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Age, growth and population structure of jumbo flying squid, *Dosidicus gigas*, based on statolith microstructure off the Exclusive Economic Zone of Chilean waters

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*The jumbo flying squid, *Dosidicus gigas*, support an important squid fishery off the Exclusive Economic Zone of Chilean waters. However, we only have limited information about their biology. In this study, age, growth and population structure of *D. gigas* were studied using statoliths from 533 specimens (386 females and 147 males) randomly sampled in the Chinese squid jigging surveys from 2007 to 2008 off the Exclusive Economic Zone of Chile. Mantle lengths (MLs) of the sample ranged from 206 to 702 mm, and their ages were estimated from 150 to 307 days for females and from 127 to 302 days for males. At least two spawning groups were identified, the main spawning peak tended to occur between August and November (austral spring group), and the secondary peak appeared during March to June (austral autumn group). The ML–age relationship was best modelled by a linear function for the austral spring group and a power function for the austral autumn group, and the body weight (BW)–age relationship was best described by an exponential function for both the groups. Instantaneous relative growth rates and absolute growth rates for ML and BW did not differ significantly between the two groups. The growth rate of *D. gigas* tended to be high at young stages, and then decreased after the sub-adult stage (>180 days old). This study suggests large spatial and temporal variability in key life history parameters of *D. gigas*, calling for the collection of more data with fine spatial and temporal scales to further improve our understanding of the fishery biology of *D. gigas*.*

Keywords: *Dosidicus gigas*, statolith, age and growth, population structure, off Exclusive Economic Zone of Chilean waters

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INTRODUCTION

The jumbo flying squid, *Dosidicus gigas*, is the largest omastrephid squid and only can be found within the Eastern Pacific Ocean from northern California to southern Chile. *Dosidicus gigas* support a major fishery off Chile, Peru and the Gulf of California, with combined annual landings of 671–819 thousand t during 2004 to 2007 (FAO, 2009). In the Chilean waters, *D. gigas* are highly abundant and support one of the most important fisheries with an annual catch of 122,000–300,000 t during 2005 to 2007 (Zúñiga *et al.*, 2008; FAO, 2009).

Many studies were conducted on fishery biology of *D. gigas* in the Gulf of California and off the Peruvian coast (e.g. Masuda *et al.*, 1998; Argüelles *et al.*, 2001; Morales-Bojórquez *et al.*, 2001; Nigmatullin *et al.*, 2001). Some of the previous studies also described the fishery biology of *D. gigas* in offshore and coastal waters of Chile (Rocha & Vega, 2003; Chong *et al.*, 2005; Zúñiga *et al.*, 2008). Rocha & Vega (2003) reported

that *D. gigas* were landed year-round, mainly concentrated in waters off central Chile. González & Chong (2006) analysed maturation of *D. gigas* specimens and hypothesized the presence of at least two cohorts of the species to explain differences in the maturation observed between winter and spring. Ibáñez & Cubillos (2007) described spatial and seasonal changes in the size–structure and reproductive activity of *D. gigas* in waters off central-south Chile (34°–40°S). Zúñiga *et al.* (2008) found a seasonal periodicity in the monthly variation of the *D. gigas* catch along the Chilean coast, and suggested the existence of two reproductive cycles for *D. gigas* based on the periodicity in the monthly catch of *D. gigas* along the Chilean coast during the time period from 2002 to 2005. Liu *et al.* (2010) described the fishery biology of *D. gigas* off the Chilean Exclusive Economic Zone (EEZ) waters based on data collected in the three scientific surveys undertaken by the Chinese squid jigging vessels during 2006 to 2008. However, little information was available on the age, growth and population structure of *D. gigas* in the Chilean EEZ waters.

Discovery of periodically deposited increments in cephalopod statoliths led to a proliferation of age and growth studies in many commercially important species (Jackson, 1994). Because growth increments in squid are only deposited after

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hatching (Balch *et al.*, 1988), we also can back-calculate their hatching dates and assign the sampled squids into different seasonal spawning groups according to their hatching dates (Laptikhovsky *et al.*, 1993). The objectives of this study are to employ statolith increment analysis to determine the age and growth of *D. gigas* off the Chilean EEZ waters and to yield a preliminary estimation of population structure, based on data collected in the three scientific surveys for *D. gigas* by the Chinese squid jigger vessels during 2006 to 2008 in the waters outside the EEZ of Chilean waters.

MATERIALS AND METHODS

Sampling and ageing

Samples of *D. gigas* were randomly collected from the three scientific surveys by the Chinese squid jigging vessels in the waters confined by 22°–30°30'S 75°30'–78°W and 37°30'–41°S 78°30'–82°W during January to June 2007 and by 20°–24°30'S 74°30'W–82°W from January to May 2008 (Figure 1). Samples were randomly collected on a monthly basis in the course of three surveys. The samples were frozen on board immediately, and brought back to the laboratory for further processing.

Statoliths of 386 females (206–702 mm (mantle length) ML) and 147 males (232–541 mm ML) were collected. Measurements of ML (mm) were taken to the nearest 1 mm and body weight (BW, g) to 1 g. The statolith of each sample was extracted for age determination. The standard ageing methodology of a statolith was used in this study (Dawe & Natsukari, 1991). The number of increments for each statolith was counted independently by two readers.

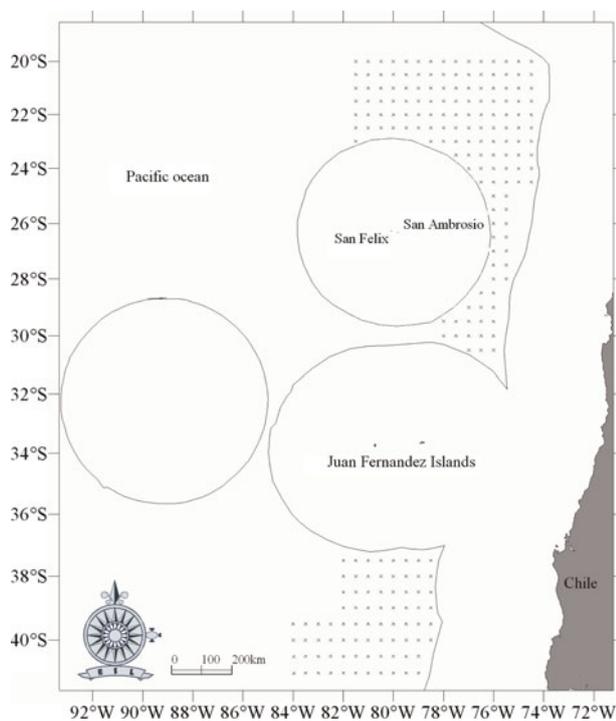


Fig. 1. Sampling localities of *Dosidicus gigas* off the Exclusive Economic Zone of Chilean waters.

The average was used if the range of counts was within 10% of the mean (Yatsu *et al.*, 1997). Increments were counted from the nucleus to the edge of the dorsal dome, where increments were most clearly visible. However, it was sometimes necessary to extrapolate from adjacent areas to resolve increment counts in local unclear areas.

Increments observed in a statolith were assumed to be laid down daily, as was confirmed for other squid species of Ommastrephidae (Bigelow, 1991; Nakamura & Sakurai, 1991; Uozumi & Ohara, 1993; Yatsu, 2000). The hatching date was back-calculated from the count of increments and the date of capture.

Data analysis

Based on the distribution of hatching dates, different seasonal spawning groups were defined (Argüelles *et al.*, 2001). We applied and evaluated the following models to quantify the growth patterns of *D. gigas* for different seasonal spawning groups:

Linear function (Rodhouse & Hatfield, 1990):

$$ML_t = c + dt \tag{1}$$

Exponential function (Bigelow, 1991; Villanueva, 1992):

$$ML_t = ce^{dt} \tag{2}$$

Power function (Jackson, 1994):

$$ML_t = ct^d \tag{3}$$

Logistic function (Dimmlich & Hoedt, 1998):

$$ML_t = \frac{L_\infty}{1 + \exp[-K(t - t_0)]} \tag{4}$$

Von Bertalanffy function (Argüelles *et al.*, 2001):

$$ML_t = ML_\infty \times \{1 - \exp[-K(t - t_0)]\} \tag{5}$$

Gompertz function (Bigelow, 1991):

$$ML_t = ML_\infty \times \exp\{1 - \exp[-K(t - t_0)]\} \tag{6}$$

where ML_t is mantle length (mm) at age t ; t is age (day); c , d , K and t_0 are the model parameters to be estimated; ML_∞ is the asymptotic mantle length; and t_0 is a hypothetical age when ML_t equals zero.

The Schnute function (Schnute, 1981; Arkhipkin & Roa, 2005) was also used:

$$ML_t = \left[ML_1^b + (ML_2^b - ML_1^b) \left(\frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right) \right]^{1/b} \tag{7}$$

where t_1 and t_2 are the youngest and oldest squid sampled, respectively. ML_1 and ML_2 are the estimated mean lengths of t_1 and t_2 days old squid, respectively.

For the above seven growth models, the likelihood and the Akaike information criterion (AIC) of each model were

calculated using the following equation:

$$L(data/\theta) = \prod_{i=1}^n \frac{1}{\sqrt{2\pi}\delta} \exp\left[-\frac{(ML_i - f(t))^2}{2\delta^2}\right] \quad (8)$$

$$AIC = -2 \ln(L_{max}) + 2m \quad (9)$$

where $L(data/\theta)$ is the likelihood of observing the data given parameters θ ; vector θ denotes parameters to be estimated; ML_i and $f(t)$ are the ML values observed and estimated from the growth model, respectively, for the i^{th} sample; n is the number of observations; m is the number of model parameters; and L_{max} is the maximum value of $L(data/\theta)$. The model which yields the smallest AIC value was selected as the best model.

Instantaneous relative growth rates (IRGRs, % d⁻¹) and absolute growth rate (AGR, mm d⁻¹ or g d⁻¹) were calculated for each 30-day interval for different spawning seasons. The IRGR and AGR were calculated as:

$$IRGR = \frac{\ln(S_2) - \ln(S_1)}{t_2 - t_1} \times 100 \quad (10)$$

$$AGR = \frac{S_2 - S_1}{t_2 - t_1} \quad (11)$$

respectively, where S_1 and S_2 were estimated ML or BW values at the beginning (t_1) and end (t_2) of the time interval (Ricker, 1958). The effect of spawning season on growth rates was evaluated through an analysis of covariance (ANCOVA).

RESULTS

Size-structure

The ML and BW of the sampled squid ranged from 206 to 702 mm and 208 to 11,300 g, respectively (Figure 2). For female squids, the average ML and BW reached 378.9 mm and 1840.3 g, respectively, and the squid with ML values ranging from 300 to 500 mm and BW from 1000 to 2500 g were dominant in the samples, consisting of 84.4% and 67.3% of the total samples, respectively (Figure 2). For male squids, the average ML and BW attained 361.3 mm and 1704.3 g, respectively, and the squid with ML of 300–500 mm and BW of 1000–2000 g consisted of 87.4% and 56.6% of the total sample, respectively (Figure 2).

Age, hatching date and spawning population

Three main growth zones (postnuclear, dark and peripheral) were observed in the dorsal dome of *D. gigas* statolith (Figure 3). Daily growth increments could be seen clearly (Figure 3). Ages of specimens were ranged from 127 to 307 days and most were from 210 to 270 days, consisting of 58.7% of all the samples (Figure 4). The ages of female squids were from 150 to 307 days with the dominant ages ranging from 210 to 270 days, which consisted of 74.35% of all the female samples (Figure 4). While for male squids, ages varied from 127 to 302 days, and the dominant ages were between 240 and 300 days, accounting for 76.87% of all the male samples (Figure 4).

All the squids sampled in this study were hatched during January to December 2008 (Figure 5A), suggesting that the

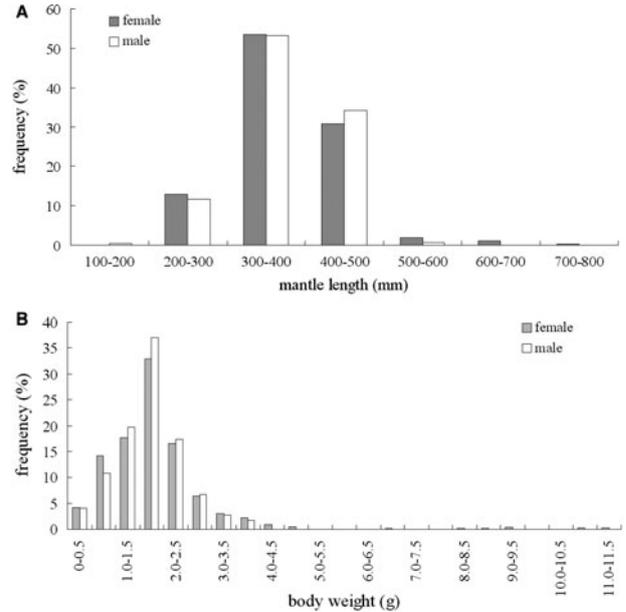


Fig. 2. A statolith of *Dosidicus gigas* showing a composition of seven reading frames in increments.

squid spawned almost throughout the year. The peak hatching dates were from August to November (austral spring), consisting of 52.91% of all the samples. The second hatching dates were from March to June (austral fall), which consisted of 30.77% of the sampled squids (Figure 5A). This suggests that there were two dominant groups for *D. gigas* off the Chilean EEZ waters: the austral spring spawning group and austral autumn spawning group (Figure 5A).

Growth models

The best age-ML models and age-BW models for both the spawning groups identified based on the AIC were:

$$ML = 1.6338 \times age + 8.106 \quad (R^2 = 0.8227, N = 164, \text{Figure } 5B)$$

$$BW = 51.685 \times e^{0.0151age} \quad (R^2 = 0.7934, N = 164, \text{Figure } 5C)$$

for the spring spawning group (Fig. 5B and 5C); and

$$ML = 5.3334 \times age^{0.6835} \quad (R^2 = 0.6532, N = 282, \text{Figure } 5B)$$

$$BW = 156.93 \times e^{0.0102age} \quad (R^2 = 0.5975, N = 282, \text{Figure } 5C)$$

for the autumn spawning group (Figure 5B, C).

Growth patterns

The average IRGRs ($P = 0.8653$) and AGRs ($P = 0.8094$) did not differ significantly between the two spawning groups. The ANCOVA revealed no significant differences for IRGRs ($P = 0.8119$) and AGRs ($P = 0.6269$) between the two spawning groups for BW.

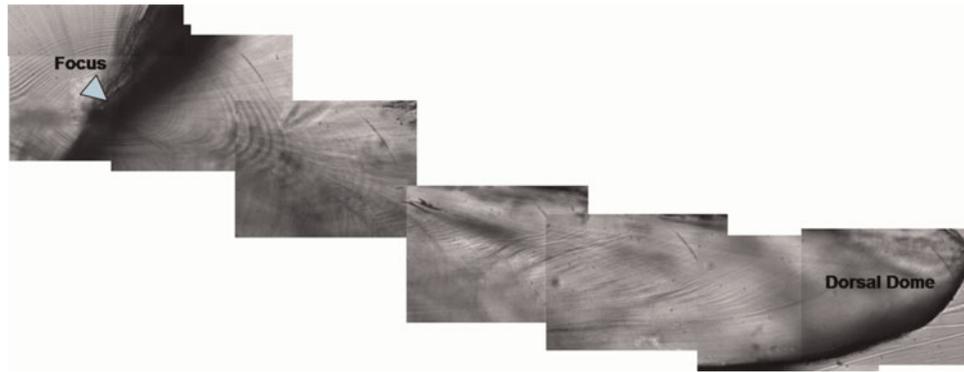


Fig. 3. The distribution of mantle length (ML, mm) (a) and body weight (BW, g) (b) for *Dosidicus gigas* off the Exclusive Economic Zone of Chilean waters.

The IRGR and AGR varied with sizes of squid. Taking the spring spawning group as an example, the IRGR and AGR of ML reached the highest with the values of 0.72 and 2.25 at ages of 181 to 210 days, respectively (Table 1), and the IRGR of BW also reached the peak (2.63%) at ages of 211 to 240 days while the highest AGR of BW (40.59 mm per day) was at ages of 241 to 270 days (Table 1).

DISCUSSION

Hatching dates of specimens based on capture dates and ages were estimated in this study suggesting that *D. gigas* might spawn throughout the year. Based on the distribution of hatching dates (Figure 5A), two modes for different spawning groups could be identified, one in August to November and the other from March to June. This is consistent with the conclusion identified in Zúñiga *et al.* (2008) who suggested that there were two cohorts per year off Chile based on the seasonal pattern of monthly catch. Clarke & Paliza (2000) reported the existence of the two spawning periods within a year for *D. gigas* in the southern hemisphere, one of the peaks occurring in austral autumn (April–May) and the other in austral spring (October–November). González & Chong (2006) also suggested the presence of at least two cohorts of *D. gigas* based on the differences in the maturation of specimens observed between winter and spring. But Liu *et al.* (2010) reported that *D. gigas* might spawn all year around with a peak spawning time from November to next January in the waters of 20°–24°30'S and 74° 30'–82°W. The population structure of *D. gigas* in the eastern Pacific Ocean is complicated. In general, three groups of *D. gigas* were identified with different ML values at maturity (Nigmatullin *et al.*, 2001). In the Gulf of

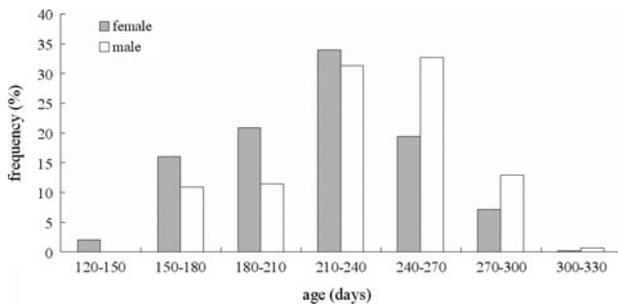


Fig. 4. The age distribution of *Dosidicus gigas* off the Exclusive Economic Zone of Chilean waters.

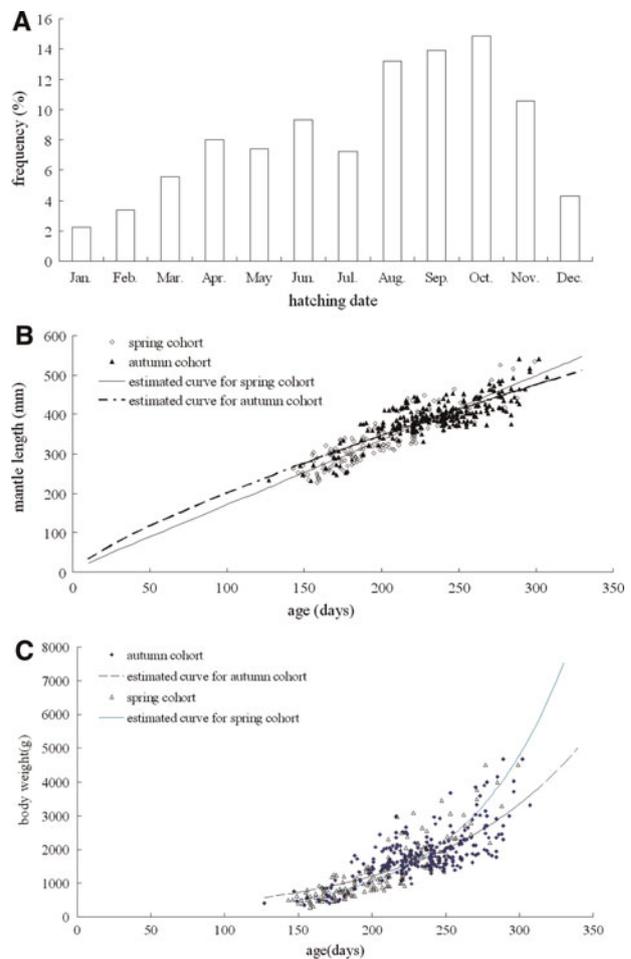


Fig. 5. The distribution of back-calculated hatching dates (a), estimated growths of mantle length (ML) (b), and body weight (BW) (c) of *Dosidicus gigas* off the Exclusive Economic Zone of Chilean waters.

California, the cohort analysis revealed five cohorts with different hatching times (Ehrhardt *et al.*, 1983). Morales-Bojórquez *et al.* (2001) estimated catchability-at-length for *D. gigas* and suggested the existence of three different cohorts off the coast of Guaymas (Sonora, Mexico). In Peruvian waters, Tafur *et al.* (2001) reported there were two main spawning peaks, but mature individuals were observed throughout the year. Argüelles *et al.* (2001) revealed the presence of two cohorts estimated by the date of hatching, one hatched in autumn/winter and recruited to the fishery in spring/summer and the other

Table 1. Instantaneous relative growth rates (IRGRs) and absolute growth rate (AGR) for mantle length (ML) and body weight (BW) of the austral spring spawning group and austral autumn spawning group of *Dosidicus gigas* off the Exclusive Economic Zone of Chilean waters.

	Age-class (d)	Sample size	Mantle length			Body weight		
			Average ML (mm)	IRGR	AGR (mm.d ⁻¹)	Average BW (g)	IRGR	AGR (g.d ⁻¹)
Spring group	121–150	5	255.8	\	\	532.1	\	\
	151–180	44	280.9	0.31	0.84	655.6	0.75	4.45
	181–210	46	348.4	0.73	2.25	971.9	1.26	10.21
	211–240	42	399.5	0.46	1.71	2137.0	2.63	38.83
	241–270	20	444.1	0.35	1.49	3354.5	1.51	40.58
	271–300	7	484.4	0.29	1.34	3678.7	0.31	10.81
Autumn group	121–150	3	250.2	\	\	540.9	\	\
	151–180	57	278.0	0.35	0.93	631.1	0.51	3.00
	181–210	34	363.0	0.89	2.83	1479.7	2.84	28.29
	211–240	82	429.2	0.56	2.21	2146.3	1.24	22.22
	241–270	73	464.6	0.26	1.18	2576.1	0.61	14.33
	271–300	31	495.5	0.21	1.03	3018.2	0.53	14.74
	301–330	2	518.0	0.15	0.75	3324.3	0.32	10.21

hatched in spring/summer and recruited to the fishery in autumn/winter. Clearly, the results derived in this study are similar to those of other studies conducted in different geographical areas and different time periods, suggesting the existence of multiple cohorts in a given year for *D. gigas* over the range of their distribution.

Statolith ageing in this study generally confirmed high growth rates of *D. gigas*. *Dosidicus gigas* can attain large sizes in less than 1 year. The oldest mature squid was found in this study to be 307 days old, with its size reaching 495 mm ML and body weight of 3300 g. The smallest immature squid was 127 days old with a size of 234 mm ML and body weight of 412 g. We conclude that the life span of *D. gigas* is likely to be about one year off the EEZ of Chilean waters, which generally conforms to the Ommastrephidae squid life history (Arkhipkin, 2004). Although some large specimens (>750 mm ML) of the large sized group were found to live for longer than one year (up to 1.5–2.0 years; Nigmatullin *et al.*, 2001; Markaida *et al.*, 2004), we did not find such individuals in this study.

Squid of each cohort tended to follow different growth models (Nigmatullin *et al.*, 2001). The logistic model best described growth (BW–age and ML–age) for *D. gigas* in the Gulf of California (Markaida *et al.*, 2004), and an exponential model for age–ML of *D. gigas* was fitted for each maturity stage and hatching season by size-group in Peruvian waters (Argüelles *et al.*, 2001). Growth in adult phases for *D. gigas* could be approximated by linear functions (Arkhipkin & Murzov, 1987; Masuda *et al.*, 1998). In the absence of larval and juvenile squid of this study, seven growth models including logistic model and exponential model were evaluated, and we found that the ML–age relationships were best described by a linear function and a power function, respectively, for the austral spring and autumn spawning groups; while the BW–age relationships of the two groups were both best described by exponential functions. However, we should note that the models identified might not be suitable to describe the growth of larval and juvenile squid because they were not included in the sample of this study.

Dosidicus gigas hatched in different seasons were found to have different growth rates off the EEZ of Chilean waters, however such differences were not significant between the two spawning groups ($P > 0.05$). The IRGR and ARG of

ML for the austral spring spawning group tended to be higher than those of the austral autumn spawning group before the age of 240 days, and for the age of 211–270 days squid the IRGR and ARG of BW for the austral spring spawning group were obviously greater than those of the austral autumn spawning group (Table 1). In the Peruvian waters, the IRGR of *D. gigas* ranged between 0.61 (austral summer) and 0.76 mm d⁻¹ (austral winter) for small squids, while larger squids had lower growth rates of 0.23 (austral summer) to 0.29 mm d⁻¹ (austral spring; Argüelles *et al.*, 2001). In the Gulf of California, the ARG of *D. gigas* can attain over 2 mm d⁻¹ for more than 5 months, and no differences in growth were noted between the groups hatched in different seasons (Markaida *et al.*, 2004). This suggests large spatial and temporal variability in growth for *D. gigas*, possibly responding to environmental gradients.

We found that the growth rate of *D. gigas* might be high at young ages, and decreased after they reached sub-adult stages (age >180 days for the spring and autumn spawning groups; Table 1). The maximum ARG and IRGR of ML for the austral spring and autumn spawning groups were reached at 181–210 days old, and the maximum ARG of BW ranged from 211 to 240 and from 181 to 210 days old, respectively, for the austral spring and autumn spawning groups (Table 1). In the Gulf of California, the ARG values of ML for the female (2.65 mm.d⁻¹) and male (2.44 mm.d⁻¹) *D. gigas* were reached at 230–250 and 210–230 days old respectively, and the maximum ARG of BW for females was 104 g.d⁻¹ at 350 days old and for males 72 g.d⁻¹ at 310 days old. Argüelles *et al.* (2001) reported that the IGRG of *D. gigas* ranged between 0.48 (maturing) and 0.58 (mature) for small squid, while the larger sized squid ranged between 0.08 (maturing) and 0.10 (mature) in the Peruvian waters.

Growth was found to be different between female and male *D. gigas* (Markaida *et al.*, 2004). Although we did find differences in growth rates between sexes, we were not able to conduct a statistical test to evaluate temporal and spatial differences in growth between female and male *D. gigas* because of small sample sizes when we divided sex-specific samples into different sampling time and spawning groups. We are planning to collect more samples in future to evaluate temporal and spatial differences in growth between female and male *D. gigas* with respect to environmental variability.

In summary, we conclude that *D. gigas* distributed off the EEZ of Chilean waters varied between 206 to 702 mm ML in size. The age of *D. gigas* estimated by counting daily growth increments in statoliths did not exceed one year old. At least two spawning groups were identified, the main spawning peak tends to occur between August and November, the secondary peak appears during March to June, but the hatching period was extended throughout the year. The best growth models differed between the two groups, but growth rates did not differ significantly between the two spawning groups. Population structure, age and growth of *D. gigas* identified in this study off the EEZ of Chilean waters seemed to be inconsistent with those in the eastern Pacific Ocean, suggesting large spatial variability in the key life history parameters for *D. gigas*. We suggest more extensive sampling of data with finer spatial and temporal scales and collaboration among different countries or regions to improve our understanding of spatial and temporal variability in the fishery biology of *D. gigas*.

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