

AGE AND GROWTH MODELLING FOR EARLY STAGES OF THE JUMBO SQUID *DOSIDICUS GIGAS* USING MULTI-MODEL INFERENCE

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ABSTRACT

Age and growth were estimated for early growth stages of the jumbo squid *Dosidicus gigas* in the Gulf of California, based on daily growth increments in statoliths. Three individual growth functions that showed non-asymptotic patterns (two cases of the Schnute general model, and Tanaka model) were fitted to length-at-age data. Using Akaike's Information Criterion and multi-model inference, we selected the best model to describe the growth pattern. We found that the Schnute general model was the best growth function describing mantle length-at-age data for paralarvae and juveniles of *D. gigas*, showing a power pattern. Absolute daily growth rate ranged from 0.03 to 1.66 mm day⁻¹, with lower values for paralarvae and higher values for juveniles.

INTRODUCTION

Dosidicus gigas is the most abundant commercial squid in the central Gulf of California. Although the fishing activity is well known in this area, life-history parameters of *D. gigas* have not been fully assessed and are critical for understanding squid biology, as well as for proper management through stock assessment modelling (Morales-Bojórquez et al. 2001; Morales-Bojórquez and Nevárez-Martínez 2010). Thus, knowledge of *D. gigas* has been limited to fishery-dependent data, and several aspects of recruits and adult squid population. In contrast, little is known about the demography of the paralarvae of *D. gigas*, and how their parameters vary spatially and seasonally in the Gulf of California, although recent information about this issue has been reported by Camarillo-Coop et al. 2010, 2013; and Rosa et al. 2013.

Rapid growth appears to enhance survival of paralarvae due to high predation during the early life stages (Boyle and Rodhouse 2005). Studies have suggested that individuals that grow rapidly and achieve a larger body size spend less time in the most vulnerable early life stages (Cushing 1982). Understanding the factors responsible for differences in growth during the early

life stages of *D. gigas* can be used to assess important factors regulating survival, as well as recruitment success (Boyle and Rodhouse 2005), it is defined as the number of individuals that reach a specified stage of the life cycle (e.g., metamorphosis, settlement, selected by the fishery). The scarcity of information on age and growth of early life stages of *D. gigas* is presently an impediment to describing spawning locations, hatch dates, and transport from offshore to recruitment areas (advection), and availability for the fishing fleets in the Gulf of California.

Growth rates are critical to survival of paralarvae, as well as the dynamics of recruitment (Vidal et al. 2005). In general, if squid have several phases of early development or the number and duration of stages are large, then natural mortality increases. According to Nesis 1979, the limits of these phases or stages are defined by body size, and not the age at which the change happens. For example, the cephalopod *Spirula spirula* has a single discontinuity in growth of its mantle, arms, tentacles, and fins. The discontinuity is characterized by morphological changes expressed through relative growth (Nesis 1979). These changes correspond to the transition from paralarval to juvenile phase (Clarke 1966). For the short fin squid *Illex argentinus*, the first discontinuity in growth coincides with the transition from the paralarval to juvenile phase, which occurs in a narrow range of 14–17 mm ML (Vidal 1994). Between 25 and 35 days the larval growth rate of *Stenoteuthis pteropus* shows a decreasing trend when the species changes from larvae to juvenile (Laptikhovskiy et al. 1993). Vidal 1994 explained that, to be efficient predators, rhyntoteuthions must be good swimmers. Fast growth and slendering of the body is a result of relatively slow growth of mantle weight, which causes the loss of the spherical shape and favors the development of the cylindrical shape, which increases the efficiency of jet propulsion. Paralarval growth in length of *Ommastrephes bartramii* is typically described by an

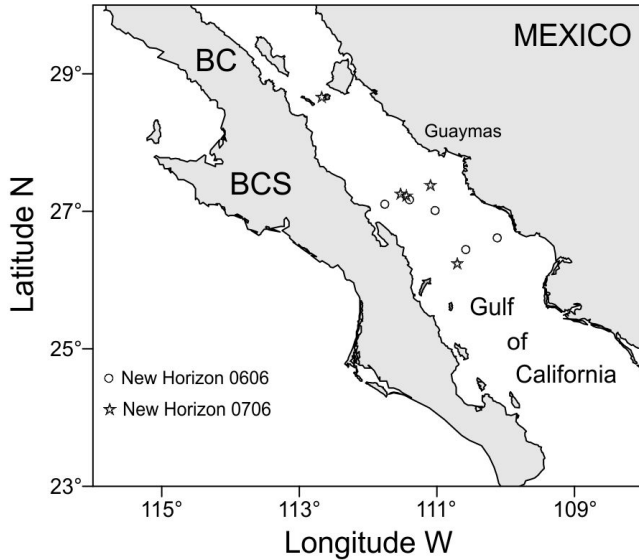


Figure 1. Study area in the central Gulf of California, Mexico. Sampling sites of two field surveys are shown.

exponential equation (Bigelow and Landgraf 1993). Arkhipkin 2004 analyzed the diversity in growth of squids (suborder Oegopsina), reporting that the tropical species show non-asymptotic growth in comparison to polar and deepwater species where the asymptotic growth is commonly observed. Fast growth has clear benefits in allowing paralarvae to pass more quickly through its most vulnerable life history stages and to develop faster physically and physiologically in order to improve its ability to detect and capture prey, as well as predator avoidance and resistance to environmental variability (Bigelow 1992).

Fishery management and conservation of *D. gigas* in the Gulf of California is very important. Lack of basic biological information of early stages of *D. gigas* reduces our understanding of the population dynamics of recruits and adult stock (Camarillo-Coop et al. 2010, 2013; Zepeda-Benitez et al. in press). In this study an appropriate growth model was identified to fit length-at-age data for early stages of *D. gigas* in the Gulf of California based on multi-model inferences and generalized growth models. The implications of these growth models, as well as the choice of models, are discussed in relation to the new population biology of early stages of *D. gigas*.

MATERIAL AND METHODS

Squid sampling data collection

Two research surveys on board the RV *New Horizon* were conducted in the central Gulf of California in June 2006 and June 2007 (fig. 1). Samples of the early life stages of *D. gigas* were collected in the Guaymas and del Carmen Basins; paralarvae were captured with a 500 μm

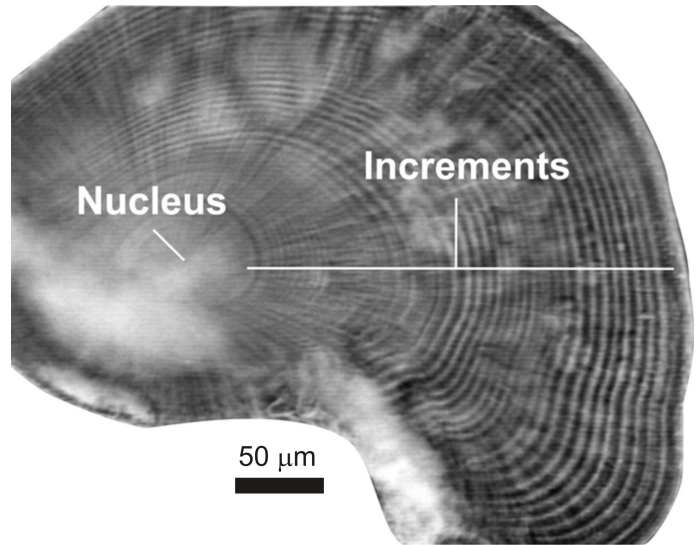


Figure 2. Microstructure of a statolith of a juvenile (18.6 mm ML) of *Dosidicus gigas*.

mesh bongo net (Diekmann and Piatkowski 2002) and juveniles with a dipnet. A total of 12 paralarvae and 93 juveniles were fixed in 95% ethanol. Measurements of mantle length (ML) and body weight (BW) were taken to the nearest 0.01 mm and 0.1 g, respectively. Statoliths from each specimen were extracted and stored in 95% ethanol for age determination. Sizes ranged from 2.8 to 67.8 mm ML; the most common size frequency interval was identified as a mode at 24–26 mm ML.

Statolith reading

The statoliths were mounted on microscopic slides for reading growth increments on the dorsal dome based on the Arkhipkin method (Dawe and Natsukari 1991). For juveniles, the statoliths were ground and polished, since in this development stage the concave and convex regions of statolith are not well developed. Consequently, any side can be used for grinding in juveniles. González et al. 2010 explained that for paralarvae (*Loligo vulgaris*) the concave and convex surfaces must be ground. The procedure is not clearly defined; however both techniques allow the observation of growth lines. Paralarvae statoliths required only polishing. Increment counting started at the nucleus and proceeded to the edge of the dorsal dome. Counts were carried out independently by two readers where they read the increments with transmitted light at 400 \times (fig. 2). Each increment was assumed to be deposited daily, as has been determined to occur for other squid of the family Ommastrephidae (Dawe et al. 1985; Nakamura and Sakurai 1991). The age of each individual was defined to be the average of the two independent counts. The index of average percent-age error (IAPE) and coefficient of variation (CV) were

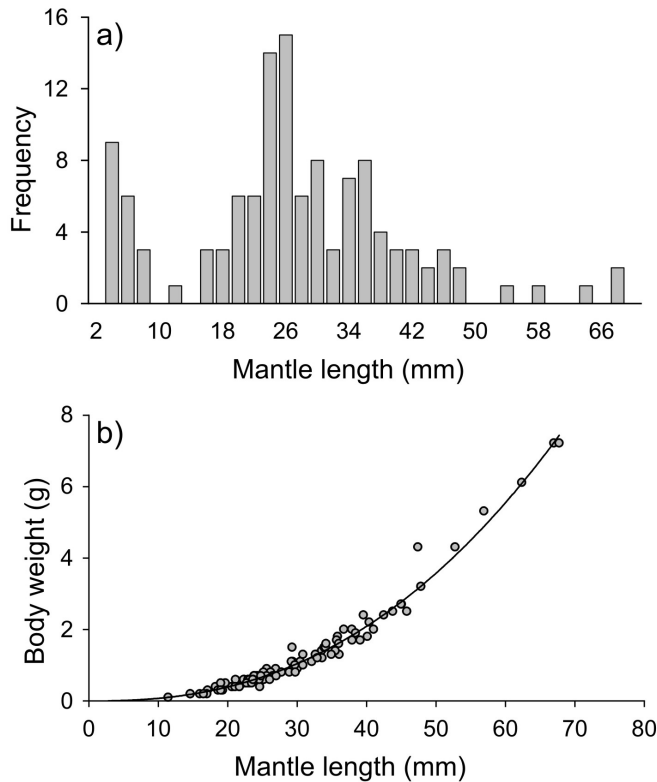


Figure 3. (a) Mantle length interval and (b) Mantle length to body weight relationship analyzed for early growth stages of *Dosidicus gigas*.

calculated to assess the reliability of the counts between readers (Campana et al. 1995).

Growth modelling

We used models that do not show an asymptotic growth because the early development of the *D. gigas* has accelerated growth. We used two cases of the non-asymptotic models proposed by the Schnute general growth model (Schnute 1981): a) $\rho = 0, \eta \neq 0$, and b) $\rho = 0, \eta = 0$, where ρ is the constant relative rate of the relative growth rate and η is the incremental relative rate of the relative growth rate. We also used an indeterminate growth model (Tanaka 1982). These models were fitted to length-at-age data, and specific details about the growth function are in Appendix 1.

Parameter estimation and confidence intervals

The θ_i parameters represent the estimated parameters in the non-asymptotic models (Schnute or Tanaka models), and were estimated using a negative log-likelihood function:

$$-\ln L(\theta_i | data) = \sum_i \left[-\frac{1}{2} \ln(2\pi) \right] - \left[\frac{1}{2} \ln(\sigma^2) - \left(\frac{\ln L(t) - \ln \hat{L}(t)^2}{2\sigma^2} \right) \right]$$

The parameters were estimated by maximizing the negative log-likelihood estimator (Hilborn and Mangel 1997) using the Newton algorithm (Neter et al. 1996). For the standard deviation (σ), the analytical solution is:

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

where n is the number of ages observed in the early stages of *D. gigas*. Confidence intervals were estimated using the bootstrap method described by Fournier and Archibald 1982.

Model selection

We compared the fits of the different candidate growth models using Akaike’s information criterion (*AIC*) (Burnham and Anderson 2002). The small-sample *AIC_c* was determined as follows:

$$AIC_c = 2 \times -\ln L(\theta_i | data) + 2 \times \theta_i + \frac{2 \times \theta_i (\theta_i + 1)}{n - \theta_i - 1},$$

where θ_i is the number of estimated parameters, n is the number of observations, and $-\ln L(\theta_i | data)$ is the objective function for each candidate growth model. The model with the lowest *AIC_c* value was selected as the best model (Haddon 2001).

Growth rates

Absolute daily growth rates (DGR), and instantaneous growth rate (G) were calculated for each 5-day interval (Forsythe and Van Heukelem 1987; González et al. 2010), with data that included paralarvae and juveniles.

RESULTS

The mantle length-body weight relationship was estimated for juveniles ($R^2 = 0.97$) and total weight varied from 0.1 to 7.2 g (figs. 3a, 3b). Power coefficient was analyzed using a Student’s *t*-test to determine the type of growth. It was estimated as a value of 2.41, which was statistically different from the theoretical value of 3.0 ($p < 0.05$), indicating that growth in juvenile of *D. gigas* is faster in length than in body mass.

Statoliths were measured from the rostrum to the dorsal dome. Length varied from 0.09 to 0.63 mm, corresponding to mantle length of 4.1 mm (paralarvae) and 67.8 mm (juvenile), respectively. The mantle length-statolith length (ML-SL) showed correlation between the two variables ($R^2 = 0.85$), which indicates that there is a proportionality between somatic growth and statolith growth of paralarvae and juveniles. The results of the index of average percent error and the coefficient of variation were 2.03% and 2.87%, respectively, indicating that the readings carried out by the two readers were similar. Estimated age varied from 1 to 59 days,

TABLE 1
 Parameters and confidence intervals estimates by Monte Carlo simulations for different growth models.

Model	Parameter	Value	Mean	S.E.	CV	Bias	%Bias	Lower 5%	Upper 95%
Schnute ($\rho = 0, \eta \neq 0$)	η	0.334	1.171	0.088	0.075	0.837	71.497	1.012	1.351
	λ_1	3.331	2.784	0.146	0.052	-0.548	-19.669	2.495	3.022
	λ_2	46.093	34.912	0.996	0.029	-11.181	-32.027	33.131	37.047
	τ_1	1							
	τ_2	59							
Schnute ($\rho = 0, \eta = 0$)	λ_1	4.030	8.319	0.725	0.087	4.289	51.559	7.072	9.877
	λ_2	54.328	84.084	23.630	0.281	29.756	35.388	62.684	213.587
	τ_1	1							
	τ_2	59							
Tanaka	γ	0.737	0.049	0.094	1.929	-0.689	-1419.267	0.002	0.854
	χ	49.760	20.956	2.329	0.111	-28.804	-137.451	16.185	25.646
	δ	70.204	22.302	0.587	0.026	-47.903	-214.793	21.527	23.774
	φ	0.004	0.211	0.154	0.733	0.207	98.127	0.084	0.761

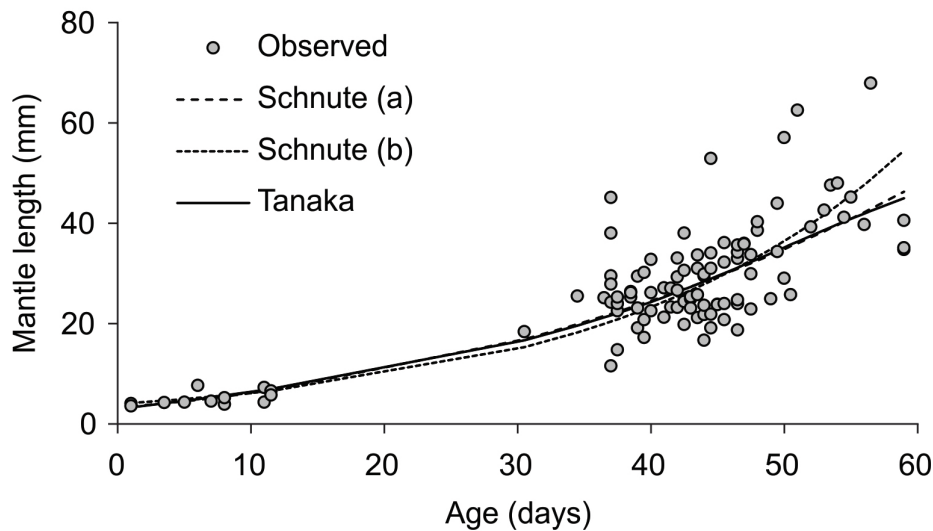


Figure 4. Growth models fitted to mantle length-at-age data for *Dosidicus gigas*. Tanaka model, and two cases of Schnute model assuming $\rho = 0, \eta \neq 0$ (a), and assuming $\rho = 0, \eta = 0$ (b). The best candidate growth model was Schnute (b).

which corresponds to paralarvae of 3.4 mm ML (the age paralarvae interval varied between 1 and 12 days; and the larger specimen was 7.5 mm) and juveniles of 34.9 mm ML, respectively. The parameters of the non-asymptotic growth models fitted to the length-at-age data are shown in Table 1.

The Schnute general model, assuming $\rho = 0, \eta \neq 0$ (fig. 4), described an empirical power function; consequently, biological parameters about individual growth were not estimated.

For each candidate model AIC_c , Δ_i and w_i values are shown in Table 2. Based on the lowest AIC_c (-10.64) and the highest w_i (0.984) values, the Schnute general model ($\rho = 0, \eta = 0$) was the function that describes the best fit the mantle length-at-age data. The other candidate models showed AIC_c differences (Δ_i) greater than 9, which indicates that these functions should not be considered.

TABLE 2
 Growth model selection for *Dosidicus gigas*.

	θ	AIC_c	Δ_i	w_i
Schnute ($\rho = 0, \eta = 0$)	2	-10.64	0.00	0.984
Schnute ($\rho = 0, \eta \neq 0$)	3	-1.28	9.36	0.009
Tanaka	4	-0.79	9.85	0.007

The highest absolute daily growth rates (DGR) for the paralarval stage was 0.16 mm day⁻¹, which occurred during the first five days of life, followed by a gradual decrease to 0.03 mm day⁻¹ (fig. 5a). Individuals between 12 and 31 days were not available. Juveniles at 35 days increased their absolute daily growth rate to a maximum of 1.66 mm day⁻¹ in individuals at 55 days. The estimations showed an increment in absolute daily growth rate, and a subsequent fall that probably can be explained by the smaller sample of size-at-age of organisms greater than 55 days old, although a linear trend was observed

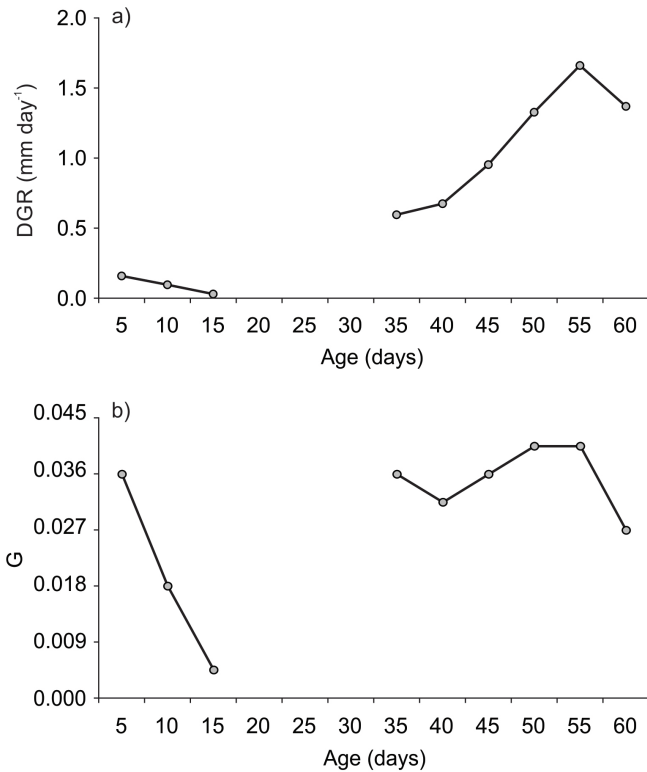


Figure 5. (a) Absolute daily growth rate (DGR), and (b) Instantaneous growth rate (G) of statoliths during early growth stages of *Dosidicus gigas*.

from 35 to 60 days old. The instantaneous growth rate decreases through the calculated range for paralarvae, decreasing from 0.036 (at age 1–5 days) to 0.005 (at age 11–15 days) (fig. 5b). For individuals from 35 days and older the instantaneous growth rate showed a new increment with an average of 0.035.

DISCUSSION

The central Gulf of California is known as a spawning region for *Dosidicus gigas* (Gilly et al. 2006a). This region is also the main fishing area during autumn and winter and is near the coastal city of Guaymas in the State of Sonora. During spring and summer fishing intensity of this resource moves westward near Santa Rosalía in the State of Baja California Sur (Markaida et al. 2005; Gilly et al. 2006b). This seasonal pattern is characterized by the presence of mature males and females, which is routinely reported in the Gulf of California (Ehrhardt et al. 1986; Velázquez-Abunader et al. 2012). Hernández-Herrera et al. 1998 concluded that the spawning season of the *D. gigas* occurs from February to May off Guaymas, Sonora. However, Ehrhardt et al. 1986 concluded that the spawning seasons are not well defined and vary annually, based on changing oceanographic conditions. From the mantle length-body weight relationship, juveniles have power coefficient less than 3. A similar pattern was reported by Laptikhovskiy et al. 1993 for the

paralarvae of *Sthenoteuthis pteropus*. It was found that during early-stages development, the length and weight proportions changed and mantle length increased faster than weight. Consequently, organisms were found to be slimmer as they grew, and this shape change is related to muscle growth playing a role in improving paralarval locomotion in order to enhance survivability.

The growth increments in paralarvae and juvenile statoliths were clearly visible, for all individuals ages were determined, however an older age (59 days) was estimated for a juvenile of 34.9 mm ML, and the age of the larger organism (67.8 mm ML) was 57 days; the youngest organism aged corresponds to a paralarvae of one day and 3.4 mm ML. Rosa et al. 2013 described results found by Arkhipkin and Murzov 1986 explaining that individuals of *Dosidicus gigas* between 28 and 32 increments (4–4.5 weeks) had a mantle length between 9 to 10 mm, showing an exponential growth in these age classes. Yatsu et al. 1999 conducted artificial fertilization experiments of *Dosidicus gigas*; they did not report increments in the statoliths, suggesting that this was an effect of artificial rearing; they also reported mantle length at hatching measured 0.9–1.3 mm based on frozen specimens, and explained that the mean mantle length gradually increased, observing high variability within and among ages for this ontogenic development stage. In contrast, our observations were based on wild paralarvae and the individuals were not frozen. Comparatively, the morphological characteristics of wild organisms cannot be similar to those individuals obtained by artificial fertilization and captivity.

Absolute growth refers to the total increase in body material or body dimensions, while the absolute growth rate is defined as absolute growth over a given time period. If this rate is constant over time, then we have linear growth. Comparatively, an exponential growth is represented by the instantaneous growth rate (Pitcher and Hart 1982). According to Arkhipkin 2004, early stages of *D. gigas* have higher instantaneous growth rates than other members of the Ommastrephidae; their growth rate declined from 5%–8% in paralarvae and juveniles, and between 0.2%–0.4% in adults. These growth rates are influenced by different biotic and abiotic factors and cause changes throughout the life cycle of squid. The most important factors are availability of food and temperature (Forsythe 1993; Jackson and Moltschanivskiy 2001a). During ontogenetic development at the paralarvae stage, the proboscis begins its division between 5 and 6 mm ML (Nesis 1970, 1983). In our study, squid at this size decline in their absolute daily growth rate to 0.03 mm day⁻¹. In our study all the paralarvae were in process of the proboscis division, and the decline in DGR possibly attributable to this morphological change; during this morphological reorganization the yolk sac

is absent and the capture apparatus (tentacles) begins to develop to make way for a more complex feeding that is mainly composed of crustaceans (Balch et al. 1985; Vecchione 1991; Laptikhovskiy et al. 1993; Vidal and Haimovici 1998).

The growth curve that was derived from the Schnute general model ($\rho = 0, \eta \neq 0$) is equivalent to a linear or quadratic growth model. However, our data does not show this tendency; consequently, this growth model was not the best candidate. For the Schnute general model, the τ_0 parameter could be estimated; nonetheless, the parameter is undefined; and does not have the usual significance related to size 0 (Schnute 1981). The Δ_i of this model ($\rho = 0, \eta \neq 0$) was greater than 9, which means that this growth function should not be considered as a candidate growth model. A similar value was estimated for the Tanaka growth model. According to Burnham and Anderson 2002, if $\Delta_i > 10$, then the candidate growth model can be omitted because it did not represent the observed growth pattern; if $4 < \Delta_i < 7$, there was partial support for the model, and the candidate growth model could explain the individual growth pattern; and if $\Delta_i < 2$, then the candidate growth model had substantial support to explain the early growth pattern of *D. gigas*. The Schnute general model ($\rho = 0, \eta = 0$) describes a power function and was identified as the best growth model candidate, where the Akaike weight was 0.984. This solution ($\rho = 0, \eta = 0$) describes a curve that starts at the t -axis (t is time in days) and continues upward with unbounded, accelerated growth, which is restricted to the early development stages (Schnute 1981). This model has also been used for other squid species. For adult *Loligo noctiluca* (Jackson and Moltschanivskiy 2001b) only the Schnute model was used. For juvenile and adult *Illex argentinus* (Schwarz and Alvarez-Perez 2010), four growth functions (exponential, potential, Gompertz, and Schnute) were used; the authors concluded that the Gompertz growth model described females, and the Schnute growth model was the best growth model for males. For both models, the existence of two growth phases was observed, an initial rapid growth and a subsequent decline in growth rate.

Cephalopods show plasticity in their growth rates and thus identifying a pattern of growth is not easy (Jackson 2004). From our results, paralarval and juvenile *Dosidicus gigas* grow following a power function; it represents a special case of the Schnute growth model ($\rho = 0, \eta = 0$) and was used in this study. During these early stages, the squid did not show a specific age where growth rate changes or length-at-age growth inflection. Consequently, Schnute ($\rho = 0, \eta \neq 0$) and Tanaka models did not adequately describe growth within early stages for this species because they did not identify the change

from one period of growth to another. These changes are usually characterized by a discontinuity in development, which is commonly associated with major ontogenic events, such as transformation of the body shape (Balch et al. 1985; Vecchione 1991; Arkhipkin and Roa-Ureta 2005). Our study showed that the early stages of wild paralarvae of *Dosidicus gigas* grow following the Schnute growth model ($\rho = 0, \eta = 0$).

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APPENDIX 1

The Schnute general growth model (Schnute 1981), assuming $\rho = 0, \eta \neq 0$ is:

$$L(t) = \left[\lambda_1^\eta + (\lambda_2^\eta - \lambda_1^\eta) \times \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{1/\eta}$$

The case, assuming $\rho = 0, \eta = 0$ is:

$$L(t) = \lambda_1 \times \exp \left[\ln(\lambda_2/\lambda_1) \times \frac{t - \tau_1}{\tau_2 - \tau_1} \right]$$

where τ_1 is the first specified age, τ_2 is the second specified age, λ_1 is the size at age τ_1 , and λ_2 is the size at age τ_2 . Using $\rho = 0, \eta \neq 0$, we estimated age of theoretical zero size (τ_0) as:

$$\tau_0 = \tau_1 + \tau_2 - \left[\frac{(\tau_2 \times \lambda_2^\eta) - (\tau_1 \times \lambda_1^\eta)}{\lambda_2^\eta - \lambda_1^\eta} \right]$$

The Tanaka model (Tanaka 1982) assumes a non-asymptotic growth phase based on indeterminate growth. The model has four parameters with an initial period of slow growth, a period of exponential growth, followed by an indefinite period of slow growth. The parameterized form of the model is:

$$L(t) = \frac{1}{\sqrt{\phi}} \ln | 2\phi(t - \chi) + 2\sqrt{\phi^2(t - \chi)^2 + \phi\gamma} | + \delta$$

where ϕ is the rate of change of the growth rate, χ is the age at which the growth rate is maximum, γ is the maximum growth rate, and δ is a parameter that shifts the mantle length at which growth is maximum (Ebert 1999).