$\ln W = \ln A + B \cdot \ln L \quad (4)$$

$$\ln W = \ln A_1 + B_1 \cdot \ln T \quad (5)$$

The values of $A$ and $B$ in Equations (2) and (4) have been estimated as: $A = -3.155 \cdot 10^{-5}$; $B = 2.996$ ($r = 0.99; n = 330$).

Instantaneous growth rates were calculated for $S$. oualaniensis for successive 30-day intervals of the growth curve with the equation (Forsythe and Van Heukelem, 1987):

$$G = \frac{((\ln W_2) - (\ln W_1))/((T_2 - T_1)) \times 100 \text{ } (\%)}{100 \text{ } (\%)} \quad (6)$$

where $W_1$ and $W_2$ are values of length (transformed to weight) at time $T_1$ and $T_2$.

**Results**

**Microstructure of gladius increments in $S$. oualaniensis**

Growth lines in the middle plate of the gladius are narrow and well-defined (Fig. 2). The boundaries between increments are observed as narrow light stripes; high magnification reveals that the stripes consist of numerous folds on the gladius dorsal surface (Fig. 3). The increments are more distinct and narrow near the border of the middle plate than in the axial region (Fig. 4). Gladii of young squid are characterized by broader growth increments in comparison to adults; increment width to gladius width ratio varies from 1:3 to 1:5 (Fig. 5). The increment width to gladius width ratio in adults varies from 1:8 to 1:14.

Prior to the calculation of growth rates, all squid were divided into two groups according to differences in gladius morphology and some biological characters. The first group was called the “tropic population”, because these squid were distributed in tropical regions of the Indian and Pacific Oceans. The northern border of their distribution in the Arabian Sea lies between 15°N and 17°N and they were absent in the Red Sea and the Aden Gulf (Fig. 7). Gladii in this group are characterized by a pair of doubled (“forked” in the anterior part) ribs along the margins of the middle plate of the proostracum (Fig. 6). The conus is wide and short. Dorsal mantle length (DML) in mature females is from 20 to 25 cm and in mature males from 15 to 20 cm.

The second group was called the “Arabian population”, because these squid were distributed in the Arabian and Red Seas, in the Aden Gulf and the Gulf of Oman (Fig. 7). Gladii in this group have a pair of simple (not forked in the anterior part) ribs along the margins of the middle plate (Fig. 6). The conus is narrow and long. Two different size forms of mature $S$. oualaniensis females were observed in the Arabian population: a large-sized form with the DML varying from 45 to 62 cm and the medium-sized form (DML from 20 to 27 cm). Among the 7900 specimens examined there were just a few large mature females with mantle lengths of 30 to 38 cm. Males could not be classified in this manner, but the dimensions of mature specimens varied from 16 to 32 cm. Geographic distribution of both forms in the Arabian population is partially overlapping. Large- and medium-sized females are found together in the Arabian Sea and the Gulf of Aden; the southern border of their distribution lies between 11°N and 12°N. Medium-sized squid occur in the Red Sea as well.

**Growth of $S$. oualaniensis from tropic populations**

Individual growth of three females and three males was studied. All males were mature, their DML ranged from 15.1 to 18.7 cm. Among the three females were two immature specimens (DMLs of 20.2 and 24.9 cm) and one mature specimen (DML 25.7 cm). Growth rates were calculated for females in the DML range from 8 to 25.7 cm, and for males in the DML range of 5 to 18.7 cm.
Figure 3. Sthenoteuthis oualaniensis; the same specimen as in Figure 2. The gladius increments in the axial region of the middle plate (magnified).

Figure 4. Sthenoteuthis oualaniensis; the same specimen as in Figure 2. The gladius increments near the edge of the middle plate.
The "initial" age of females with a DML of 8 cm was estimated as 95 days and that of males with a DML of 5 cm was about 70 days on the basis of statolith methods (Arkhipkin and Bizikov, 1991).

Length growth curves for both sexes are shown in Figure 8. The female growth curve is generally well-defined and is approximated by a linear regression (1) with the following coefficients: $A = -42.147; B = 1.255$ ($r = 0.99$). From the equation, females grow from 8 cm to 25 cm DML in an average period of 137 days. The male growth curve is slightly S-shaped with a slow retardation of absolute growth rates by the time of spawning. Males grow from 5 cm DML to 18 cm DML in about 153 days.

Weight growth curves for both sexes are typically power-like (Fig. 9). The values of coefficients in Equation (3) were estimated as follows:

**Females**

$A = 1.532 \times 10^{-7}$

$B = 4.021$ ($r = 0.99$)

**Males**

$A = 1.392 \times 10^{-7}$

$B = 3.927$ ($r = 0.99$)

Both length and weight curves show that females grow faster than males.

The average rates of relative growth in weight calculated for successive 30-day intervals according to Equation (6) for females and males are represented in Figure 10 and do not differ dramatically between the sexes. As the diagram shows, relative growth rates decline uniformly during ontogeny; weight increases declined from 4.2% at 4 months of age to 1.33% at 8 months and length values decreased from 1.32% at 4 months to 0.51% at 8 months.

Growth of *S. oualaniensis* from the Arabian population

Thirty-one females (DML from 10.1 to 60.7 cm) and 7 males (DML 9.7 to 27.5 cm) were examined. Individual growth was reconstructed for females in the DML range 3 to 60.7 cm and for males in the DML range 3 to 27.5 cm. Based on maturity stage-at-length and growth rates, 26 females (DML from 10.1 to 60.7 cm) were classified as large-sized form and 5 females as medium-sized form.

Length growth curves of females from both groups are shown in Figure 11. The growth of large-sized females is...
slightly S-shaped. The initial age of squid with a DML of 3 cm was estimated as 50 days (Arkhipkin, 1989; Arkhipkin and Bizikov, 1991). Based on this estimate, the age of large females was calculated as 100 days at DML 8 cm, 156 days at DML 14 cm, 200 days at DML 21 cm, 300 days at DML 36 cm, and 368 days at DML 50 cm. The largest females (up to DML 60 cm) show higher individual growth rates compared with those with average growth rates (Fig. 12).

The length growth curves for males and medium-sized females are similar (Fig. 13). They are approximated quite well by linear regression (1) with the values of coefficients estimated as follows:

<table>
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<th>Group</th>
<th>A</th>
<th>B</th>
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<tr>
<td>Medium-sized females</td>
<td>A = -9.73 B = 0.768 (r = 0.99)</td>
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<tr>
<td>Males</td>
<td>A = -11.5 B = 0.787 (r = 0.99)</td>
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The weight growth curves for males and both size groups of females are typically power-like (Fig. 14). The values of power regression coefficients according to Equation (3) were estimated as:

<table>
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<tr>
<th>Group</th>
<th>A</th>
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<tbody>
<tr>
<td>Large-sized females</td>
<td>A = 6.2 * 10^{-8} B = 4.17 (r = 0.99)</td>
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<tr>
<td>Medium-sized females</td>
<td>A = 5.11 * 10^{-6} B = 3.14 (r = 0.99)</td>
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<tr>
<td>Males (not shown)</td>
<td>A = 6.54 * 10^{-6} B = 3.21 (r = 0.99)</td>
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Relative length and weight growth rates (Fig. 15) show gradual declines during ontogeny. Both length and weight growth rates are higher in large-sized females than in medium-sized females and males, the latter two being nearly coincident.

The individual growth of two mature males and three mature females was reconstructed. All three females were in spawning condition and their ovaries were partly spent.

In general, the individual curves of males (Fig. 16) have the same linear pattern as the summarized one. However, distinct periodicity of growth occurred in both specimens. The period of growth rate oscillation varied from 30 to 60 days.

The diagrams of individual growth rates of mature females (Fig. 17) apparently reflect the dynamics of growth during the spawning period. The curves for three large-sized spawning females (DML 55.2, 58.8 and 60.1 cm) were reconstructed for the 80-day period before capture. All the curves have similar roughly sinusoidal shapes with a period of oscillation of approximately 30 days. It appears that during spawning relatively rapid growth with daily increments of 1.5-3.6 mm alternates with phases of slow growth when daily increments drop to 0.4-1.2 mm. At the beginning of the 80-day interval (left end of the diagrams) all females had
Figure 7. Distribution of two groups of Sthenoteuthis oualaniensis: solid line delimiting the spotted area = Arabian population; broken line delimiting the hatched area = tropical population.
Figure 8. *Sthenoteuthis oualaniensis*; length growth of squids from tropical population.

Figure 9. *Sthenoteuthis oualaniensis*, body weight growth of squids from tropical population.

Figure 10. *Sthenoteuthis oualaniensis*, tropical population: daily relative growth rates of mantle length reconstructed by gladii method.

Figure 11. Length growth of *Sthenoteuthis oualaniensis* females (Arabian population).
Figure 12. *Sthenoteuthis oualaniensis*. Individual growth curves of two of the largest spawning females from the Arabian population (DML 58 and 58.8 cm). The lower curve is the average one for large-sized females.

Figure 13. Length growth of male and mid-sized females of *Sthenoteuthis oualaniensis* (Arabian population).

Figure 14. Body weight growth of *Sthenoteuthis oualaniensis* females (Arabian population).

Figure 15. Daily relative growth rates of the body weight of *Sthenoteuthis oualaniensis* (Arabian Population).
high growth rates of approximately 2.3–3.8 mm per day. This corresponds to a mantle length between 43 and 48 mm.

Discussion

As the gladius consists of three independently growing shell layers (see Introduction) it may be used for squid aging in two alternative ways. First, if the width of the increments of a chosen layer does not correlate with the width of mantle increments, it is possible to count the total number of increments and thus determine the absolute age of a squid in the same way as when using statoliths. The growth curve in this case is derived by approximation of length versus age data. Second, if the increments of a chosen layer show high correlation with the mantle increments, it is possible to determine individual growth rates at different sizes and calculate individual growth curves as in the present study. However, in this case, individual absolute age has not been estimated because of the faintness of the increments in the posterior region of the gladius.

As an example of the first approach, the age and growth of Antarctic squid *Kondakovia longimana* (Onychoteuthidae) were recently studied following the first type of aging using the cross-section of the gladius at the level of rostrum (Bizikov, 1991). Zones of slow and rapid growth were found on the rostrum cross-section, apparently reflecting seasonal variation of squid growth. The periodicity of *Kondakovia* rostrum increments was confirmed to be daily, as the periods of its slow growth corresponded to the cold season of the Antarctic winter while periods of accelerated growth corresponded to summer. As the study showed, *K. longimana* has very slow growth with regular winter retardation and longevity of about 5 years. Within the mantle range from 8.5 to 47 cm, the growth of *K. longimana* is well approximated by the linear regression (1) with the value of coefficients $A = -11.82; B = 0.64 (r = 0.95)$. The same results on the growth performance and life cycle longevity of *K. longimana* were obtained from the size-frequency analysis (Jarre et al., 1991).

In the present study, the gladius of *S. oualaniensis* was used for size-specific growth rate determination (the second type of ageing), thus additional statolith data were necessary to estimate the age at the initial point on the growth curves. The study revealed that *S. oualaniensis* has very rapid growth with distinct retardation at maturity which results in very steep, slightly S-shaped, or roughly linear growth curve. The growth rates vary greatly among different intraspecific groups. The life cycle of *S. oualaniensis* in both population and size groups is about one year. Relative daily growth rates decline progressively during ontogeny: 4–4.5% of body weight (BW) in young squid (8–9 cm DML); 2–3% BW in immature squid, and 0.7–0.9% BW in mature squid. Large females continue to grow slowly (0.8% BW) even during the spawning period. Males were usually smaller than females due to earlier maturation and consequent decrease of somatic growth.

An important advantage of gladius increment analysis is its ability to trace the individual growth of squid. Roughly lunar growth periodicity was found in both sexes of *S. oualaniensis*. However, the sharp decrease and periodical cessation of growth in large spawning females apparently relates to the start and periodicity of spawning.

The fact that Arabian population large-size females have growth rates twice as high as those of medium-size females clearly shows that size is not directly related to age and that mature females of both size groups are apparently of comparable age (about one year). However, the absence of mature females of 30–38 cm DML among the 7900 specimens examined strongly suggests that there are two size forms of females in the Arabian Sea.

Ecological differences that were found between these two forms give additional support to this conclusion. During the cruise of RV “Hydrobiolog” (1987) the author spent more than 100 h observing this species from a manned submersible. In the daytime, medium-size females were found in the 50–200 m layer and large females in the 400 to 1100 m layer. At night they were found in the 0–100 m and the 50–500 m layer, respect-
Growth of *Sthenoteuthis oualaniensis* 

The growth data obtained here for Arabian large-sized female *S. oualaniensis* correspond well with those calculated earlier using gladius and statoliths simultaneously (Arkhipkin and Bizikov, 1991). Apparently it testifies to the precision of both methods as well as to the similarity of the ecological situation in the open Arabian Sea during the winter seasons of 1987 and 1990.

The results of the present study confirm the gladius to be a recording structure that may be effectively used for squid growth investigations in the laboratory as well as under research cruise conditions. Application of the gladius for squid growth analysis opens possibilities for cephalopod life history reconstruction research.

Figure 17. *Sthenoteuthis oualaniensis*. Diagrams of daily individual increments of mantle length (mm d$^{-1}$) of three spawning large-sized females from the Arabian population.
enables us to analyse the real growth of a particular specimen while the statoliths method deals just with the statistical correlation of length (weight) versus age. However, the major problem is still the validation of gladius increment periodicity for as many species as possible. The joint application of both statolith and gladius methods is highly desirable. Such an application will provide us with valuable information on squid life history at the individual as well as the population level that cannot be obtained when using these two methods separately.

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References