

RESEARCH ARTICLE

Age and growth estimates of the jumbo flying squid (*Dosidicus gigas*) off Peru

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Abstract – Mantle length (ML) and age data were analyzed to describe the growth patterns of the flying jumbo squid, *Dosidicus gigas*, in Peruvian waters. Six non-asymptotic growth models and four asymptotic growth models were fitted. Length-at-age data for males and females were analysed separately to assess the growth pattern. Multi-model inference and Akaike's information criterion were used to identify the best fitting model. For females, the best candidate growth model was the Schnute model with $L_{\infty} = 106.96$ cm ML (CI 101.23–110.27 cm ML, $P < 0.05$), age at growth inflection 244.71 days (CI 232.82–284.86 days, $P < 0.05$), and length at growth inflection 57.26 cm ML (CI 55.42–58.51 cm ML, $P < 0.05$). The growth pattern in males was best described by a Gompertz growth model with $L_{\infty} = 127.58$ cm ML (CI 115.27–131.80 cm ML, $P < 0.05$), $t_0 = 21.8$ (CI 20.06–22.41, $P < 0.05$), and $k = 0.007$ (CI 0.006–0.007, $P < 0.05$). These results contrast with the growth model previously reported for *D. gigas* in the region, where the growth pattern was identified as non-asymptotic.

Keywords: Age / Statoliths / Multi-model inference / Peru

1 Introduction

The flying jumbo squid *Dosidicus gigas* is a monocyclic ommastrephid species and endemic in the eastern Pacific Ocean. Its longevity varies between 1 and 1.5 years reaching 120 mm mantle length. Females are larger than males, and the sex ratio (female:male) has high variability, changing in different areas of the eastern Pacific Ocean between 1:1 and 14:1 (Morales-Bojórquez and Pacheco-Bedoya, 2016b). The fecundity of *D. gigas* is around 32 million eggs. It is a multiple spawner with 10 to 14 spawning batches during its short life span (Markaida and Nigmatullin, 2009). The number of cohorts per year varies between one and six (Taipe *et al.*, 2001; Markaida and Nigmatullin, 2009; Keyl *et al.*, 2011; Rosa *et al.*, 2013; Zepeda-Benitez *et al.*, 2014a). Mechanisms that can, in theory, cause variability in the population structure are environmental factors, population area, spatial distribution

of individuals, abundance and density dependence of the squid population, and schooling behavior (Morales-Bojórquez *et al.*, 2001). Changes in the number and abundance of flying jumbo squid cohorts are a demographic response that has implications for availability and accessibility to fishing fleets (Keyl *et al.*, 2011; Rosa *et al.*, 2013). The species has the highest abundance in the southern hemisphere, mainly between Ecuador and northern Peru. It is possible that both coastal states share the same stock (Morales-Bojórquez and Pacheco-Bedoya, 2017), which would make this a transboundary stock (Maguire *et al.*, 2006).

Recent comparative and analytical studies have shown that understanding individual growth is fundamental for estimating life histories, demography, ecosystem dynamics, and fisheries sustainability (Montgomery *et al.*, 2010; Pardo *et al.*, 2013). Individual growth is associated with a number of life-history traits including natural mortality, lifespan and reproductive allocation, which are traits that influence the response of species to exploitation (Sullivan *et al.*, 1990). Age and growth studies are of practical importance for describing the status of a

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harvested population. Variability in individual growth can affect the important management quantities such as: age-at-first maturity, age of recruitment, survival, and reproductive potential. Thus, knowing factors influencing individual growth is key for jumbo flying squid populations (Morales-Bojórquez and Nevárez-Martínez, 2010). According to Pecl (2004) and Schwarz and Alvarez-Perez (2010), squid growth follows one of two patterns: the first is non-asymptotic (Boyle and Rodhouse, 2005) and the second one asymptotic (Arkhipkin *et al.*, 1996; Arkhipkin and Roa-Ureta, 2005). To handle this duality in squid growth patterns, Lipinski (2002) proposed a conceptual growth model for cephalopods, which describes three growth phases. The first phase is characterized by relatively slow paralarvae growth, the second phase represents juveniles and adults where fast growth can be observed, and the last phase is characterized by diminished or lack of growth, commonly observed in spawners.

In the literature, there are few age and growth studies for *D. gigas* in the Humboldt and California Current. Argüelles *et al.* (2001) estimated an exponential growth pattern for *D. gigas* in Peruvian waters. In the south (Chilean waters), Chen *et al.* (2011) reported that the species exhibited a linear growth pattern in spring spawners, while a power function was identified for autumn spawners, indicating differential growth between cohorts. The linear function was also estimated in the Costa Rica Dome (Chen *et al.*, 2013). Markaida *et al.* (2004) and Mejía-Rebollo *et al.* (2008) reported that growth of *D. gigas* in the California Current is best described by a logistic curve. Zepeda-Benitez *et al.* (2014a) found that the species exhibits asymptotic growth, as described by the general Schnute function, based on results of a multi-model approach to modeling the growth of males, females and combined sexes of jumbo flying squid in the Gulf of California. Given these reported differences in growth patterns, Zepeda-Benitez *et al.* (2014a) assumed that the growth of *D. gigas* in the eastern Pacific Ocean followed a non-asymptotic pattern in the Southern Hemisphere and an asymptotic pattern in the Northern Hemisphere.

Model selection is grounded in likelihood theory, a robust framework that supports most modern statistical approaches (Burnham and Anderson, 2002). Multi-model inference has two advantages:

- analyses are not restricted to evaluating a single growth model where significance is measured against some arbitrary probability threshold. Instead, competing growth models are compared to one another by evaluating the relative support in the observed data for each growth model;
- candidate growth models can be ranked and weighted, thereby providing a quantitative measure of relative support (Hobbs and Hilborn, 2006).

The aim of this study was to determine the growth pattern of jumbo flying squid in Peruvian waters based on a multi-model inference approach.

2 Materials and methods

2.1 Squid sampling

A research survey onboard R/V Hakurei Maru VIII was conducted in Peruvian waters (Exclusive Economic Zone, 3°

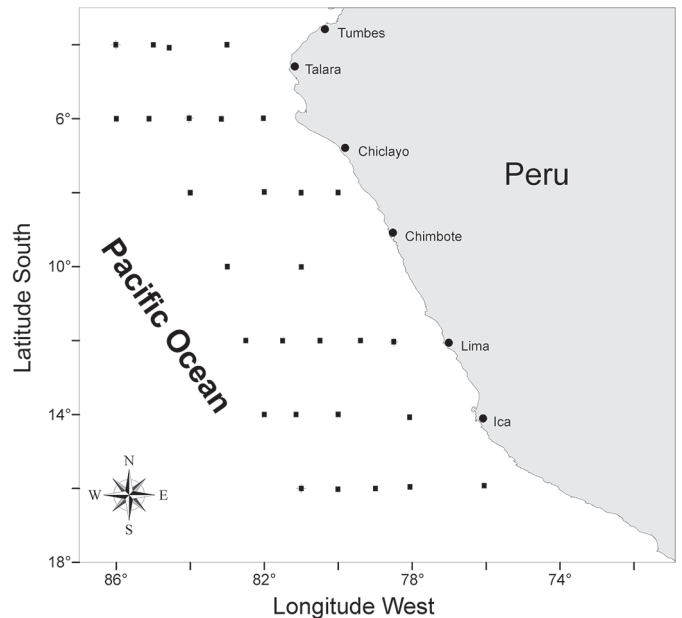


Fig. 1. Study area in Peruvian waters. The filled squares denote the sampling locations of *Dosidicus gigas* onboard the R/V Hakurei Maru VIII.

59.9' S and 83° 0.4' W, and 16° 1.22' S and 80° 0.5' W) from 17 December 2011 to 14 January 2012. A total of 29 stations were sampled. Squids were caught at night with artificial lights (from 19:00 to 05:00 h) using 43 automatic computerized jigging machines. Individuals were caught from the surface to 82 m. For each 10 h night period, initial and final positions of the vessel were recorded (Fig. 1).

Statoliths of 226 individuals (161 females, and 65 males) were collected and stored in 70% ethanol for age determination. Measurements of mantle length (ML) and total weight (TW) were taken to the nearest 0.1 cm and 0.1 g, respectively. The survey covered the entire spatial distribution of *D. gigas* in Peruvian waters. In this region, jumbo-flying squid has shown high inter-annual variability in the number of cohorts produced each year, ranging from one cohort to six cohorts (Keyl *et al.*, 2011). Consequently, several ages and mantle length sizes are present in the population at any given time. Variability in the number of cohorts has been reported for several fishing grounds in the eastern Pacific Ocean, allowing for age and growth to be measured on short time scales, commonly less than a year (Morales-Bojórquez and Pacheco-Bedoya, 2016a, 2016b); or over just two or three months in Peruvian, Ecuadorian, and Chilean waters (Chen *et al.*, 2011, 2013; Liu *et al.*, 2013, 2015, 2017; Hu *et al.*, 2016).

To estimate the relationship between ML and TW for females and males the power equation $TW = aML^b$ was used, where a is the average condition factor and b is the coefficient of allometry, indicating isometric growth when equal to three and allometric growth when significantly different from three (Aguirre-Villaseñor *et al.*, 2008). The estimated value of b was analyzed with Student's t -test (Zar, 1999) to determine whether growth was isometric or allometric.

Table 1. Asymptotic and non-asymptotic growth models analyzed for *Dosidicus gigas* from the Peruvian waters.

Model	Function	θ_i	Source	Observations
Schnute ($\rho \neq 0, \eta \neq 0$)	$L(t) = \left[\lambda_1^\eta + (\lambda_2^\eta - \lambda_1^\eta) \times \frac{1 - e^{-\rho(t-\tau_1)}}{1 - e^{-\rho(\tau_2-\tau_1)}} \right]^{1/\eta}$	4	Schnute (1981)	Asymptotic
Schnute ($\rho=0, \eta \neq 0$)	$L(t) = \left[\lambda_1^\eta + (\lambda_2^\eta - \lambda_1^\eta) \times \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{1/\eta}$	3	Schnute (1981)	Non-asymptotic
Schnute ($\rho=0, \eta=0$)	$L(t) = \lambda_1 \times e^{\left[\ln\left(\lambda_2/\lambda_1\right) \times \frac{t-\tau_1}{\tau_2-\tau_1} \right]}$	2	Schnute (1981)	Non-asymptotic
Gompertz	$L(t) = L_\infty e^{\left[-e^{-\kappa(t-t_0)}\right]}$	3	Alp <i>et al.</i> (2011)	Asymptotic
Linear	$L(t) = \alpha + (\beta \times x)$	2	Schnute (1981)	Non-asymptotic
Power	$L(t) = \alpha \times x^\beta$	2	Mercier <i>et al.</i> (2011)	Non-asymptotic
Extended power	$L(t) = \alpha \times x^{\beta-\frac{\delta}{x}}$	3	Mercier <i>et al.</i> (2011)	Non-asymptotic
Persistence	$L(t) = \alpha \times x^{\beta \times e^{\left(\frac{\delta}{x}\right)}}$	3	Mercier <i>et al.</i> (2011)	Non-asymptotic
Richards	$L(t) = L_\infty * \left[1 - e^{-\kappa(t-t_0)}\right]^\mu$	4	Ebert (1999)	Asymptotic
Jolicoeur	$L(t) = \frac{L_\infty}{1 + (\varphi * t^{-\mu})}$	3	Jolicoeur (1985)	Asymptotic

2.2 Statolith reading

The statoliths were prepared for reading based on the Arkhipkin method (Dawe and Natsukari, 1991). Only the right statolith was used for age determination. Samples were ground and polished on both sides. Finally, a drop of Canada balsam was applied. A cover glass was used to cover the polished surface and the statoliths were left to dry for 18 hours at 70 °C. The growth increments in the statoliths were counted from the nucleus to the edge of the dorsal dome; the counts were performed by one reader using an optical microscope with transmitted light at 400×. Statoliths were analyzed in random order, the increment counts were recorded with no prior knowledge of the mantle length or sex of each specimen, and each replicate count was conducted without consulting the previous count, thereby avoiding any bias in the replicates. According to Campana (2001), ageing error can be expressed as follows:

- discrepancies on reproducibility of repeated measurements on a given structure (precision);
- differences between the closeness of the age estimate to the true value (accuracy).

Thus, three counts were made at different times. The age validation for *D. gigas* has not been verified. However, daily increments have been validated for other squids of the same family (Dawe *et al.*, 1985; Nakamura and Sakurai, 1991). Consequently, the increments observed in the statoliths of jumbo flying squid were assumed to have been laid down daily.

The index of average percent error (IAPE) and the coefficient of variation (CV) (Campana *et al.*, 1995) were calculated to assess the reliability of the counts:

$$IAPE = \frac{100}{N} \sum_{j=1}^N \left[\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{\bar{X}_j} \right],$$

$$CV = \frac{100}{N} \sum_{j=1}^N \sqrt{\frac{\sum_{i=1}^R (X_{ij} - X_j)^2}{R-1}}{\bar{X}_j},$$

where *N* is the number of squids aged, *R* is the number of readings, *X_{ij}* is the *i*_{th} age determination of the *j*_{th} squid, and \bar{X}_j is the mean age of the *j*_{th} squid.

2.3 Growth modeling

Asymptotic and non-asymptotic growth models were applied to our data set, analyzing females and males (Tables 1 and 2). These models were selected based on:

- ease of use and prevalence in the literature (Markaida *et al.*, 2004; Mejia-Rebollo *et al.*, 2008; Chen *et al.*, 2011, 2013; Zepeda-Benitez *et al.*, 2014a, 2014b);
- the fact that growth patterns in squid species have been described as being either asymptotic or non-asymptotic depending on the biology of the species (Arkhipkin *et al.*,

Table 2. Parameters associated with asymptotic and non-asymptotic growth models.

Parameter	Units	Description
τ_1	Time	First specified age
τ_2	Time	Second specified age
λ_1	cm	Size at age τ_1
λ_2	cm	Size at age τ_2
ρ	Time ⁻¹	Constant relative rate of relative growth rate
η	Dimensionless	Incremental relative rate of relative growth rate
L_∞	cm	Asymptotic size
κ	Dimensionless	Growth coefficient
t_0	Time	^a
α	Dimensionless	Intercept
β	Dimensionless	Slope
δ	Dimensionless	Scale parameter
μ	Dimensionless	Shape parameter
φ	Dimensionless	Scaling parameter to adjust for size $\neq 0$ at time 0

^a This parameter is the theoretical age of the fish at zero size under the assumption that the von Bertalanffy growth curve describes the growth accurately right down to zero length. The definition changes according to candidate growth models, e.g., the Logistic, Johnson, and Gompertz models correspond to the inflection point for each curve; for generalized von Bertalanffy growth model, t_0 has similar interpretation as in the von Bertalanffy assuming the equation to be valid at all ages; a similar assumption is applied to the Richards growth model (Katsanevakis, 2006). The t_0 parameter is largely artificial, in so far as it defines the age at which the organism would be of zero length if it grew throughout its life with the same pattern of growth as in the early stages.

1996; Pecl, 2004; Arkhipkin and Roa-Ureta, 2005; Ceriola and Jackson, 2010; Schwarz and Alvarez-Perez, 2010; Zepeda-Benitez *et al.*, 2014a, 2014b).

Thus, the following candidate growth models were considered:

- linear;
- power;
- extended power;
- persistence;
- Gompertz;
- Richards;
- Jolicoeur;
- Schnute ($\rho \neq 0$ and $\eta \neq 0$; $\rho = 0$ and $\eta \neq 0$; and $\rho = 0$ and $\eta = 0$) (Schnute, 1981; Jolicoeur, 1985; Ebert, 1999; Alp *et al.*, 2011; Mercier *et al.*, 2011; Zepeda-Benitez *et al.*, 2014a).

For the Schnute growth model supplementary equations for estimating age at growth inflection, length-at-age at growth inflection, and theoretical age at length zero are detailed in Appendix A. As comparison, the von Bertalanffy (1938) growth model was also considered, although this model is not

recommended for growth modeling of squid (Jackson *et al.*, 2000).

2.4 Model fitting

Parameters θ_i of the i th growth models were estimated using a negative log-likelihood function assuming a lognormal distribution:

$$-\ln L(\theta_i | data) = \frac{n}{2} [\ln(\sigma^2) + \ln(2\pi)] + \sum_{j=1}^n \left[\left(\frac{[\ln L_j - \ln \hat{L}_j]^2}{2\sigma^2} \right) \right],$$

where L_j is the observed mantle length for the j^{th} individual, \hat{L}_j is the estimated mantle length for the j^{th} individual, n is the number of individuals in the sample. Parameters were estimated by maximum likelihood using a Newton-Raphson algorithm (Neter *et al.*, 1996). The analytical solution for the standard deviation (σ) was:

$$\sigma = \sqrt{\frac{1}{n} \sum_{t=1}^n [\ln L(t) - \ln \hat{L}(t)]^2}.$$

The lognormal distribution was used to account for variation in size-at-age increasing with age. This means errors were assumed to be multiplicative (Quinn and Deriso, 1999). The optimization process for estimating parameters for each candidate growth model, bootstrap routine, confidence intervals, and model selection were implemented in Visual Basic Application ver. 6.0TM.

2.5 Confidence intervals

Confidence intervals for fitted parameters θ_i must be estimated considering the correlation (covariance) between parameters, if it exists (Hilborn and Walters, 1992). An alternative approach to estimating confidence intervals analytically is to use a bootstrap, which has the advantage of accounting for correlations between parameters (Haddon, 2001). Confidence intervals were estimated using the bootstrap method described by Fournier and Archibald (1982). For this, the 226 individuals (161 females and 65 males) were resampled with replacement 2000 times and the candidate growth models were fitted to each bootstrap dataset with 226 simulated individuals; this process created datasets for females and males with the same statistical properties as the original dataset, as well as a set of estimated parameters, which can be used to study the empirical distribution of the estimates. So, the bootstrap standard deviation (sd) is an estimate of the standard error (SE) of the parameter estimate. The bootstrap mean (\bar{x}) is an estimate of the mean value of the θ_i estimate; consequently, the coefficient of variation (CV) was estimated as $CV = sd/\bar{x}$ (Deriso *et al.*, 1985). The bias (B) and percent bias ($\%B$) were estimated, as follows: $B = \bar{x} - \theta_i$ and $\%B = \left(\frac{\bar{x} - \theta_i}{\theta_i} \right) \times 100\%$ (Jacobson *et al.*, 1994), where θ_i represents the estimated parameters for candidate growth model i fitted to the original data. The confidence intervals

were estimated using the bias-corrected percentile method (Haddon, 2001).

2.6 Model selection

We compared the fits of the ten candidate growth models using Akaike's information criterion (*AIC*) (Burnham and Anderson, 2002). The *AIC* penalizes the complexity of the model, given by the number of parameters, to attain an optimum between parsimony and accuracy (Pardo *et al.*, 2013). Consequently, it represents an efficient tool for selecting among competing models (Katsanevakis, 2006). The *AIC* was estimated as:

$$AIC = \{2[-\ln L(\theta_i^{MLE}|data)]\} + (2\theta_i),$$

where θ_i^{MLE} represents the number of estimated parameters, and $-\ln L(\theta_i^{MLE}|data)$ is the likelihood function for each growth model, and data represents the full dataset for females and males, separately. The model with the lowest *AIC* value (denoted AIC_γ) was selected as the best model (Burnham and Anderson, 2002). Models with *AIC* values which differed little from AIC_γ were also retained. Differences were estimated as $\Delta_k = AIC_\gamma - AIC_k$ for candidate growth model *k*. Models with $\Delta_k > 10$ were omitted, models with $4 < \Delta_k < 7$ were considered to have partial support, while models with $\Delta_k < 2$ were interpreted as being similar to the best model to explain the growth pattern of *D. gigas* (Burnham and Anderson, 2002). Moreover, the plausibility of model *k* was estimated as its Akaike weight (w_k):

$$w_k = \frac{e^{(-0.5\Delta_k)}}{\sum_{i=1}^{10} e^{(-0.5\Delta_i)}}.$$

The weights sum to 1 and are interpreted as evidence in favor of growth model *k* (Katsanevakis, 2006).

3 Results

3.1 Statolith reading and length-weight relationships

All 229 statoliths were read and included in the analyses. Mantle length range varied from 15 to 120 cm, including juveniles, recruits and adults. Corresponding ages varied from 101 to 442 days. The IAPE and CV values for all individuals combined were 3.57 and 4.58%, respectively, indicating high consistency among readings. In the sample, female *D. gigas* had mantle lengths mainly between 40 and 60 cm, while males were between 20 and 40 cm ML. Thus most sampled individuals measured 20 and 60 cm ML, with larger individuals (80–120 cm ML) being rare (Fig. 2a). A similar pattern was found for age. Sampled females were mostly 180 to 240 days old, and males 120 to 150 days. The proportion of sampled jumbo flying squid younger than 270 days and older than 240 days was low (Fig. 2b). Positive allometric growth was found for females, $TW = 0.024 \text{ ML}^{3.1}$ ($r^2 = 0.98$, Student's *t*-test, $P < 0.05$) and for males, $TW = 0.005 \text{ ML}^{3.4}$ ($r^2 = 0.99$, Student's *t*-test, $P < 0.05$) (the null hypothesis $b = 3$ was defined as isometric growth against the alternative hypothesis $b \neq 3$ identified as allometric growth).

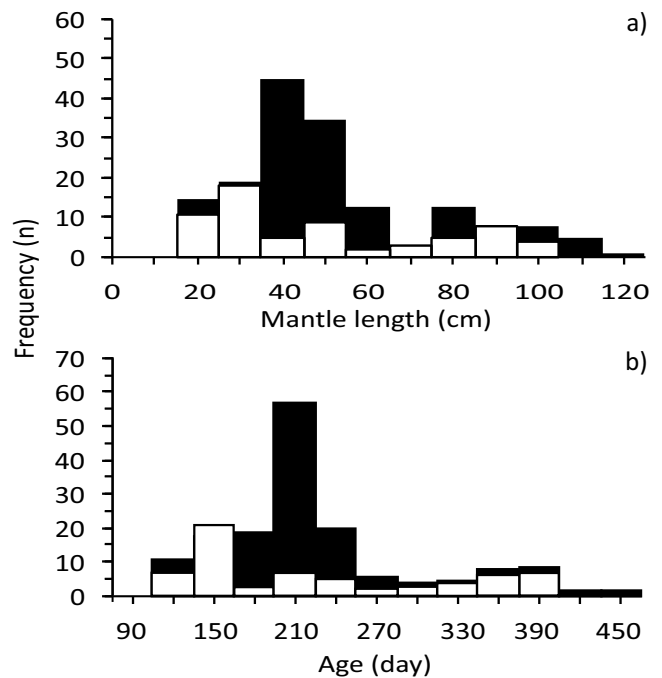


Fig. 2. Mantle length frequency distribution (a), and age composition (b) of *Dosidicus gigas* caught in Peruvian waters onboard the R/V Hakurei Maru VIII. Black bars are females and white bars are males.

3.2 Candidate growth models and model selection

The best fitting growth model for female *D. gigas* was the Schnute model ($\rho \neq 0, \eta \neq 0$) describing an asymptotic growth pattern (Fig. 3, Table 3). This candidate growth model had the lowest *AIC* and an Akaike weight of 0.99 (Table 4). The remaining candidate growth models showed Akaike differences higher than 9, consequently, they were not considered any further. For males, the Gompertz growth model had the lowest *AIC*, and an Akaike weight of 0.46 (Fig. 3, Tables 3 and 5). However, the Schnute model fitted similarly well ($\Delta_i = 1.88$), while there was also some evidence in support of the Richards ($\Delta_i = 2.07$) and the Jolicoeur ($\Delta_i = 2.12$) models. In summary, both female and male *D. gigas* in Peruvian waters grow asymptotically. The results indicated a different growth pattern between females (Schnute model $\rho \neq 0$ and $\eta \neq 0$), and males (Gompertz model, though the Schnute model had a similar fit). Note that the von Bertalanffy growth model showed poor performance for females and males. It exhibited a lack of convergence and parameter values lacked biological sense or interpretation (Appendix B).

4 Discussion

This study analyzed the growth pattern of *D. gigas* in Peruvian waters based on a multi-model approach. Previously, growth modeling for jumbo flying squid was done in the region using a single growth model (Argüelles *et al.*, 2001). In the statistical approach documented here, model selection offers a way to draw inference regarding competing growth hypotheses (Katsanevakis, 2006). Some differences were found between the age structures reported in this study in comparison to 1992

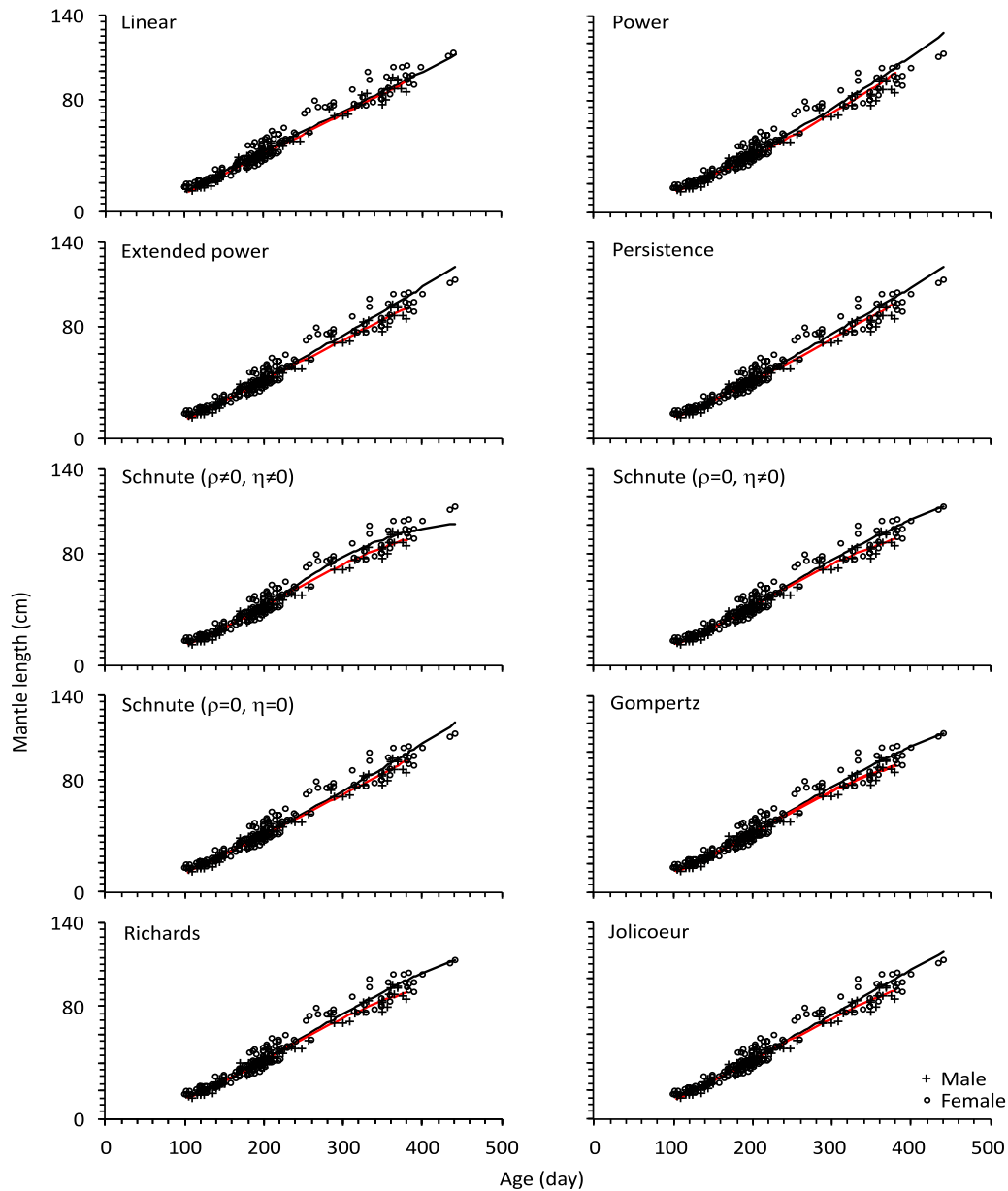


Fig. 3. Asymptotic and non-asymptotic growth models fitted to the *Dosidicus gigas* data set, analyzing females (black line) and males (red line). Three Schnute growth models were fitted: (a) ($\rho \neq 0, \eta \neq 0$); (b) ($\rho = 0, \eta \neq 0$); (c) ($\rho = 0, \eta = 0$).

(Argüelles *et al.*, 2001). The age of *D. gigas* analyzed in 1992 varied from 115 to 354 days, i.e. less than one year. In comparison, in this study, age varied from 101 to 442 days, thus included individuals older than one year. Argüelles *et al.* (2001) reported exponential growth for *D. gigas* in the region. The mantle length-at-age data were analyzed by these authors to derive:

- mantle length-at-age relationships by hatching season and size group;
- mantle length-at-age relationships by maturity stage and size group.

In the present study, the growth patterns for *D. gigas* individuals of different hatching season and mantle length

groups were analyzed together. Nigmatullin *et al.* (2001) classified male and female individuals into three groups according to mantle length (small, medium and large) and mentioned that the longevity of all groups is one year, although individuals with large mantle length (> 75 cm) might be 1.5 to 2 years, showing different growth pattern. The reason for this variation may be associated with the different age intervals used in each study and plasticity in life-history strategies of *D. gigas* in the eastern Pacific Ocean (Hoving *et al.*, 2013). Identifying growth patterns based on size groups is not easy, given the necessity to follow each cohort. If cohorts could be followed for *D. gigas*, then it would be possible to identify whether the size-at-age data showed growth compensation (*i.e.*, when cohort mantle length-at-age variability decreases

Table 3. Parameters and confidence intervals estimates by Monte Carlo simulations for different growth models applied to *Dosidicus gigas* (Schnute model for females, and Gompertz model for males).

Model	Parameter	Value	Mean	S.E.	CV	Bias	%Bias	Lower C.I.	Upper C.I.
Schnute ($\rho \neq 0, \eta \neq 0$)	ρ	0.015	0.015	0.001	0.037	0.000	-0.785	0.014	0.016
	η	-1.407	-1.417	0.053	-0.037	-0.010	0.677	-1.561	-1.345
	λ_1	16.50	16.39	5.446	0.033	-1.066	-0.650	14.85	17.25
	λ_2	102.11	101.45	35.455	0.035	-6.602	-0.651	90.37	106.56
	τ_1	101							
	τ_2	442							
Gompertz	L_∞	127.58	127.26	33.009	0.026	-3.137	-0.247	115.27	131.80
	κ	0.007	0.007	0.000	0.026	0.000	-0.401	0.006	0.007
	t_0	21.87	21.80	4.298	0.020	-0.697	-0.320	20.60	22.41

Table 4. Growth model selection for females of *Dosidicus gigas* caught in Peruvian waters.

Model	$-\ln L(\theta_i \text{data})$	AIC	Δ_k	w_k
Schnute ($\rho \neq 0, \eta \neq 0$)	610.55	-1213.09	0.00	0.99
Gompertz	605.02	-1204.04	9.05	0.01
Richards	604.89	-1210.79	11.31	0.0
Persistence	599.35	-1192.69	20.40	0.0
Jolicoeur	598.84	-1191.68	21.42	0.0
Extended power	596.01	-1186.02	27.08	0.0
Power	591.82	-1179.64	33.46	0.0
Linear	580.76	-1157.51	55.58	0.0
Schnute ($\rho = 0, \eta \neq 0$)	298.41	-590.83	622.26	0.0
Schnute ($\rho = 0, \eta = 0$)	235.57	-467.13	745.96	0.0

$-\ln L(\theta_i|\text{data})$ denotes the objective function value; AIC: Akaike's information criteria; Δ_k : shows differences in AIC; w_k : represents Akaike weight.

Table 5. Growth model selection for males of *Dosidicus gigas* caught in Peruvian waters.

Model	$-\ln L(\theta_i \text{data})$	AIC	Δ_k	w_k
Gompertz	267.49	-528.82	0.00	0.46
Schnute ($\rho \neq 0, \eta \neq 0$)	267.57	-526.94	1.88	0.18
Richards	267.48	-526.75	2.07	0.16
Jolicoeur	266.43	-526.70	2.12	0.16
Extended power	264.65	-523.14	5.68	0.02
Linear	262.08	-520.04	8.78	0.0
Persistence	261.89	-517.62	11.20	0.0
Power	252.53	-500.94	27.89	0.0
Schnute ($\rho = 0, \eta \neq 0$)	136.03	-265.90	262.93	0.0
Schnute ($\rho = 0, \eta = 0$)	99.78	-195.44	333.38	0.0

$-\ln L(\theta_i|\text{data})$ denotes the objective function value; AIC: Akaike's information criteria; Δ_k : shows differences in AIC; w_k : represents Akaike weight.

with time or age) or growth depensation (*i.e.*, when cohort mantle length-at-age variability increases with age) (Gurney and Veitch, 2007; Gurney *et al.*, 2007).

Our analyses for females and males revealed asymptotic growth for the species. The advantage of the Schnute model

($\rho \neq 0, \eta \neq 0$) is that it has more inflexion points, and if early stages of growth are included in the analysis then the model can identify them. Non-asymptotic growth models for *D. gigas* were also fitted by Markaida *et al.* (2004) and Mejía-Rebollo *et al.* (2008) and the best growth model was selected based on

the largest coefficient of determination (r^2) and the least coefficient of variation (CV) in estimated parameters. According to Burnham and Anderson (2002), adjusted r^2 and CV values are useful measures for the explained variation but they are not useful for growth model selection (Schwarz and Alvarez-Perez, 2010; Chen *et al.*, 2011, 2013).

The best candidate growth model selected by AIC was the Schnute growth model ($\rho \neq 0$, $\eta \neq 0$) for female flying jumbo squids; bias in parameter estimates was less than 1%. For male squids, the best candidate growth model was the Gompertz model and the bias was also less than 1%. Discrepancies between the asymptotic growth patterns found here and the non-asymptotic growth estimated for 1992 (Argüelles *et al.*, 2001) might be explained by the complex intra-specific population structure of the *D. gigas*. The species quickly responds to environmental variability driven by El Niño and La Niña events in both the Humboldt Current and California Current Systems, rapidly changing processes such as somatic growth, maturation (early or delayed), and life cycle duration (Taípe *et al.*, 2001; Waluda and Rodhouse, 2006; Bazzino *et al.*, 2007; Rosa *et al.*, 2013; Arkhipkin *et al.*, 2015). According to Zepeda-Benitez *et al.* (2014a), females *D. gigas* grow faster than males and become larger.

Flying jumbo squid populations are dominated by females (unequal sex ratio) making the mantle length structure and age composition mainly influenced by females. For Peruvian waters, the sex ratio (female:male) has been reported as 7:1 (Rubio and Salazar, 1992) and 3:1 (Ye and Chen, 2007). For Chilean waters, the sex ratio has been found to vary from 3:1 to 9:1 (Chong *et al.*, 2005). Finally, in the Mexican Pacific, the sex ratio has been reported as 2:1, 4:1, 5:1 and 14:1 (Hernández Herrera *et al.*, 1996; Markaida and Sosa-Nishizaki, 2001; Díaz-Urbe *et al.*, 2006; Markaida, 2006; Bazzino *et al.*, 2007). Thus, dominance of female jumbo squid seems to be a common feature in the eastern Pacific Ocean. Given this, any growth curves fitted to the data set of combined sexes without balancing the number of individuals by sex will be determined by females and depend on the sex ratio. Argüelles and Tafur (2010) reported that the growth of flying jumbo squid varied with the temperature regime, with both sex reacting independently. Thus, female and male *D. gigas* may respond differently to the same environmental conditions. In the Humboldt Current System off Peru, the change between a 1-year life cycle and non-asymptotic growth in 1992 (Argüelles *et al.*, 2001), and the opposite pattern in 2012 (life cycle greater than one year, almost 1.5 years, and asymptotic growth) was explained by differences in water temperature (Arkhipkin *et al.*, 2015). Years with warmer waters lead usually to a shorter life cycle (one year) while colder temperatures extend the life cycle to more than one year, as much as close to two years.

Chen *et al.* (2013) did not report differences in the growth pattern by sex for *D. gigas* in Costa Rican waters, and similar results were reported by Zepeda-Benitez *et al.* (2014a) for the jumbo squid population in Mexican waters. The conceptual growth model for cephalopods proposed by Lipinski (2002) describes three phases:

- relatively slow paralarvae growth;
- rapid growth by juveniles and adults;
- diminished or no growth commonly observed for spawners.

Thus, a unique growth model for *D. gigas* must handle these changes in growth rates during the life cycle. Only sufficiently flexible models can achieve this, such as the Schnute ($\rho \neq 0$, $\eta \neq 0$) and Gompertz models, both have parameters expressing reasonable biological interpretations (Schnute, 1981). Understanding the population dynamics of *D. gigas* requires monitoring the stock at appropriate spatial and temporal scales. Data partially collected may be insufficient, affecting the detectability of relevant process such as:

- recruitment;
- changes in spatial distribution of the squid schools due to environmental variability;
- variability in the number of cohorts.

The spatial extent of the research survey in this study covered the entire distribution of *D. gigas* in Peruvian waters. Consequently, the age and mantle length structure of the whole population was well sampled and the growth patterns identified for *D. gigas* (females and males) represented the growth for the early summer season in Peruvian waters.

For studying growth of squid populations, a challenge is that an asymptote is less clearly visible in length-at-age data compared to fishes. Using a multi-model allows to confront the candidate growth models with data in an objective manner, overcoming the limitations of visual perception. In recent years, there have been many advances in the quantitative analysis of age and growth of different squid species (Arkhipkin and Shcherbich, 2012; Zepeda-Benitez *et al.*, 2014a). To establish the growth pattern of *D. gigas* throughout its distribution area is difficult, because the pattern changes from asymptotic to non-asymptotic growth according to the region (Peru, Chile, Ecuador, Costa Rica, Mexico), the duration of the life cycle can be modified by environmental conditions (Arkhipkin *et al.*, 2015), the number of cohorts changes and the maturation in females can be early or delayed (Keyl *et al.*, 2011). It is presently understood that growth patterns are affected by biological and environmental causes. Thus, growth modeling cannot be limited to a single growth model. Multi-model inference allows analyzing different alternative models and improving the biological knowledge of jumbo flying squid in the region.

For cephalopods, growth studies have been based on statoliths which implies that increments from the nucleus to the edge of the dorsal dome can be counted and correspond to daily rings (Boyle and Rodhouse, 2005). For vertebrates (e.g. tuna), alternative data sources such as length frequency and length increment data derived from tagging experiments have also been used to estimate mean length-at-age and the variability of length-at-age (Schnute and Fournier, 1980; Francis, 1988; Fournier *et al.*, 1990; Labelle *et al.*, 1993; Restrepo *et al.*, 2010). Usually, these types of data have been used independently, however the comparison among data sources has been useful to identify the uncertainty in growth parameters. A recent approach incorporating different data sources for modeling length-at-age has been based on integrated growth models (Kirkwood, 1983; Eveson *et al.*, 2004; Restrepo *et al.*, 2010; Aires-da-Silva *et al.*, 2015; Luquin-Covarrubias *et al.*, 2016).

For jumbo flying squid, an integrated growth model will allow the implementation of a joint likelihood function for different data sources, thus the level of uncertainty of the growth parameters can be diminished with the availability of data (Aires-da-Silva *et al.*, 2015; Luquin-Covarrubias *et al.*, 2016). Theoretically, different data sources will often be most informative about different portions of the life cycle and different aspects of growth. The use of an integrated growth model would allow for the different data sources to complement each other and provide a more robust and comprehensive basis for modeling growth, avoiding significantly overestimating or underestimating growth parameters (Maunder and Punt, 2013; Maunder and Piner, 2014; Aires-da-Silva *et al.*, 2015; Luquin-Covarrubias *et al.*, 2016). According to , the different data sources are informative of a particular ontogenetic stage. Therefore, direct aging data provide information from recruits to older individuals. This information can be collected from fishery-dependent data (fishery vessel reports) and fishery-independent data (scientific surveys at sea). Tag–recapture data are one observation per fish, thus, valuable information (length and time) about how individuals grow is collected (Laslett *et al.*, 2002). Finally, length–frequency data collected from commercial catches are commonly informative about younger ages. An integrated growth model has been successfully applied to improve the growth parameters and the theoretical growth trajectories for different species (Kirkwood, 1983; Restrepo *et al.*, 2010; Aires-da-Silva *et al.*, 2015; Luquin-Covarrubias *et al.*, 2016). Although an integrated growth model for modeling length-at-age data in *D. gigas* can be plausible, the evidence found in this study indicated that the species exhibits an asymptotic growth pattern in Peruvian waters.

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Appendix A Schnute growth model and parameters

Given that the Schnute growth model ($\rho \neq 0, \eta \neq 0$) was the best candidate growth model selected by AIC for females, the equations that explicitly were used to estimate asymptotic size (1), age at growth inflection (2), length-at-age of growth inflection (3), and theoretical age of the squid at zero size (4) were as follows (Schnute, 1981):

$$L_{\infty} = \left[\frac{(e^{\rho\tau_2}\lambda_2^{\eta}) - (e^{\rho\tau_1}\lambda_1^{\eta})}{e^{\rho\tau_2} - e^{\rho\tau_1}} \right]^{1/\eta} \quad (1)$$

$$\tau^* = \tau_1 + \tau_2 - 1 / \rho \ln \left[\frac{\eta \{ (e^{\rho\tau_2}\lambda_2^{\eta}) - (e^{\rho\tau_1}\lambda_1^{\eta}) \}}{\lambda_2^{\eta} - \lambda_1^{\eta}} \right] \quad (2)$$

$$L^* = \left[\frac{(1 - \eta) \{ (e^{\rho\tau_2}\lambda_2^{\eta}) - (e^{\rho\tau_1}\lambda_1^{\eta}) \}}{e^{\rho\tau_2} - e^{\rho\tau_1}} \right]^{1/\eta} \quad (3)$$

$$\tau_0 = \tau_1 + \tau_2 - 1 / \rho \ln \left[\frac{(e^{\rho\tau_2}\lambda_2^{\eta}) - (e^{\rho\tau_1}\lambda_1^{\eta})}{\lambda_2^{\eta} - \lambda_1^{\eta}} \right] \quad (4)$$

Schnute (1981) explained that the general growth model includes asymptotic and non-asymptotic curves; the model gives to the length-at-age data the freedom to select the most appropriate model. For this reason, this study analyzed the following cases: i) $\rho \neq 0$ and $\eta \neq 0$; ii) $\rho = 0$ and $\eta \neq 0$; and iii) $\rho = 0$ and $\eta = 0$.

Appendix B von Bertalanffy growth model

We analyzed the performance of the von Bertalanffy growth model. However, the model was not informative for jumbo flying squid. The negative log likelihood function showed a lack of convergence, and the theoretical growth model did not fit the age-length data, consequently the estimated parameters of the von Bertalanffy growth model were highly biased without biological sense or interpretation (Fig. B1, Table B1). The von Bertalanffy growth model failed to show the growth pattern in females and males. Jackson *et al.* (2000) explained that due to the degree of plasticity in squid growth similar sized individuals might have considerably different ages. Additionally, if growth is rapid with a high degree of individual plasticity, then it is difficult to discern an asymptotic size. Consequently, the von Bertalanffy (1938) growth model is a wrong model to explain the growth pattern in squid (Boyle and Rodhouse, 2005).

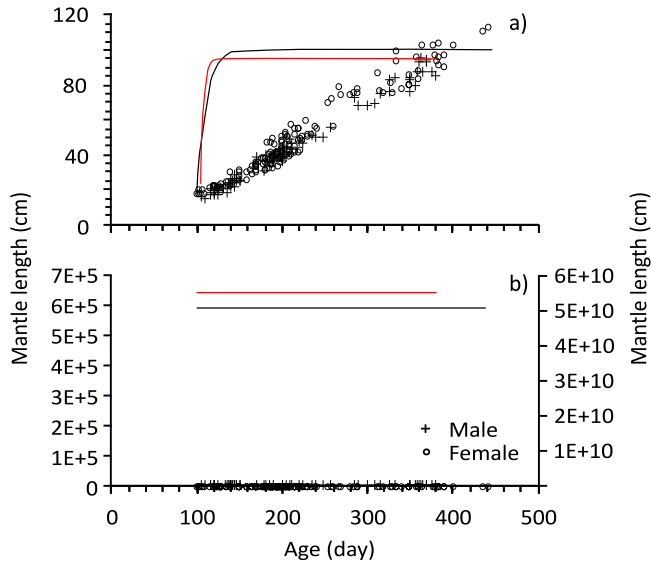


Fig. B1. Age-at-mantle length data fitted to von Bertalanffy growth model; (a) denotes the growth models with initial values; (b) shows the two growth models optimized exhibiting a lack of convergence. In both figures, the black line is females and the red line represents males.

Table B1. Initial and optimized parameters for the von Bertalanffy growth model applied to jumbo flying squid *Dosidicus gigas* in Peruvian waters.

Parameter	Females		Males	
	Initial	Optimized	Initial	Optimized
L_{∞} (cm)	100	53687092200	95	600194
k	0.1	282622	0.29	53687091
t_0	9	-4250976868	10	-8462631

L_{∞} is average maximum mantle length reached by older individuals; k represents the growth coefficient; t_0 parameter is the theoretical age of the squid at zero size under the assumption that the von Bertalanffy (1938) growth curve describes the growth accurately right down to zero length. Even if this unlikely assumption is true, squid will be born with some positive length, so t_0 will usually be negative.

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