FOLIA MALACOLOGICA
Folia Malacol. 29(3): 153–162
ISSN 1506-7629 (print) • ISSN 2300-7125 (on-line)
The Association of Polish Malacologists
Faculty of Biology, Adam Mickiewicz University
Bogucki Wydawnictwo Naukowe
Poznań, September 2021
https://doi.org/10.12657/folmal.029.017

GROWTH RATES OF THE CHOKKA SQUID *LOLIGO REYNAUDII* D’ORBIGNY, 1845 (CEPHALOPODA: MYOPSIDA: LOLIGINIDAE) OFF SOUTH AFRICA, INVESTIGATED OVER TWO YEARS

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Abstract: Growth of adult chokka squid *Loligo reynaudii* d’Orbigny was modelled using mantle length and age data derived from samples collected over two years (2003 and 2004) from a single, large cohort of mature and spawning squid. A total of 588 statoliths were examined (310 males, 278 females) from individuals of 71–425 mm mantle length (ML). The maximum size of chokka squid was 425 mm ML for males and 263 mm ML for females. The Francis Growth Model and Linear Growth model were selected for further analysis from six models considered. Males and females attain similar ages, although mantle length-based daily growth rates ranged from 0.75 to 1.02 (0.88 quantile _50) mm/day for males and 0.32–0.45 (0.38 quantile _50) mm/day for females, explaining the sexual dimorphism apparent in the sizes of individuals of this species.

Key words: age; growth models; growth rates; length frequency

INTRODUCTION

Although the chokka squid (*Loligo reynaudii* d’Orbigny, 1845) can be considered one of the most comprehensively studied squid species worldwide, relatively few data on growth rates (absolute or relative) are currently available. Estimates of age and other important parameters such as growth rate, age-at-maturity and life span are crucial in the understanding of the population dynamics of marine organisms (Jackson 1990). The value of these parameters towards achieving sound management of fisheries in general and squid stocks in particular is well known and documented in a number of publications (Hatanaka 1986, Bigelow 1992, Arkhipkin 1994, Hatfield et al. 2001, Grist & Jackson 2004, SCHWARZ & PEREZ 2010, JIN et al. 2019). Estimates for these parameters can be obtained from age estimates based on hard structures such as gladii, beaks and statoliths, which are shown to bear periodic growth increments (e.g. JIN et al. 2019).

A preliminary study of age and growth of the chokka squid *L. reynaudii* (LIPIŃSKI & DURHOLTZ 1994) that used data from only 31 individuals, indicated significant differences between males and females. Reviews of chokka biology (SAUER et al. 2013, VAN DER VYVER et al. 2016, LIPIŃSKI et al. 2016) and recent ageing study (LIPIŃSKI et al. 2020) provide no estimates of chokka squid growth rates.

This study aimed at providing growth rates of the chokka squid with age estimates derived from statolith daily increment analyses (details in LIPIŃSKI et al. 2020). Age data, coupled with the mantle length measurements of the aged individuals, are used to estimate growth rates of a large cohort of spawning squid, which is subject to exploitation and management (SAUER et al. 2013, VAN DER VYVER et al. 2016, LIPIŃSKI et al. 2016).

MATERIALS AND METHODS

Details of the sampling and statolith analyses are provided by LIPIŃSKI et al. (2020) and some details are repeated here. Details of images of increments, periodicity, validation for chokka species are provided in references given in LIPIŃSKI et al. (2020). The study was conducted on material sampled from the south-east coast of South Africa in the area between Plettenberg Bay (24°E) and Port Alfred (26°E), the main spawning grounds of the species. Squid were caught using hand jigging in 2003 and both hand jigging and trawling in 2004 (trawling: 36% of males and 57% of females collected in that year). All sampling was conducted on spawning grounds where mature squid move freely between spawning concentrations (see SAUER et al. 1992, LIPIŃSKI et al. 1998). Even small sampled individuals were mature (stage V) with few exceptions of maturity stage IV (LIPIŃSKI & UNDERHILL 1995). All individuals were measured (mantle length in bins 1 cm below) and then randomly sub-sampled for statolith extraction. Length distributions of the squid sampled were visually compared with those from the overall survey; there were no differences between these distributions (LIPIŃSKI et al. 2020: fig. 6). Statoliths (both left and right) were dissected from fresh animals (LIPIŃSKI et al. 2020 – references therein) washed in distilled water and stored in 70% ethanol. Both statoliths were later air-dried and prepared for light microscopy (LIPIŃSKI et al. 2020 – references therein). The statolith preparations were viewed under transmitted light using a Carl Zeiss Axioscope 5 compound microscope and photographed using a Carl Zeiss high resolution digital camera mounted on the microscope. An experienced statolith reader then conducted a single count with no repetitions of the total number of increments in better prepared statolith of the pair, using the digital images. A total of 613 statoliths were prepared for analysis, of which 588 were used for this study. The length and age data are summarised in Tables 1a and 1b for easy reference.

Six growth models (linear, exponential, power, Gompertz, Schnute and Francis) were initially considered, and fitted to the mantle length-at-age data. However, of the six models, only four yielded acceptable fits to the data. The Gompertz and exponential growth models could not be fitted to the data because numerical issues with no solutions were found, and these were not considered further. The models fitted are given below:

Linear growth model:

$$\mathrm{ML} = a + b(\mathrm{age})$$

Power growth model:

$$\mathrm{ML} = a(\mathrm{age})^{b}$$

Francis growth model (OGLE 2016):

$$\mathrm{ML} = L_1(L_3 - L_1)\left[\frac{1 - r^{2\left(\frac{\mathrm{age} - t_1}{t_3 - t_1}\right)}}{1 - r^2}\right]$$

where $r = \frac{L_3 - L_2}{L_2 - L_1}$.

Schnute growth model (OGLE 2016):

$$\mathrm{ML} = L_1 + (L_2 - L_1)\left[\frac{1 - e^{-k(t - t_1)}}{1 - e^{-k(t_2 - t_1)}}\right]$$

where a, b, k, L_1, L_2, L_3 are model parameters from the above five models to be estimated. For the Francis growth model L_1, L_2, L_3 are mean length at ages t_1, t_2, t_3, t_1 and t_3 are ages of relatively young and old age individuals and $t_2 = \frac{t_1 + t_3}{2}$. For the Schnute growth model L_1, L_2 are mean length at age t_1 and t_2, where t_1 and t_2 are ages of relatively young and old age individuals.

The four models (Linear, Power, Schnute and Francis) were fitted to length at age data for males and females separately, and to both sexes combined.

Table 1a. Summary of mantle lengths (mm) corresponding to individuals collected during the November/December 2003 and 2004 research surveys that provided reliable estimates of age

Sampling period	Vessel (gear)	Females			Males			Total (M & F)
		Total	Range	Mean ± SE	Total	Range	Mean ± SE	
Nov/Dec 2003	Algoa (jig)	66	150–263	205 ± 2.46	106	182–425	309 ± 4.16	172
Nov/Dec 2004	Algoa (jig)	123	83–240 (jig+trawl)	176 ± 1.78	134	71–375 (jig+trawl)	244 ± 5.07	421
	Algoa (trawl)	92			72			

Table 1b. Summary of estimated age distributions of male and female chokka squid collected during survey years 2003 and 2004 (quoted from LIPIŃSKI et al. 2020)

Sampling period	Estimated age (days)					
	Female			Male		
	Total no.	Range	Mean ± SE	Total no.	Range	Mean ± SE
Nov/Dec 2003	66	278–478	350 ± 5.58	106	281–484	364 ± 4.50
Nov/Dec 2004	212	175–464	326 ± 2.70	204	168–397	325 ± 3.15

Selection of the best performing model was based on the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), Root Mean Squared Prediction Error (RMSPE) and Mean Absolute Error (MAE). Confidence intervals were estimated using a bootstrapping approach where, once the model is fitted, the residuals were randomly sampled and added to the response variable (length) and then the model was re-fitted. This process was repeated 1,000 times. Both the computation of the confidence intervals for the estimated parameters and the prediction are based on the bootstrap generated parameters. For all growth models fitted, the standard model diagnostics were checked: plots of residuals vs. fitted values (if models are valid this plot should show relatively random distribution of points), and quantile-quantile plots of residuals (to check if the residuals deviate from theoretical expectation under normal distribution).

Daily growth rate (mm/day) DGR and Instantaneous Growth Rate (IGR) were estimated as shown below for each 20-day interval, following RICKER (1979):

$$\mathrm{DGR} = \frac{\mathrm{ML}_1 - \mathrm{ML}_2}{t_1 - t_2}$$

$$\mathrm{IGR} = \frac{\ln(\mathrm{ML}_1) - \ln(\mathrm{ML}_2)}{t_1 - t_2}$$

where ML_1 and ML_2 are the estimated/predicted mantle length at time t_1 and t_2, respectively. In addition to the point estimates, we also computed 95% confidence interval by bootstrapping as part of the growth model fitting.

All the analyses, visualisation and report generation were in R (R CORE TEAM 2020). Multiple R packages were utilised for data processing, visualisation, analysis, and summary of results including ALATHEA (2015), ELZHOV et al. (2016), HENRY & WICKHAM (2019), ALLAIRE et al. (2020), ROBINSON & HAYES (2020), WICKHAM et al. (2020a, b) and XIE (2020).

RESULTS

The length frequency distributions of *L. reynaudii* for each of the years 2003 & 2004 and for both years combined are presented in Figure 1 (Kernel density). The mantle length size ranged from 71 to 425 mm in males and from 83 to 263 mm in females during the two survey years.

The fits of the four growth models to the observed size at age data are illustrated in Figure 2. It is apparent that the Linear and Power models yield similar estimates of chokka squid growth, but these differ somewhat from those yielded by the Schnute and Francis models, which were almost identical. Plots of the residuals of the four growth models fitted to the data (Fig. 3) show no apparent systematic pattern, indicating no bias in the model estimates. The appreciably wider scatter of the residuals for males relative to females clearly shows the generally poorer fit of the models to the male data (apparent in the performance measures in Table 2). The Schnute and Francis growth models performed equally well in all fits to the data (Table 2) and showed better performance than did the linear and power models. The Francis growth model was, however, selected for further analyses of the year-specific data because the

Schnute model could not be fitted (no convergence to a numerical solution) to all of the year-specific cases considered. The Francis model results (Table 3, Fig. 4) indicate that at relatively young ages, growth rates of male and female *L. reynaudii* were not appreciably different, but that as ages increased, males grew substantially faster than females. Separate Francis growth models fitted to size at age data for each sampling year (2003 and 2004) show that the growth of the squid sampled in 2003 appears to be faster than that of those sampled in 2004 (Fig. 5), and that males in both years grew faster in length with increasing age compared to females. The Linear growth model (Table 4) provided an "overall" measure of growth rate as an increase in size per day: 0.75–1.02 mm/d for males, 0.32–0.45 mm/d for females and 0.64–0.86 mm/d for sexes combined.

The DGR and instantaneous growth rate (G) generally declined with age and appeared to vary between sex (Figs 6–7).

Table 2. Performance measures for four growth models (Linear, Francis, Power and Schnute) and different data types (All data, Male, and Female). Four model performance measures were considered: Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), Root Mean Squared Error (RMSE), and Mean Absolute Error (MAE)

sex	model_name	AIC	BIC	RMSE	MAE
All	Francis	6325.39	6342.79	59.96	50.60
	Linear	6326.80	6339.86	60.14	50.58
	Power	6327.48	6340.54	60.17	50.75
	Schnute	6325.39	6342.79	59.96	50.60
Male	Francis	3307.88	3322.75	55.06	42.37
	Linear	3312.42	3323.57	55.66	43.77
	Power	3313.65	3324.80	55.77	43.95
	Schnute	3307.88	3322.75	55.06	42.37
Female	Francis	2437.49	2451.87	22.13	17.28
	Linear	2456.88	2467.66	23.03	18.09
	Power	2452.78	2463.57	22.85	17.94
	Schnute	2437.49	2451.87	22.13	17.28

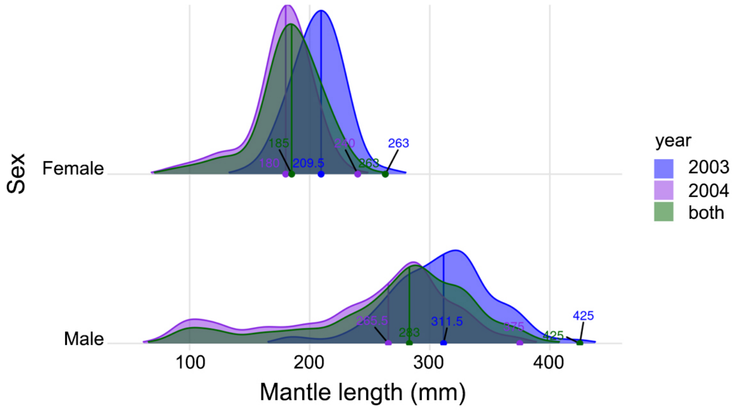

Fig. 1. Female and male length distribution of *Loligo reynaudii* between Plettenberg Bay and Port Alfred for the surveys conducted during November/December of 2003 and 2004. Median and maximum length of squid for each sex and year are represented by the dots. Kernel density graph, therefore there is no y axis

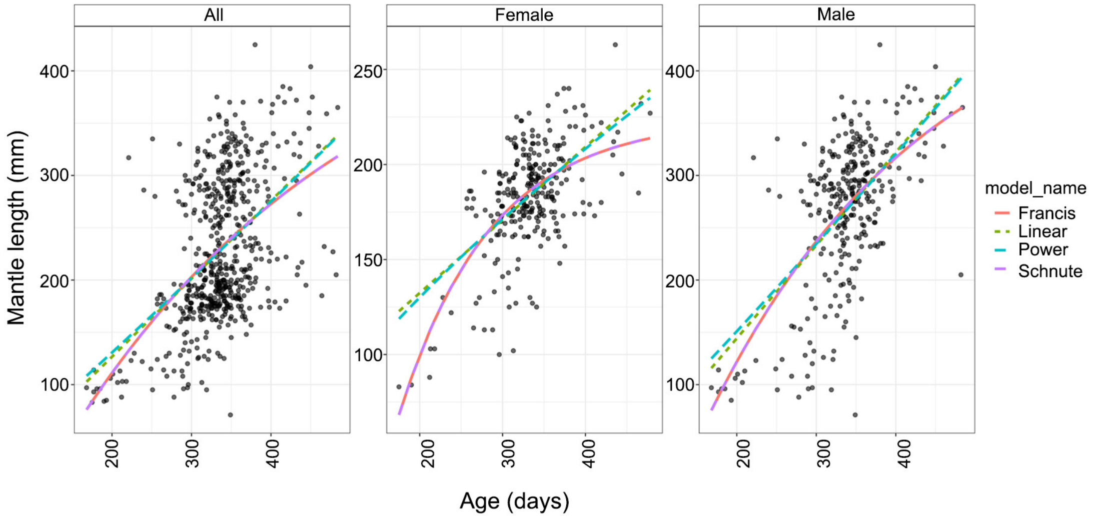

Fig. 2. Fits from the four growth models (Francis, Power, Linear and Schnute) for males, females, and all individuals combined

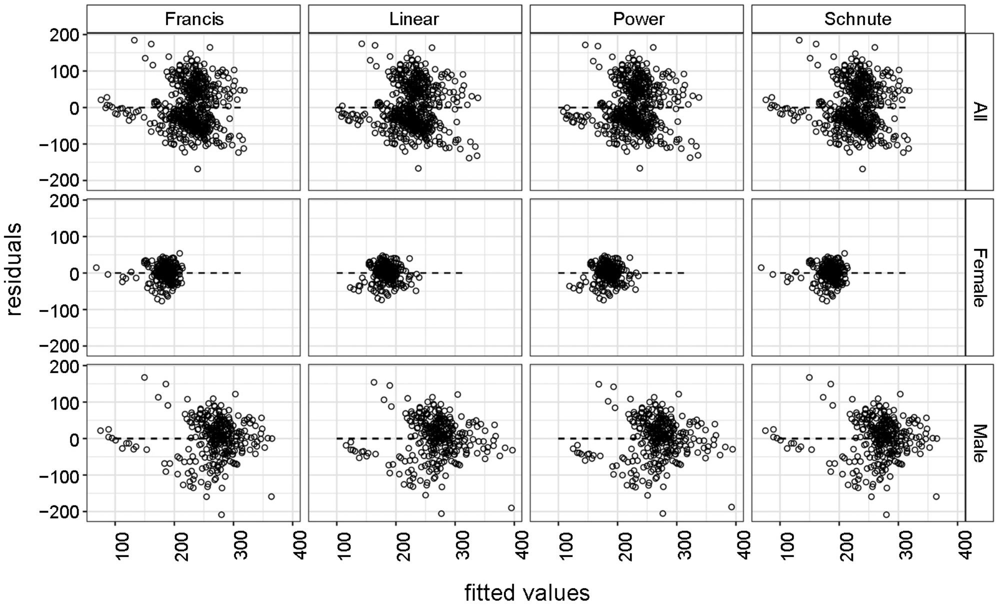

Fig. 3. Residual plots for the four growth models fitted to the size at age data for males, females and all combined

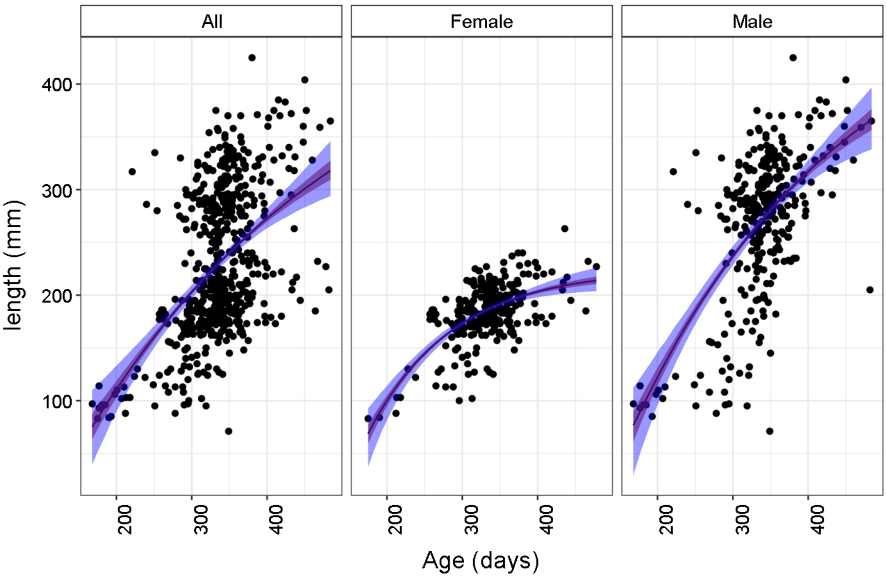

Fig. 4. Sex-specific observed mantle lengths (mm) at age (dots) pooled for both sampling years (2003 and 2004), with the Francis growth models fitted to the data. Solid lines represent the median of predicted mantle length. Light brown and light blue envelopes represent the 50% and 95% confidence intervals, respectively

Table 3. Summary statistics (median, upper and lower 2.5% quantiles) of estimated growth parameters for males, females and all data combined. Francis growth model

sex	terms	quant_2.5	quant_50	quant_97.5
All	L1	88.13	110.99	132.82
	L2	196.63	202.97	209.56
	L3	262.87	272.27	281.99
Female	L1	81.57	99.42	116.03
	L2	169.53	173.28	177.01
	L3	197.94	203.45	208.80
Male	L1	94.10	122.20	147.02
	L2	228.58	236.85	245.40
	L3	305.71	317.48	327.50

Table 4. Summary statistics of estimated growth parameters for males, females and all data combined. Linear growth model

sex	terms	quant_2.5	quant_50	quant_97.5
All	a	−59.35	−23.65	12.04
	b	0.64	0.75	0.86
Female	a	33.49	56.14	76.70
	b	0.32	0.38	0.45
Male	a	−79.28	−34.65	13.10
	b	0.75	0.89	1.02

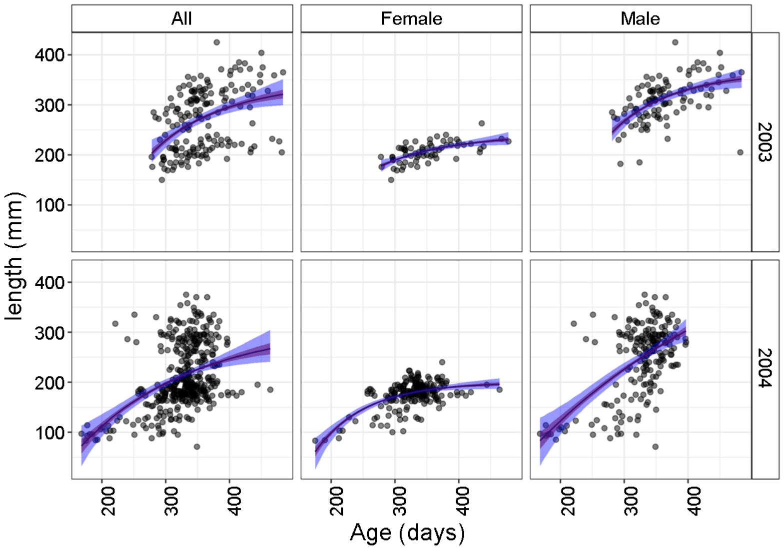

Fig. 5. Year-specific observed mantle lengths at age (dots) with the Francis growth models fitted to the data. Solid lines represent the median of predicted mantle length. Light brown and light blue envelopes represent the 50% and 95% confidence intervals, respectively

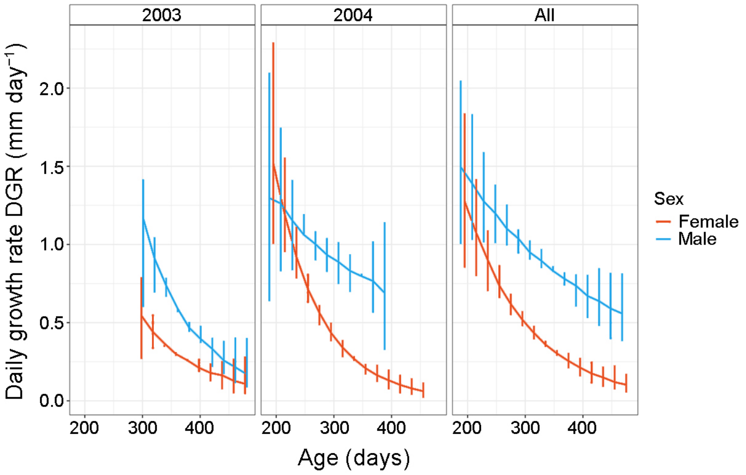

Fig. 6. Daily growth rates, mantle size (mm/day) for females and males for the two sampling years (2003 and 2004) and the combined data. Error bars represent 95% confidence interval

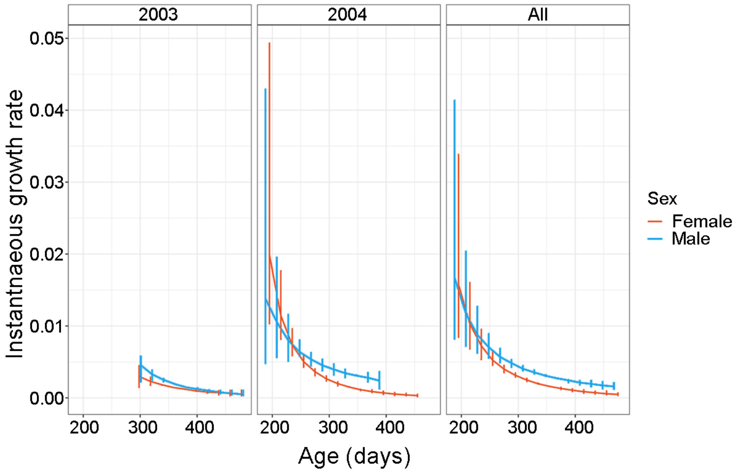

Fig. 7. Instantaneous growth rate for females and males for the two sampling years (2003 and 2004) and the combined data. Error bars represent 95% confidence interval

DISCUSSION

Considering that the data used in this study only covered the middle and later parts of the chokka squid life cycle and that the data were collected in a limited part of the species distribution range, we note that growth of the whole population of chokka cannot be discussed here. Likewise, precision of age readings (e.g. Campana 2001) was somewhat compromised, due to logistical reasons, by the use of only one statolith reader (albeit experienced in reading both otoliths and statoliths) and only one reading, as in the linked study by Lipiński et al. (2020). However, it is believed that in the light of the present results being comparable with a previous study (Lipiński & Durholtz 1994 vs. Lipiński et al. 2020) these results may be accepted, and outweigh rejection on the grounds that the requirement of precision is not met. The growth rates in this paper concern adult life stages of a single, but very important and exploited cohort. Grist et al. (2011) have warned against spurious growth models and equations arising from uncritical lumping of various cohorts with drastically different growth trajectories and patterns. The linear models fitted to the data during this study suggested that the relative growth rates of the chokka squid may be low in comparison with other values for loliginids. For example, Jin et al. (2019) found that such values for *Uroteuthis chinensis* (Gray, 1849) were 5.17 mm/d and 2.46 mm/d for males and females, respectively; for *U. edulis* (Hoyle, 1885) they were: males 1.71 mm/d, females 2.05 mm/d. This may be characteristic for the older life stages where growth rates are declining (Natsukari et al. 1988, Schwarz & Perez 2010).

Interestingly, *L. reynaudii* resembles *U. chinensis* in that the growth of males is more than double that of females. While the results of this study have therefore confirmed the sexual dimorphism in the chokka squid growth and highlighted the large inter-annual variation in growth (Figs 6–7), further work encompassing data from all life stages, seasons, areas and as many years as possible is required for a proper understanding and quantification of the growth of this species. However, growth rates from a single cohort of squid, investigated on a large sample and repeated for at least two years, highlight growth ranges, differences between sexes, differences between years, and growth type (slow – fast; variable – steady) (Figs 6–7). This simple material shows some possible interpretation complications, such as possible limited presence of sneaker males in the sample, which may have similar ages as large males but, obviously, very different growth rates (references concerning sneaker presence: Sauer et al. 2013). In addition, difference in growth between years may have been influenced by the different sampling methods, where 2003 data were collected only by jigging and 2004 data were collected both by jigging and trawl. However, this influence is considered small as ages (Lipiński et al. 2020) and length frequencies (Fig. 1) for both years were similar for smaller squid, especially males.

There are a number of reviews on growth in cephalopods (Jackson 1994, Lipiński 2002, Arkhipkin 2004, Jackson & McGlashan 2004, Arkhipkin & Roa-Ureta 2005) as well as some more recent considerations (e.g. Schwarz & Perez 2010, Grist et al. 2011, Jin et al. 2019). It has been recognised that understanding and describing cephalopod growth are difficult (Moltschaniwskyj 2004). Early studies (eg. Jackson 1990, Gonzalez et al. 1996) suggested that growth of squid could best be described by a linear model. Other studies (e.g. Yang et al. 1986, Lee et al. 1994, Hatfield et al. 2001) reported considerable differences between growth models of cephalopods grown in different conditions (e.g. in different temperature regimes). Arkhipkin (2004) pointed out that maximum relative growth rates were observed during the paralarval stage, quoting Forsythe & Heukelem's (1987) data. However, these data were obtained for paralarvae kept in aquaria (therefore fed ad libitum) and not in their natural environment (see also Grist et al. 2011: p. 117). At least some data from the latter (e.g. Natsukari et al. 1988, Bigelow 1992) show the opposite: the initial phase of paralarval growth is in fact the slowest stage (Bigelow 1992: fig. 7, first few days; Vidal et al. 2002: reporting "no net growth" during the first 10–15 days), despite exponential growth phase later. If this is confirmed with a larger sample size and for many species, a three-phase growth for cephalopods may be most plausible: paralarval (linear followed by exponential during the "vertical movement" phase of the paralarvae), juvenile and early adult (exponential); late adult (asymptotic), as was suggested by Jackson (2004) working with loliginid squid.

The large individual variation has led to two different approaches in considering cephalopod growth: fitting available models to available length and/or weight data (most often in situ, but also from aquarium rearing) (e.g. Arkhipkin & Roa-Ureta 2005); or open-ended, flexible, currently energy balance-based models (Grist & Jackson 2004, O'Dor et al. 2005, Grist et al. 2011). However, given that growth models typically do not fit squid size at age data very well (Natsukari et al. 1988, Schwarz & Perez 2010, present data: Fig. 2) and energy balance equations are generally too broad, lacking useful detail and resolution, we are of the opinion that estimates of growth rate changes over time (e.g. Arkhipkin 1994:

fig. 9–10, Arkhipkin et al. 1999: fig. 9EF, present paper: Figs 6–7) are more useful to evaluate squid growth during the full life cycle. Of course, it should be appreciated that even if they cover the entire life cycle, they are imprecise in determining the lower and especially upper growth rates for a given species. This is because of large natural variability in that part of the life cycle, including responses to, for example, environmental factors, food availability etc. (Natsukari et al. 1988). A full understanding of these fluctuations and their determinants is (ideally) required for accurate life cycle models, population dynamics models, and fisheries management decisions.

ACKNOWLEDGEMENTS

The South African Squid Management Industrial Association (SASMIA) is acknowledged for funding the project, and the former Department of Agriculture, Forestry and Fisheries for access to the data. Many of our professional colleagues participated in the data collection – their input is gratefully acknowledged. Prof. Coleen Moloney (UCT) and Dr Lisa Hendrickson (NMFS NOAA, USA) are thanked for the discussions on cephalopod growth and various comments and inputs. Finally, The Rhodes University (Department of Ichthyology and Fisheries Science) provided logistics and support.

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Received: March 22nd, 2021
Revised: May 1st/June 14th, 2021
Accepted: June 23rd, 2021
Published on-line: July 11th, 2021