Growth model selection for the jumbo squid *Dosidicus gigas* from the Gulf of California, Mexico

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ABSTRACT: We analyzed mantle length and age data of the whole ontogenic cycle of the jumbo squid *Dosidicus gigas* in the Gulf of California, Mexico, to describe its growth pattern. Several individual growth models that included asymptotic and non-asymptotic patterns were fitted to the data, and Akaike's information criterion and multimodel inference were used to identify the model that best fit the data. The length-at-age data were divided into males and females (recruits and adults) for analysis separately and then combined to assess the overall growth pattern. The Schnute general model ($\rho \neq 0$, $\eta \neq 0$, where ρ is the constant relative rate of the relative growth rate, η is the incremental relative rate of the relative growth rate) was the function that best described the growth of females, males and both sexes of *D. gigas* together. For females, the Akaike difference and Akaike weight were 0 and 0.91, respectively; for males, the Akaike difference was also 0, but the Akaike weight was 0.39, showing that alternative growth models could explain the individual growth; these growth models were the Gompertz (L_0, length at time zero), Gompertz (L_∞, asymptotic length) and Schnute ($\rho \neq 0$, $\eta = 0$) models. We estimated the age and mantle length at which the growth rate changes for both sexes, estimating an age of 162.36 d (separately, 167.51 d for females and 158.98 d for males), and a length of 299.52 mm for the growth inflection point (separately, 312.84 mm for females and 292.86 mm for males). Once *D. gigas* reaches this point, the species exhibits more gradual growth until reaching an asymptotic mantle length of 859.45 mm (for females, 904.80 mm, and for males, 828.49 mm). A comparison of the growth patterns of *D. gigas* reported in the Eastern Pacific indicated non-asymptotic growth of this species in the Humboldt Current and Costa Rica Dome; in contrast, asymptotic growth was identified for the western coast of Baja California and Gulf of California. The reason for this difference is unclear, and this issue will be a topic of future studies.

KEY WORDS: Age · Asymptotic growth · Multimodel inference · Schnute's model

INTRODUCTION

The jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) is widely distributed in the Eastern Pacific, ranging from Alaska to Chile (Cosgrove 2005, Wing 2006, Zeidberg & Robison 2007). In Mexico, most commercial catches of jumbo squid are harvested from the central Gulf of California (Fig. 1). In this fishery,

there are a number of different fishing fleets: (1) 2 fleets from Baja California Sur, (2) 3 fleets from Baja California, and (3) 2 fleets from Sonora, Mexico. Fishing takes place off Baja California Sur during the spring and summer and off Sonora during the fall and winter (Velázquez-Abunader et al. 2012). The fishing season in Baja California occurs during summer and fall.

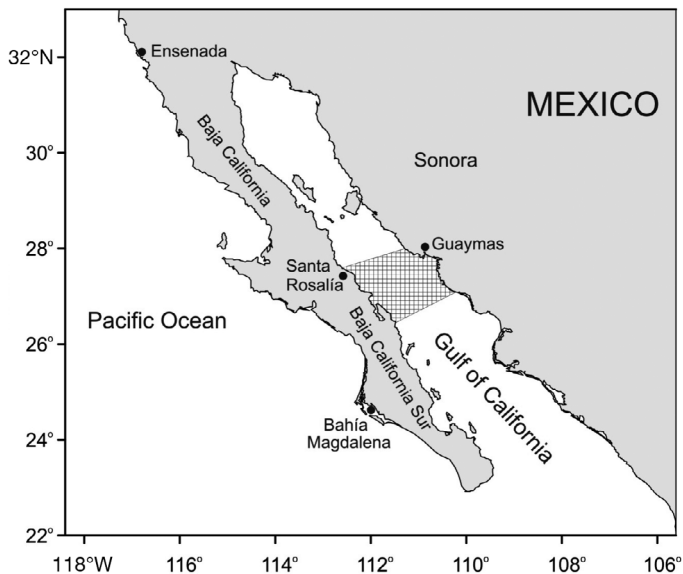*Corresponding author: emorales@cibnor.mx

Fig. 1. Study area in the central Gulf of California, Mexico. The grid shows the main distribution area of *Dosidicus gigas*

In the Gulf of California, the jumbo squid is considered an important commercial resource. Consequently, several studies have been conducted to understand the population dynamics of this species. These studies have provided information on the distribution and abundance of the squid in the Gulf of California (Nevárez-Martínez et al. 2000) and migration patterns within the Guaymas Basin (Markaida et al. 2005, Gilly et al. 2006). Reproduction in *D. gigas* occurs throughout the year, which supports the hypothesis of multiple cohorts within the squid population (Markaida & Sosa-Nishizaki 2001, Díaz-Uribe et al. 2006, Markaida 2006). Fishery management recommendations are based on biological reference points and variations in the recruitment pattern of this population (Hernández-Herrera et al. 1998, Morales Bojórquez et al. 2001b, 2001c, 2008, 2012, Nevárez-Martínez et al. 2006, 2010).

In contrast, studies on age determination and growth are scarce for this species in the region. In the Gulf of California, Markaida et al. (2004) employed fishery-dependent data to describe the age and growth of large specimens of the jumbo squid *D. gigas* that supported the fishery in the Gulf of California in 1995 to 1997. Mejía-Rebollo et al. (2008) described jumbo squid growth off the coast of the Baja California Peninsula and concluded that squid from the Gulf of California grow faster than squid from waters off the western coast of Baja California.

The variability in the biomass and availability of jumbo squid has been linked to their life history

(Ehrhardt et al. 1983, Morales-Bojórquez et al. 2001a). Growth rate is a critical component of the life history of this species, and detailed knowledge is required to provide sound scientific advice for the implementation of fishery management strategies (Hernández-Herrera et al. 1998). The relationship between age and growth of the jumbo squid from the Mexican Pacific has previously been investigated. However, dissimilarities in some parameter estimates, such as growth rates for adult individuals, have been observed. No studies have been published to date that fully describe the age and growth of jumbo squid in the Gulf of California. Markaida et al. (2004) and Mejía-Rebollo et al. (2008) used individuals from the adult population (105 to 442 d) and basic criteria to analyze the growth pattern of this species, primarily basing their analysis on the determination coefficient (R^2) and coefficient of variation (CV) values. However, although adjusted R^2 and CV values are useful as measures of the explained proportion of the variation, they are not useful in growth model selection (Burnham & Anderson 2002, Schwarz & Alvarez-Perez 2010, Chen et al. 2011, 2013). In recent years, there have been many advances in the quantitative analysis of age and growth of different species of squid. According to Katsanevakis (2006), multimodel inference is a reliable alternative method for identifying growth curves.

The study of the growth pattern of *D. gigas* has involved fitting candidate models to a set of length-at-age data (Chen et al. 2011, 2013). The information theory modeling approach uses the principle of parsimony, which implies the selection of the model with the smallest possible number of parameters for an adequate representation of the data. The Akaike's information criterion (AIC) approach is commonly used in age and growth studies where model complexity (number of parameters) is balanced with goodness-of-fit (sum of squares as objective function) (Katsanevakis 2006, Katsanevakis & Maravelias 2008). This approach helps with evaluation of multiple growth functions which are important for describing the growth of a species (Cailliet et al. 2006). The growth patterns in squid species have been described to be both asymptotic as well as non-asymptotic according to length-at-age data available and biology of the species. Authors studying shelf water habitats of tropical and subtropical species (e.g. myopsin squid and cuttlefish) have mostly found rapid (exponential) growth for a substantial period of the life cycle followed by a rather short period of decreased growth rate at the end of ontogenesis. Both exponential and power functions have been used to

fit the length-at-age data for these squid, leading to the conclusion that squid do not grow asymptotically (Pecl 2004, Ceriola & Jackson 2010). Conversely, authors studying both slope and open ocean species (primarily oegopsin squid) have often found that growth in these individuals slows down earlier in ontogenesis than in tropical or subtropical myopsins and displays asymptotic tendencies by the end of their life cycle. Length-at-age data for these species were commonly best described by asymptotic functions (Arkhipkin et al. 1996, Arkhipkin & Roa-Ureta 2005, Miyahara et al. 2006, Schwarz & Alvarez-Perez 2010). This paper presents the first growth curve for *D. gigas* from paralarvae to adult individuals in the population based on a statistical confrontation of asymptotic and non-asymptotic models.

MATERIALS AND METHODS

Squid sampling data collection

Two research surveys on board the R/V 'New Horizon' were conducted in the central Gulf of California during June 2006 and June 2007. Samples of the early life stages of *Dosidicus gigas* were collected from the Guaymas and del Carmen Basins; paralarvae were captured using a bongo net with a 500 µm mesh and juvenile specimens using a spoon net; 12 paralarvae and 93 juveniles were collected and fixed in 95 % ethanol. For this stage, measurements of mantle length (ML) and total weight (TW) were taken to the nearest 0.01 mm and 0.1 g, respectively. Statoliths from each individual were extracted and stored in 95 % ethanol for age determination. Recruits (n = 80) and adult (n = 163) samples were collected from fishery-dependent data every 2 wk in Santa Rosalía B.C.S., Mexico during the 2001−2002 fishing season. Given that our study is partially based on individuals harvested, different measures of recruitment are valid; in this study, recruitment was defined as individuals of a certain age or length added to the exploited stock each year as a result of growth and/or migration into the fishing area (Hilborn & Walters 1992, Quinn & Deriso 1999). The recruits were individuals from 310 to 480 mm ML; this ML interval represented the second mode observed in our length-at-age data set. Similar sizes of recruitment were reported by Hernández-Herrera et al. (1998) and Velázquez-Abunader et al. (2012). The adults were the individuals larger than 490 mm ML. The fishery is conducted by a fleet of small boats owned by local fishermen. The fishing gear is based

on jigs with 4 to 6 rings of hooks (Nevárez-Martínez et al. 2000). Measurements of ML (mm) and mantle weight (MW, g) were taken for each individual; the statoliths were extracted and stored in 70 % ethanol for age determination.

To estimate the relationship between the length and weight, we used the power equation TW = $a \times$ ML^b for juveniles and MW = $a \times$ ML^b for adults, where a is a coefficient related to the body form (also known as a scaling coefficient), and b is an exponent indicating isometric growth when equal to 3 and allometric growth when significantly different from 3 (Esmaeili & Ebrahimi 2006, Aguirre 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. Allometric growth has 2 cases: (1) if $b < 3$, the squid grows faster in length than in weight, and (2) if $b > 3$, the squid grows faster in weight than in length. We hypothesized that the chronology of these allometric changes would be related to the chronology of important early life-history events and would therefore reflect an evolutionary ontogenetic response to functional demands. It has already been suggested that allometric growth patterns closely match the expected priorities for executing the necessary biological roles (Osse 1989, Gisbert 1999). Therefore, in this study, the chronology of relevant shifts in allometric growth measured from b parameter is used to denote morphological changes in the ontogenic pattern of *D. gigas*.

Statolith reading

The statoliths were prepared for reading based on the Arkhipkin method (Dawe & Natsukari 1991). For paralarvae and juveniles, statoliths were mounted on microscopic slides; for juveniles, the dorsal dome was ground and polished with sandpaper. For adults, the statoliths were ground and polished on both sides. Finally, a drop of Canada balsam was applied, and a cover glass was used to cover the polished surface, and the statolith was left to dry for 18 h at 70°C. Observation and counts of the increments on the statoliths from the nucleus to the edge of the dorsal dome were performed independently by 2 readers using an optical microscope with transmitted light at 400×.

Boyle & Rodhouse (2005) explained that the validation of cephalopod based on 1 ring, 1 day is generally accepted, although this relationship needs more analysis. However, for different families of cephalopods, such as Ommastrephidae, Loliginidae, and Idiosepiidae, this daily pattern of ring formation has directly

been validated using tetracycline and strontium in individuals in captivity. For *D. gigas*, the proportionalities between mantle length and statolith length and between mantle length and statolith radius were assessed; the relationships were significant statistically, showing that the statolith is a useful structure for describing the growth in this species (Markaida et al. 2004). Yatsu (2000), using paralarvae of *D. gigas* that were artificially fertilized and reared, reported a linear relationship between statolith length and age (days). In our study, the increments observed in the statoliths of *D. gigas* were assumed to be laid down daily, as has been validated for other squids of the family Ommastrephidae (Dawe et al. 1985, Nakamura & Sakurai 1991).

The age of each individual was defined as the average of the counts of both readers. To avoid bias in the readings, when the difference between readers was >5%, the statolith was read again. The index of average percent error (IAPE) and the CV (Campana et al. 1995) were calculated to assess the reliability of the reading counts between readers; this means that these quantitative indices measure the consistency among determinations. Both indices were estimated separately for a first group comprising the paralarvae and juveniles and a second that included recruits and adults. IAPE and CV were expressed as follows:

$$\text{IAPE} = \frac{100}{N} \sum_{j=1}^{N} \left[\frac{1}{R} \sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \right] \quad (1)$$

$$\text{CV} = \frac{100}{N} \sum_{j=1}^{N} \frac{\sqrt{\dfrac{\sum_{i=1}^{R} (X_{ij} - X_j)^2}{R-1}}}{X_j} \quad (2)$$

where N is the number of squid aged, R is the number of readings, X_{ij} is the i_{th} age determination of the j_{th} squid, and X_j is the mean age of the j_{th} squid.

Growth modeling

Arkhipkin & Roa-Ureta (2005) hypothesized that if the range of the age studied is long enough (>two-thirds of the whole lifespan), all squid species would demonstrate S-shape growth (Sachs cycle) as modeled by Gompertz or Schnute curves. The use of a large sample size (usually >150 specimens) helps to improve the statistical fit of these curves. Our analysis incorporates most of the ontogeny of the life cycle of jumbo squid, including paralarvae, juveniles, recruits and adults, for the first time. For this reason, we believe that our sample acceptably covers the

entire ontogenetic development of the species. For part of the juvenile stage, we did not include individuals from 100 to 300 mm ML; these squid are not available to fishing fleets, given the selectivity of the fishing gear (jigs), which is for squid >300 mm ML. During the juvenile stage, increases in vertical migratory capacity make them unavailable to surface (bongo or spoon) nets. According to Schwarz & Alvarez-Perez (2010), if early stages and juveniles of indeterminate sex are incorporated into length-at-age analyses, then it is possible to have a wider representation of ontogeny for males, females and both sexes. We used this criterion in our length-at-age analysis, using ML of individuals < 100 mm.

Asymptotic and non-asymptotic models were applied to our data set. We used 2 cases ($\rho \neq 0$, $\eta \neq 0$ and $\rho \neq 0$, $\eta = 0$, where ρ is the constant relative rate of the relative growth rate, n is the incremental relative rate of the relative growth rate) of the asymptotic model proposed by the Schnute general growth model (Schnute 1981) and the Gompertz model (L_∞) (Alp et al. 2011), assuming asymptotic length. The following non-asymptotic models were used: (1) power, (2) extended power and (3) persistence as described by Schnute (1981) and Mercier et al. (2011). Additionally, we used a modified non-asymptotic version of the Gompertz model; in this model, L_∞ is substituted by L_0 (length at time zero) (Quiñonez-Velázquez et al. 2000). The models in this study were selected based on ease of use and their prevalence of use in the literature (Markaida et al. 2004, Mejía-Rebollo et al. 2008, Chen et al. 2011, 2013).

Asymptotic models

We analyzed the asymptotic growth of jumbo squid based on the Schnute general model (Schnute 1981) and the Gompertz model (L_∞) (Alp et al. 2011), assuming asymptotic length. The Schnute model was proposed considering the biological principles of individual growth and suitably describes properties of growth curves such as inflection points and asymptotic limits. The inflection points can show different growth values associated with different life stages, mainly for early stages and adult stage. These values are defined as the age of growth inflection, length-at-age of growth inflection and average asymptotic length. The data were analyzed according to case 1 and 2 described by Schnute (1981); for both cases, parameters ρ and η were assumed as $\rho \neq 0$, $\eta \neq 0$, and $\rho \neq 0$, $\eta = 0$. This means that depending on the parameters ρ and η, squid growth may be

accelerate, decelerate or both. The model represents S-shaped growth curves with a period of accelerated development in the paralarval and juvenile stages followed by decelerated growth, during which the adult squid approaches a final limiting ML. The assumption is that such an S-shaped growth curve shows that the growth acceleration is proportional to the growth rate (ρ) and to a linear function of the relative growth rate (η) (Schnute 1981).

The Schnute general growth model assuming $\rho \neq 0$, $\eta \neq 0$ is as follows:

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

The case assuming $\rho \neq 0$, $\eta = 0$ is described as follows:

$$L(t) = \lambda_1 \times \exp^{\left[\ln\left(\lambda_2 / \lambda_1\right) \times \frac{1 - \exp^{-\rho(t - \tau_1)}}{1 - \exp^{-\rho(\tau_2 - \tau_1)}} \right]} \quad 4)$$

where τ_1 is the first specified age, τ_2 is the second specified age, λ_1 is the length at age τ_1, and λ_2 is the length at age τ_2. Using $\rho \neq 0$, $\eta \neq 0$, we estimated the age of theoretical zero length (τ_1), asymptotic length (L_∞), age of growth inflection ($\tau^\star$) and length at age of growth inflection ($L^\star$). These equations are expressed as follows:

$$\tau_0 = \tau_1 + \tau_2 - \frac{1}{\rho} \times \ln\left[\frac{(\exp^{\rho \times \tau_2} \times \lambda_2^\eta) - (\exp^{\rho \times \tau_1} \times \lambda_1^\eta)}{\lambda_2^\eta - \lambda_1^\eta} \right] \quad (5)$$

$$L_\infty = \left[\frac{(\exp^{\rho \times \tau_2} \times \lambda_2^\eta) - (\exp^{\rho \times \tau_1} \times \lambda_1^\eta)}{\exp^{\rho \times \tau_2} - \exp^{\rho \times \tau_1}} \right]^{1/\eta} \quad (6)$$

$$\tau^\star = \tau_1 + \tau_2 - \frac{1}{\rho} \times \ln\left[\frac{\eta \times \{(\exp^{\rho \times \tau_2} \times \lambda_2^\eta) - (\exp^{\rho \times \tau_1} \times \lambda_1^\eta)\}}{\lambda_2^\eta - \lambda_1^\eta} \right]$$
$$(7)$$

$$L^\star = \left[\frac{(1 - \eta) \times \{(\exp^{\rho \times \tau_2} \times \lambda_2^\eta) - (\exp^{\rho \times \tau_1} \times \lambda_1^\eta)\}}{\exp^{\rho \times \tau_2} - \exp^{\rho \times \tau_1}} \right]^{1/\eta} \quad (8)$$

According to Schnute (1981), if $\eta = 0$, then there is no age τ_0. Therefore, the growth parameters for the case $\rho \neq 0$, $\eta = 0$ were estimated as follows:

$$L_\infty = \exp\left[\frac{(\exp^{\rho \times \tau_2} \times \ln \lambda_2) - (\exp^{\rho \times \tau_1} \times \ln \lambda_1)}{\exp^{\rho \times \tau_2} - \exp^{\rho \times \tau_1}} \right] \quad (9)$$

$$\tau^\star = \tau_1 + \tau_2 - \frac{1}{\rho} \times \ln\left[\frac{\exp^{\rho \times \tau_2} - \exp^{\rho \times \tau_1}}{\ln\left(\lambda_2 / \lambda_1\right)} \right] \quad (10)$$

$$L^\star = \exp\left[\frac{(\exp^{\rho \times \tau_2} \times \ln \lambda_2) - (\exp^{\rho \times \tau_1} \times \ln \lambda_1)}{\exp^{\rho \times \tau_2} - \exp^{\rho \times \tau_1}} - 1 \right] \quad (11)$$

The Schnute model was used because the parameters in the model almost always have stable statistical estimates, they have reasonable biological interpre-

tations, and the submodels correspond simply to limiting parameter values (Schnute 1981).

The Gompertz model assuming asymptotic length (L_∞) (Alp et al. 2011) is as follows:

$$L(t) = L_\infty \exp^{[-\exp^{-\kappa(t - t_0)}]} \quad (12)$$

where L_∞ is the average asymptotic length, κ is a dimensionless parameter, and t_0 is a constant.

Non-asymptotic models

Generally, squid growth follows one of two patterns: non-asymptotic (Boyle & Rodhouse 2005) or asymptotic (Arkhipkin et al. 1996, Arkhipkin & Roa-Ureta 2005). According to Boyle & Rodhouse (2005), we analyzed a non-asymptotic growth pattern for jumbo squid using 4 growth candidate models:

(1) power: $L(t) = \alpha \times x^\beta$
    (Mercier et al. 2011)
(2) extended power: $L(t) = \alpha \times x^{\beta - \frac{\delta}{x}}$
    (Mercier et al. 2011)
(3) persistence: $L(t) = \alpha \times x^{\beta \times \exp\left(\frac{-\delta}{x}\right)}$
    (Mercier et al. 2011)
(4) Gompertz (L_0): $L(t) = L_0 \exp^{[\kappa \times (1 - \exp^{-\mu \times \tau})]}$
    (Quiñonez-Velázquez et al. 2000)

where α, β and δ are parameters, usually with $\alpha > 0$, $\beta > 0$, and $\delta > 0$; parameter α is the initial length (at age zero). For $\beta > 0$, these functions may be applicable to temporarily limited periods of growth (e.g. the early growth stage). For the non-asymptotic Gompertz model, L_0 corresponds to length at $t = 0$, κ is a dimensionless parameter such that $\kappa \times \mu = A_0$, A_0 is the specific growth rate at $t = 0 (A_t = A_0 \exp^{-\alpha \times t})$, $L(t)$ is the length-at-age t, μ is the specific rate of growth when $t = t_0$, and t_0 is the time at which the growth rate starts to decrease (Quiñonez-Velázquez et al. 2000).

Parameter estimation and confidence intervals

The θ_i parameters in the asymptotic and non-asymptotic models were estimated using a sum of squares algorithm (SSQ). The SSQ was estimated assuming the next objective function: $SSQ = \sum_{i=1}^{n} (\ln O_i - \ln E_i)^2$, where O_i is the observed data, and E_i is the estimated data. According to Hilborn & Mangel (1997), Haddon (2001) and Burnham & Anderson (2002), for linear and non-linear models, the parameters estimated are equivalent using SSQ or likelihood theory. This occurs if the models have normally distributed residuals with constant variance. We assume that O_i

is log-normally distributed around the candidate growth models. This assumption is based on the variation in length-at-age; that value usually increases with old individuals (the data points are more scattered for old individuals in comparison with younger individuals). In theory, the logarithm transformation can transform the data to a normal distribution and stabilize the variances (Quinn & Deriso 1999). The θ_i parameters were estimated for each growth candidate model (asymptotic and non-asymptotic models) when the SSQ was minimized with a nonlinear fit using the Newton algorithm (Neter et al. 1996).

The confidence intervals for the θ_i parameters in the candidate growth models must be estimated by considering the correlation between parameters (Hilborn & Walters 1992). There are possibilities that the confidence regions can be asymmetric rather than the symmetrical ellipses assumed by asymptotic methods, and if this occurs, the likelihood-profile method is preferred (Morales-Bojórquez & Nevárez-Martínez 2010). However, when considering more than one parameter, the confidence intervals become wider if there is any correlation (covariance) between parameters. If there is no parameter correlation, then there is no interaction between the parameters, and the confidence intervals would be unbiased. An alternative approach to estimating confidence intervals is to use bootstrapping methods, which have the advantage of automatically accounting for changes in all parameters at once (Haddon 2001). We estimated confidence intervals using the parametric bootstrap method described by Fournier & Archibald (1982). The bootstrap was parametric with residuals sampled from the assumed probability distribution, and the growth model was conditioned in that the residuals were applied to the observed data from the model that was fit to the original data (Johnson & Omland 2004, Magnusson et al. 2013). The main source of variability was measured in the age data, and the inaccuracy and imprecision were assessed using the IAPE and CV values previously estimated. Therefore, the simulated data were estimated as follows: $A_s = A_o \times \exp^{\varepsilon_i}$, where A_s is the simulated age, A_o is the observed age, and ε_i represents the residual error sampled from a normal distribution with mean 0 and variance σ^2. Each candidate growth model was bootstrapped 2000 times; this process creates a new data set with the same statistical properties as the original data set as well as a new set of estimated parameters, which can be used to study the empirical distribution of the estimates. The bootstrap standard deviation (SD) is an estimate of the standard error (SE) of the θ_i estimate. The bootstrap mean $\bar{x}$ is an estimate of the mean value of the θ_i

estimate; consequently, the CV was estimated as $CV = SD/\bar{x}$ (Deriso et al. 1985). The bias (B) and percent bias (%B) were estimated as $B = \bar{x} - \theta_i$ and $\%B = \dfrac{\bar{x} - \theta_i}{\theta_i} \times 100\%$ (Jacobson et al. 1994), where θ_i is the best i_{th} parameter estimate from each candidate growth model fitted to the original data. The confidence intervals were estimated using the bias-corrected percentile method (Haddon 2001).

Model selection

We compared the fits of the different candidate growth models using AIC. The AIC can be estimated from negative log likelihood or an SSQ function; we used the estimator proposed for the SSQ function by Burnham & Anderson (2002). The use of the AIC for model selection has a strong theoretical basis in information theory. For a given length-at-age data set, the AIC gives an estimate of the expected, relative, directed distance between the fitted model and the unknown true mechanism that generated the data. Thus, the decision rule for model selection using those statistics is to choose the model with the lowest AIC (Quinn II & Deriso 1999, Haddon 2001). For a fixed length-at-age data set, adding more parameters to the model reduces that distance but further increases uncertainty in the estimation process. That trade-off between underfitting and overfitting is directly expressed in the AIC as a term that penalizes the model scores as a function of the number of estimated parameters in the model (Wang & Liu 2006). According to Pardo et al. (2013) the AIC approach, used in age and growth studies, balances model complexity expressed in the number of parameters in each candidate growth model and goodness-of-fit expressed in the sum of squares algorithm. The AIC was used as follows:

$$AIC = n \times \ln(\hat{\sigma}^2) + 2 \times \theta_i \qquad (13)$$

where θ_i is the number of estimated parameters, n is the number of observations, and σ^2 was estimated as follows:

$$\hat{\sigma}^2 = SSQ/n \qquad (14)$$

We used AIC because $n/\theta > 40$; if n/θ was <40, then a small sample length could be assumed and the bias-corrected form AIC_c of the AIC would need to be used for model selection (Araya & Cubillos 2006, Katsanevakis et al. 2007, Kwang-Ming et al. 2009, Alp et al. 2011). The model with the lowest AIC value was selected as the best model (Haddon 2001).

The differences in AIC (Δ_i) were estimated as follows: $\Delta_i = AIC - AIC_i$, where AIC_i was the estimated value for each candidate growth model i, and AIC represents the estimated value for the best model. If $\Delta_i > 10$, then the candidate growth model might be omitted because it did not represent the observed growth pattern; if $4 < \Delta_i < 7$, there was partial support in 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 growth pattern of *D. gigas* (Burnham & Anderson 2002). Moreover, we estimated the plausibility of each model, defined as the Akaike weight (w_i) of each candidate growth model, where w_i was estimated as follows:

$$w_i = \frac{\exp^{(-0.5\Delta_i)}}{\sum_{i=1}^{j} \exp^{(-0.5\Delta_i)}} \tag{15}$$

where j represents the number of candidate growth models. The weights range between 0 and 1 and are interpreted as the weight of the evidence in favor of model i as the best model among the set of all candidate growth models examined (Katsanevakis 2006). According to Burnham & Anderson (2002), part of the multi-model inference includes ranking the fitted models from best to worst, based on the AIC differences in values, and then scaling to obtain the relative plausibility of each fitted model by a weight of evidence for the selected best model; if the weight of the best model is >0.9, model averaging is not recommended (Grueber et al. 2011).

RESULTS

A total of 348 samples of the jumbo squid *Dosidicus gigas* were captured in the central Gulf of California and analyzed. Only recruits and adults can be classified as females and males. The abundance of recruited females was 47; there were 33 recruited males, 92 adult females and 71 adult males. All the statoliths for paralarvae, juveniles, recruits and adults were read, and the number of rings were counted and included in the analyses. The growth curve for this species was estimated using samples of the different ontogenic development stages; these included (1) 12 paralarvae ranging from 3.4 to 7.5 mm in ML and 1 to 12 d of age; (2) 93 juveniles with ML ranging from 11.4 to 67.7 mm and estimated ages that varied from 37 to 57 d; (3) 80 recruits with ML between 310 and 480 mm and ages varying from 148 to 260 d; and (4) 163 adults whose ML ranged from 490 to 910 mm and whose estimated ages varied from 246 to 450 d
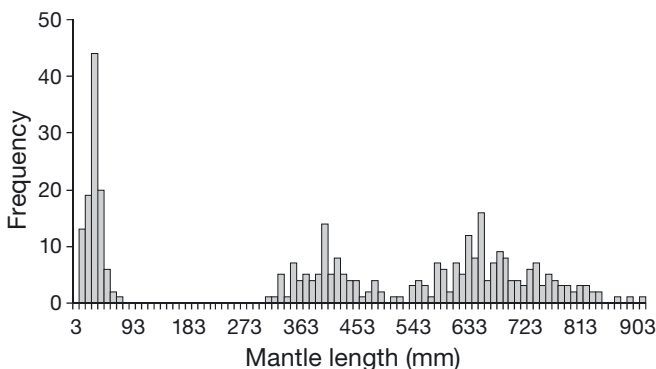

Fig. 2. Size-frequency distribution of mantle length intervals of sampled *Dosidicus gigas* (N = 348)

(Fig. 2). Individuals between 68 and 300 mm in ML were not sampled during the research surveys; consequently, this length range is not included here.

Length-weight relationships

We estimated 3 length-weight relationships as follows: (1) juveniles using TW and ML, (2) recruits and (3) adults; for the latter two stages, we used MW and ML. We estimated negative allometric growth for juveniles, described as $TW = 4 \times 10^{-4}ML^{2.35}$, $R^2 = 0.96$ (*t*-test, p < 0.05); in this stage, the squid grows faster in length than in weight. For recruits, the model was described as $MW = 3 \times 10^{-5}ML^{2.91}$, $R^2 = 0.62$ (*t*-test, p < 0.05), showing isometric mantle growth; in this stage, the individual grows at the same rate for all parts, so that its shape is consistent throughout development. Adults were described as $MW = 8 \times 10^{-7}ML^{3.49}$, $R^2 = 0.93$ (*t*-test, p < 0.05), showing a positive allometric mantle growth; in this stage, the squid grows faster in weight than in length.

Statolith reading

The IAPE and CV values estimated for paralarvae and juveniles were 2.0 and 2.8%, respectively. For recruits and adults, IAPE = 3.8%, and CV = 6.3%. The results of the IAPE showed values of <5%, meaning that there was high accuracy between readers. According to the CV values, we observed consistency between readers.

Candidate growth models fitted to females

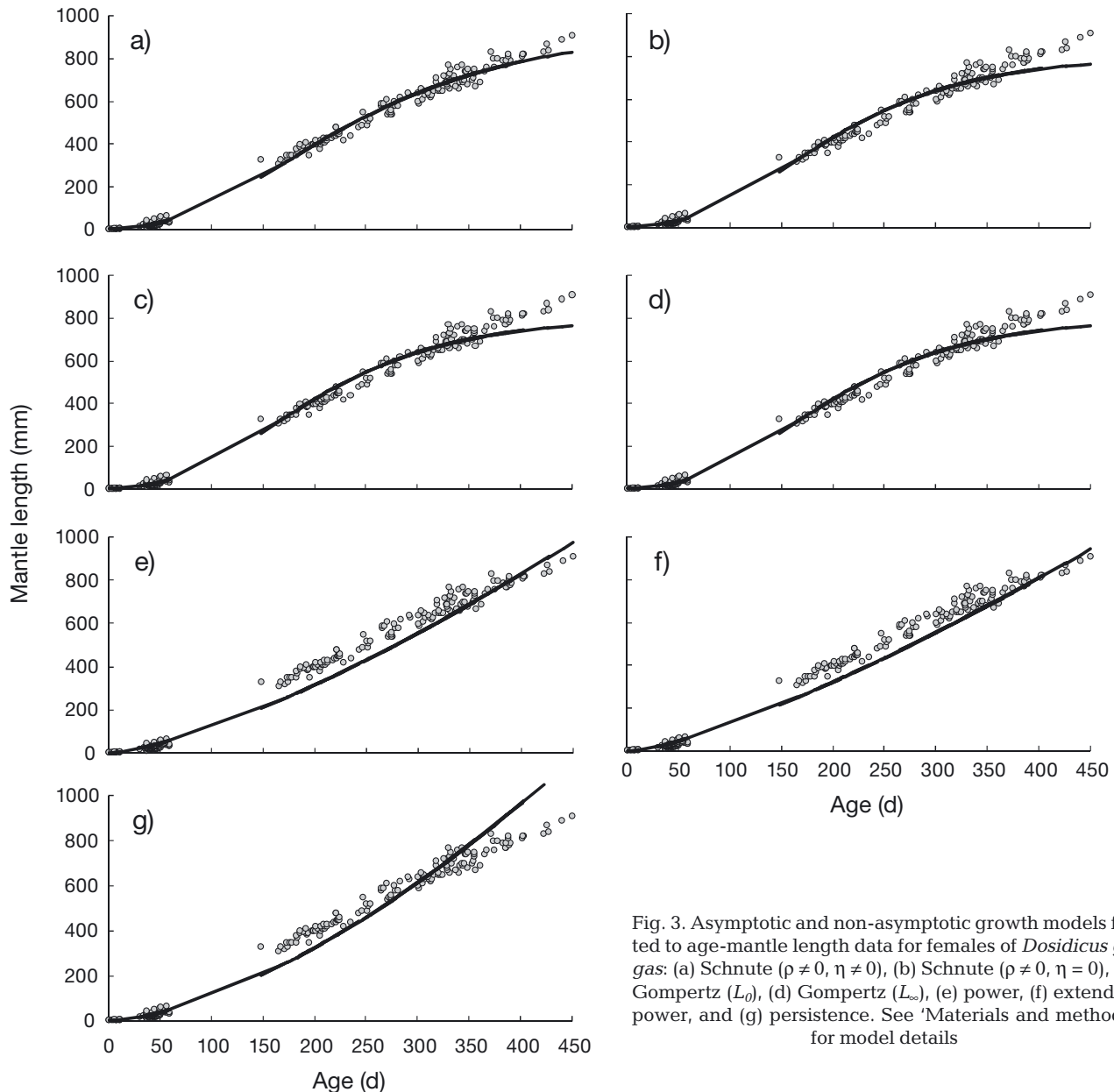The parameters of the theoretical growth curves fitted to asymptotic and non-asymptotic models for

Fig. 3. Asymptotic and non-asymptotic growth models fitted to age-mantle length data for females of *Dosidicus gigas*: (a) Schnute ($\rho \neq 0$, $\eta \neq 0$), (b) Schnute ($\rho \neq 0$, $\eta = 0$), (c) Gompertz (L_0), (d) Gompertz (L_∞), (e) power, (f) extended power, and (g) persistence. See 'Materials and methods' for model details

females are shown in Table S1 in the Supplement at www.int-res.com/articles/suppl/b021p231_supp.pdf, and the models are fitted to data in Fig. 3. The best candidate model to describe growth in females of *D. gigas* was the Schnute model $\rho \neq 0$, $\eta \neq 0$; however, the asymptotic models of Schnute $\rho \neq 0$, $\eta = 0$ and 2 versions of the Gompertz model used in this analysis were candidate models that showed a description of the age-at-length data. This was observed in the estimates of the AIC (Table 1), where the evidence in favor of Schnute model $\rho \neq 0$, $\eta \neq 0$ was 91%; this model estimated asymptotic length of 904.80 mm ML, age of growth inflection of 167.51 d and length-

at-age of growth inflection of 312.84 mm ML (details about the parameters and confidence intervals are shown in Table S2). The non-asymptotic models were not selected by AIC; consequently, they did not describe the growth of females of *D. gigas*.

Candidate growth models fitted to males

The parameters of the candidate growth curves fitted to asymptotic and non-asymptotic models for males are shown in Table S3, and the models are fit-

Table 1. Growth model selection for females of *Dosidicus gigas*. θ = number of parameters; AIC = Akaike's information criteria; Δ_i = differences in AIC; w_i = Akaike weight. See 'Materials and methods' for model details

	θ	AIC	Δ_i	w_i
Schnute (ρ ≠ 0, η ≠ 0)	4	−1278.751	0.000	0.913
Gompertz (L_∞)	3	−1271.854	6.897	0.029
Gompertz (L_0)	3	−1271.851	6.899	0.029
Schnute (ρ ≠ 0, η = 0)	3	−1271.852	6.898	0.029
Persistence	3	−1001.517	277.233	0.000
Extended power	3	−307.600	971.150	0.000
Power	2	−114.931	1163.820	0.000

ted to the data in Fig. 4. The growth pattern in males was described by the Schnute model (ρ ≠ 0, η ≠ 0); however, the evidence in favor of this model was 39.70%, while the asymptotic model of Schnute (ρ ≠ 0, η = 0) and 2 versions of the Gompertz model both showed 20.1% of evidence in favor and identical estimates for differences in AIC (1.36) (Table 2). The non-asymptotic growth functions did not describe the growth of males of *D. gigas*. The best candidate model estimated asymptotic length of 828.49 mm ML, age of growth inflection of 158.98 d and length-at-age of growth inflection of 292.86 mm ML (Table S4).
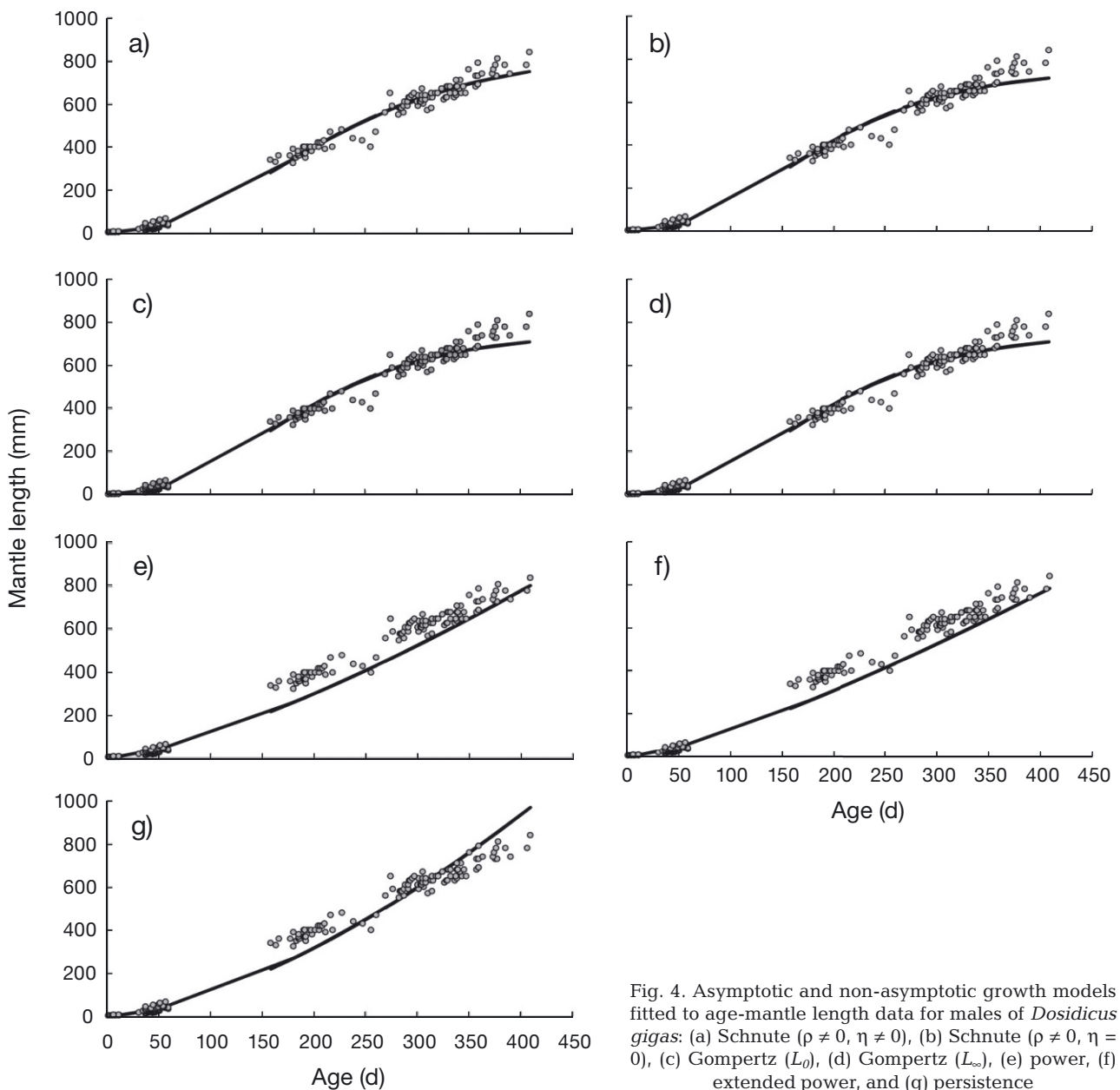

Fig. 4. Asymptotic and non-asymptotic growth models fitted to age-mantle length data for males of *Dosidicus gigas*: (a) Schnute (ρ ≠ 0, η ≠ 0), (b) Schnute (ρ ≠ 0, η = 0), (c) Gompertz (L_0), (d) Gompertz (L_∞), (e) power, (f) extended power, and (g) persistence

Table 2. Growth model selection for males of *Dosidicus giga*. See Table 1 for details

	θ	AIC	Δ_i	w_i
Schnute (ρ ≠ 0, η ≠ 0)	4	−1057.7598	0.0000	0.3968
Gompertz (L_∞)	3	−1056.4024	1.3574	0.2013
Gompertz (L_0)	3	−1056.3998	1.3600	0.2010
Schnute (ρ ≠ 0, η = 0)	3	−1056.3994	1.3604	0.2010
Persistence	3	−828.8933	228.8665	0.0000
Extended power	3	−249.9555	807.8043	0.0000
Power	2	−83.4870	974.2728	0.0000

Candidate growth models fitted to both sexes

The analysis of both sexes showed a similar result to that found for previous data of males and females, and the Schnute model (ρ ≠ 0, η ≠ 0) was the best can-

didate growth model for both sexes (Fig. 5). This result is relevant to understand the growth of this species, for which the plasticity in growth for males, females and both sexes can be described using the same candidate growth model. For the Schnute general model assuming ρ ≠ 0, η = 0 (Fig. 5a), the estimated values are shown in Table S5. The growth parameters for the non-asymptotic models (Table S6) produced different estimates of the initial length at Age 0 (α); the variation in α (0.07 to 0.42 mm) was greater than the variation of the β parameter (1.27 to 1.57), which determines the period of rapid growth during early stages. The non-asymptotic models fitted to the data are shown in Fig. 5e,f,g.

For each candidate model AIC, the Δ_i and w_i values are presented in Table 3. Based on the lowest AIC (−1913.97) and the highest w_i (99.40%) values, the
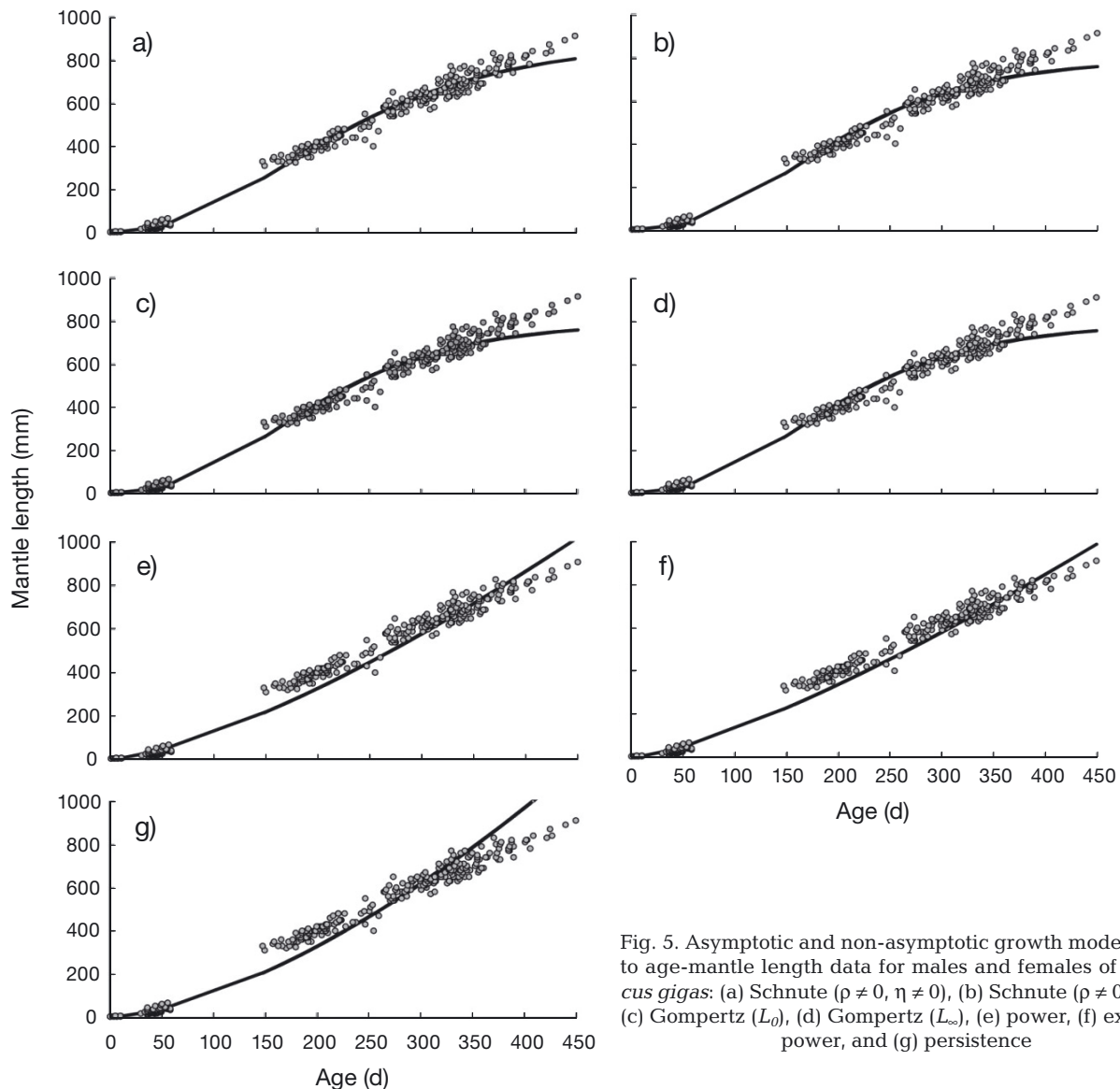

Fig. 5. Asymptotic and non-asymptotic growth models fitted to age-mantle length data for males and females of *Dosidicus gigas*: (a) Schnute (ρ ≠ 0, η ≠ 0), (b) Schnute (ρ ≠ 0, η = 0), (c) Gompertz (L_0), (d) Gompertz (L_∞), (e) power, (f) extended power, and (g) persistence

Table 3. Growth model selection for males and females of *Dosidicus gigas*. See Table 1 for details

	θ	AIC	Δ_i	w_i
Schnute ($\rho \neq 0$, $\eta \neq 0$)	4	−1913.9676	0.0000	0.9945
Gompertz (L_∞)	3	−1901.3857	12.5819	0.0018
Gompertz (L_0)	3	−1901.3850	12.5825	0.0018
Schnute ($\rho \neq 0$, $\eta = 0$)	3	−1901.3846	12.5829	0.0018
Persistence	3	−1517.7401	396.2274	0.0000
Extended power	3	−546.7402	1367.2274	0.0000
Power	2	−269.1049	1644.8627	0.0000

Schnute model ($\rho \neq 0$, $\eta \neq 0$) was the function that produced the statistically best fit for the mantle length-at-age data. This means that the growth pattern of the jumbo squid is asymptotic. Alternative asymptotic growth models such as the Schnute ($\rho \neq 0$, $\eta = 0$) and Gompertz (L_∞) models showed estimated AIC differences (Δ_i) > 10. This means that these candidate growth models might be rejected, as the jumbo squid's growth pattern is not described by them. For the non-asymptotic growth models (power, extended power, persistence and Gompertz [L_0]), the Δ_i values were also >10. The weight of evidence identified the Schnute ($\rho \neq 0$, $\eta \neq 0$) model as the best model among the set of candidate growth models examined. Weight values for the other candidate models were <1.0 % (non-asymptotic growth models). Consequently, these growth functions did not describe the growth pattern of the jumbo squid.

DISCUSSION

Theoretically, the cephalopods have a 2-phase pattern of growth; the growth of this group of organisms has been represented by different mathematical functions of individual growth (Grist & Jackson 2004). Non-asymptotic growth is commonly described for early stages of squids. Yatsu (2000) estimated the exponential growth patterns for the paralarvae of *Dosidicus gigas*, *Ommastrephes bartramii* and *Illex illecebrosus* from 1 to 35 d. This exponential growth pattern is coincident with the first part described by the 2-phase model; however, for sub-adults and adults of *D. gigas*, *Sthenoteuthis oualaniensis*, *Ommastrephes bartramii* and *Illex argentinus*, the growth model identified was a linear function. Ceriola & Jackson (2010) analyzed the age and growth of the squid *Loliolus noctiluca* off Tasmania, for which the age of the sampled organisms varied from 84 to 122 d, and concluded that the species exhibited a growth pattern described by an exponential model.

Jackson (2004) reviewed the squid growth pattern of the family Loliginidae, for which the growth is continuous and non-asymptotic.

Lipinski (2002) proposed a conceptual growth model for cephalopods, which describes 3 phases of growth. The first phase is characterized by a relatively slow paralarval growth; the second phase represents the juveniles and adults, during which fast growth can be observed; finally, the last phase could have a diminished or absent growth, commonly observed for spawners. Key aspects of this model to explain the ontogenetic growth of cephalopods are as follows: (1) the changes or inflection points among phases should be estimated (in the course of fieldwork or aquarium maintenance); (2) longevity should be known; (3) all 3 phases of growth are approximated by linearity; and (4) the parameters estimated for each phase using a linear model represent an intersection and slope values, which will be different for each phase (e.g. growth rate, initial length-at-age 0). Although the conceptual model (as above) may be useful for describing cephalopod growth, it depends on 3 independent linear models, on the availability of the inflection points and on maximum age data. Mathematically, the unitary growth model for cephalopods must consider the changes in growth rates along the cephalopod life cycle; therefore, it is necessary for an acceptable model to show sufficient flexibility. Schnute (1981) proposed a general growth model including asymptotic and non-asymptotic models previously described (Richards, Gompertz, logistic, quadratic and exponential, among others): the model estimates inflection points and asymptotic limits (if any), and the parameters in the model have reasonable biological interpretations. This model has successfully been applied to different squid species (Schwarz & Alvarez-Perez 2010, Chen et al. 2011, 2013, Arkhipkin & Roa-Ureta 2005).

The statoliths are formed from a biomineralization process and are composed of a mineral matrix (aragonite crystal form) and an organic matrix composed of proteins, phosphoproteins, glycoproteins, proteoglucids and polysaccharides (Rodhouse & Hatfield 1990, Bettencourt & Guerra 2000). Different hypothesis have been given about the formation of growth rings; Morris (1991) proposed that pH changes (related to different concentrations of magnesium) in the statocyst fluid could inhibit or favor calcification based on amino acid metabolism and squid activity levels. Lipinski (1993) suggested that periodic changes in strontium concentrations in the statocyst are directly or indirectly responsible for the definitions of growth layers and increments in the statoliths, even

more than pH changes. The origin of strontium could be the result of a combination of exogenous factors, such as temperature, salinity, strontium dissolved in seawater and feeding, and/or endogenous factors, such as stress and reproductive cycles (Gallahar & Kingsford 1996).

Changes in the ions, pH, and organic or inorganic components are related to individual metabolism, diel activity patterns and environmental conditions (Pauly 1998, Bettencourt & Guerra 2000). For *D. gigas* in the Gulf of California, the vertical and horizontal movements (Gilly et al. 2006, Bazzino et al. 2010, Hoving et al. 2013, Rosa et al. 2013) and large-scale migrations in and out of the Gulf are caused by environmental changes such as El Niño and La Niña events (Morales-Bojórquez et al. 2001a, Rosa et al. 2013). These could affect the deposition process of statoliths and the daily formation of the growth rings. The increments in rings are also affected by the supply of oxygen (Lipinski 1993, Pauly 1998). For *D. gigas*, effects on habitat utilization and food habits have been documented in relationship to the oxygen minimum zone (Stewart et al. 2013). However, measuring statolith daily growth increments is the most frequently method used to determine the age of squids. In species for which the validation has been done (Boyle & Rodhouse 2005), the total number of growth increments represents the age of an individual in days. For *D. gigas*, this periodicity (1 mark, 1 day) has not been validated (Nigmatullin et al. 2001); however, given the similarity of growth increments in validated species of the same family (Boyle & Rodhouse 2005), the hypothesis of 1 mark, 1 day is generally accepted for growth studies (Arkhipkin 2005).

Specifically for the jumbo squid *D. gigas*, our results described an asymptotic growth given that the best candidate model was Schnute model ($\rho \neq 0$, $\eta \neq 0$), with high statistical evidence for the selection of that model from among the different candidate models analyzed. Although the results of AIC were close, the Akaike differences ($\Delta_i = 0$) and Akaike weights indicated the best models for females (0.91), males (0.39) and both (0.99). In this study, we used a general growth model (Schnute 1981) and included alternative growth models as special cases such as Richards, Gompertz, logistic and von Bertalanffy, among others, which included non-asymptotic growth models. For the females, males and both sexes of *D. gigas*, the Schnute growth model assuming parameters $\rho \neq 0$, $\eta = 0$ described a similar pattern to that of the Gompertz growth function, given that the Gompertz model represents a submodel of the general growth model. According to Schnute (1981), the

general model using these parameters is an explicit condition of the Gompertz model. Therefore, the shapes and AIC values can be very close or equal. Similar results have been previously described using the general model of Richards or Schnute vs. different growth submodels (Rogers-Bennett et al. 2007, Flores et al. 2010, Shelton et al. 2006, Barreto et al. 2011). The literature shows that for the multi-model inference approach applied to individual growth, it is not unusual that different candidate growth models yield equal values of AIC (Rogers-Bennett et al. 2007, Flores et al. 2010, Helidoniotis et al. 2011). Several studies also have shown that the AIC estimates of the candidate growth models were very close; the magnitude of the change can be <0.1 (Araya & Cubillos 2006, Shelton et al. 2006, Farrell et al. 2010, Barreto et al. 2011, Grist et al. 2011, Mercier et al. 2011, Shuman et al. 2011).

Markaida et al. (2005), using mark-recapture data of *D. gigas*, showed that the daily growth rate diminishes for older individuals; their study analyzed squid between 46 and 80.7 cm ML, and the daily growth rate changed from 1.5 to 1.0 mm d^{-1}. These absolute rates expressed as relative growth rates changed from 0.22 % to 0.15 %. Asymptotic growth has been documented for the squid *Ornithoteuthis antillarum* from the central-eastern Atlantic Ocean, and the model that best described the length-at-age data was a logistic model for individuals from 10 to 182 d (Arkhipkin et al. 1998). Arkhipkin & Roa-Ureta (2005) analyzed the growth patterns of 12 species of squid (suborders Myopsina and Oegopsina) using length-at-age data including individuals ranging from the early life stages to adults. They concluded that the species grew asymptotically, primarily described by the Schnute model and Gompertz model. In Japanese waters, the diamond squid *Thysanoteuthis rhombus* showed asymptotic growth described by a logistic model. The age of the sampled individuals in this study varied from 102 to 306 d, and the growth pattern was selected according to AIC (Miyahara et al. 2006). For the squid *Illex argentinus* from the waters of southern Brazil, Schwarz & Alvarez-Perez (2010) estimated asymptotic growth for both females and males of this species; the AIC used for model selection identified the Schnute model as the best fit for males and the Gompertz model for females. The age interval analyzed was from 56 to 320 d.

A change in the growth pattern of *D. gigas* in the Eastern Pacific is observed along a latitudinal gradient from south to north: (1) in the Humboldt Current (Chilean waters), the species exhibited a linear

growth pattern for the spring spawners group, and a power function was identified for the autumn spawners group (Chen et al. 2011); (2) elsewhere in the Humboldt Current (Peruvian waters), the growth estimated for *D. gigas* was exponential (Argüelles et al. 2001); (3) in the Costa Rica Dome, the growth of this species was described by a linear function (Chen et al. 2013); (4) in the Gulf of California, Mexico, Markaida et al. (2004) estimated that a logistic model described the growth of this species; and (5) in the western coast of Baja California, Mexico, Mejía-Rebollo et al. (2008) also identified a logistic growth model for *D. gigas* (Table 4). The growth patterns of *D. gigas* reported in the Eastern Pacific show non-asymptotic growth in the Humboldt Current and Costa Rica Dome in contrast with the asymptotic growth identified in the California Current and Gulf of California.

It was difficult to establish the growth pattern of *D. gigas* throughout its distribution area because the pattern changed from asymptotic to non-asymptotic according to the region. The reason for this variation in growth pattern 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 (Hoving et al. 2013) (Table 4). In growth studies for harvested species, the use of length-at-age data for early stages is not common. The absence of this data (paralarvae and juveniles) is the primary cause of biases in the curve adjustment that influences length-at-age data distributions (Forsythe 2004). Consequently, the absence of initial observation parameters likely influences the reliability of any growth model. Alternative solutions have been suggested based on modified growth models that fix empirical length or age at birth (Pardo et al. 2013, Gwinn et al. 2010). Their approach allows one to know length-at-age data for the early stages, but in general, such models only provide one datum. Nev-

ertheless, the theoretical assumptions in their procedure help to improve the estimates of growth coefficients and asymptotic length parameters and the fitting of growth models to the data. In our study, we improved this process by using data representing the whole squid ontogenic cycle, including organisms from 1 to 450 d old; these organisms included paralarvae, juveniles, recruits and spawning adults. The number of individuals used for modeling representing the early stages was 105 organisms. This distribution means that any curve adjusted to the data is very well represented in terms of sample size, since it included recruits as well as data sets of adults (n = 243); this data set allowed for modelling of the variability in length-at-age data for *D. gigas*. Another reason for the observed variation in the growth pattern may be the differences in model selection criteria. Chen et al. (2011, 2013) used AIC for the selection of the best growth model; in contrast, Markaida et al. (2004) and Mejía-Rebollo et al. (2008) used criteria based on the maximum R^2 and minimum coefficient of variation. In our study, the asymptotic growth model identified for *D. gigas* was based on multi-model inference; this approach is accepted for age and growth modeling as the best statistical procedure for model selection. This approach has been used in age and growth studies of other taxa, such as echinoderms (Shelton et al. 2006, Flores et al. 2010), fish (Araya & Cubillos 2006, Alp et al. 2011, Barreto et al. 2011), crustaceans (Montgomery et al. 2010, Rodríguez-Domínguez et al. 2012) and other mollusks (Rogers-Bennett et al. 2007, Cruz-Vásquez et al. 2012).

For females, males and both sexes the growth pattern of *D. gigas* was described by the Schnute model ($\rho \neq 0$, $\eta \neq 0$). The growth curve was sigmoid, and the ρ and η values were useful for estimating the inflection point (age and ML) and τ_0 value. The sigmoid pattern can be explained by a 2-phase growth pattern, with the first phase describing exponential

Table 4. Growth models analyzed for *Dosidicus gigas* in the Eastern Pacific. SSQ: sum of squares algorithm

Source	Study area	Age interval (d)	Growth model	Objective function	Model selection	Confidence intervals
Argüelles et al. (2001)	Peru	115–354	Exponential	SSQ	No	No
Markaida et al. (2004)	Gulf of California	174–442	Logistic	SSQ	No	No
Mejía-Rebollo et al. (2008)	Western coast of Baja California, Mexico	105–433	Logistic	SSQ	No	No
Chen et al. (2011)	Chile	121–307	Linear/Power	Likelihood	Yes	No
Chen et al. (2013)	Costa Rica	130–289	Linear	Likelihood	Yes	No
This study	Gulf of California	1–450	Schnute ($\rho \neq 0$, $\eta \neq 0$)	SSQ	Yes	Yes

growth in the early development stages according to Forsythe & Van Heukelem (1987). We estimated the age (τ^*) and mantle length (L^*) at which the growth rate changes (growth inflection point) to be 162.36 d and 299.52 mm, respectively. Once *D. gigas* reaches τ^* and L^*, the species exhibits more gradual growth until reaching an asymptotic mantle length of 859.45 mm. In the Gulf of California, Markaida et al. (2004) fitted a logistic growth model and estimated an asymptotic mantle length of 999.1 mm for females and 945.0 mm for males. Using the same growth function, Mejía-Rebollo et al. (2008) estimated an asymptotic mantle length of 877.5 mm and 792.1 mm for females and males, respectively, in the western coast of Baja California, Mexico. Markaida et al. (2004) estimated a daily growth rate of 2.65 mm d^{-1} for males between 230 and 250 d and a rate of 2.44 mm d^{-1} for females between 210 and 230 d; these authors assumed that the daily growth rate decreased for both sexes, primarily for older individuals. Comparatively, we estimated an earlier age of growth inflection.

Based on papers published concerning growth of *D. gigas*, we observe that, although it is reported that females reach larger lengths than males, the growth pattern is the same; this means that they grow at similar growth rates. Markaida et al. (2004) and Mejía-Rebollo et al. (2008) described an asymptotic curve type for males and females of *D. gigas*, which leads us to assume that the separation by sex did not change the fitted curve. Likewise, Chen et al. (2013) used model selection and fitted a non-asymptotic (linear) curve for males and females found offshore Costa Rica. They did not report differences in the growth pattern by sex. A similar result was found in our study, and the same model described the growth patterns of females, males and both sexes. We recognize that there are fewer data points in the first part of the curve for individuals measuring from 100 to 300 mm ML (juvenile and recruits stages); however, according to the reproductive biology of females of jumbo squid, we observed that the age of growth inflection (τ^* = 167.51 d, CI = 147.00 to 192.29 d) and length-at-age of growth inflection (L^* = 312.84 mm ML, CI = 306.18 to 322.11 mm ML) are coincident for mature females reported by Markaida et al. (2004), who identified a female group that matured early from 184 d and at 323 mm ML. Mejía-Rebollo et al. (2008) reported females maturing and mature from 260 to 400 mm ML and from 105 to 205 d old, respectively, in the western coast of the Baja California Peninsula. For males, the estimates age of growth inflection (τ^* = 158.98 d, CI = 133.25 to 191.01 d) and

length-at-age of growth inflection (L^* = 292.86 mm ML, CI = 284.74 to 308.90 mm ML) were consistent with those of Markaida et al. (2004), who observed mature males from 196 d and at 314 mm ML. In contrast, larger squid were reported by Díaz-Uribe et al. (2006), who found mature males from 370 mm, and Quiñonez-Velázquez et al. (2013) reported mature males from 320 to 420 mm ML. *D. gigas* may mature from ML of 20 cm or larger (Hoving et al. 2013). This length may vary in the Gulf of California or western coast of the Baja California Peninsula. Our data showed that the maximum age in males was 409 d, whilst that of females was 450 d. Markaida et al. (2004) reported that the longevity in males of *D. gigas* is less since they mature before females. Nigmatullin et al. (2001) classified 3 groups of individuals for males and females according to ML; they defined sizes as small, medium and large and did mention that the females were larger than males in the 3 groups. The longevity of all groups is ~1 yr, although individuals of large size (>750 mm ML) could attain longevity from 1.5 to 2 yr.

In conclusion, *D. gigas* from the Gulf of California exhibits an asymptotic growth pattern described by the Schnute general model ($\rho \neq 0$, $\eta \neq 0$). The model was useful for describing the whole squid ontogenic cycle, which included organisms from 1 to 450 d of age (paralarvae, juveniles, recruits and spawning adults). This model was identified as more comprehensive since it was more flexible in estimating multiple parameters, such as age of growth inflection, length-at-age of growth inflection and an asymptotic limit; this inclusiveness was useful for jointly analyzing 2 data sets (early stages and adults).

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