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Age, Maturation and population structure of the Humboldt squid, *Dosidicus gigas* off Peruvian Exclusive Economic Zones

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1. Introduction

Humboldt squid, *Dosidicus gigas* (D'Orbigny, 1835), prevails in the southern part of the California Current system and northern region of the Humboldt Current system. It supports four major fisheries in the Eastern Pacific Ocean, squid fisheries in the Gulf of California and vicinity waters of Costa Rica Dome, Peru and central Chile (Nevárez-Martínez et al., 2000; Morales-Bojórquez et al., 2001; Taipe et al., 2001; Rocha and Vega, 2003). The population in the Peruvian waters are considered most abundant and support the most important fishery (Nigmatullin et al., 2001). An early study of *D*. *gigas* in Peru was performed by a joint Peruvian-Japanese survey during November to December in 1989 (Rubio and Salazar, 1992). After the survey a large scale of commercial fishery targeting *D*. *gigas* was developed with industrialized fishing fleets from Japan and South Korea (Taipe et al., 2001). Chinese squid jigging fleet began to explore this squid in 2001, with annual landing reaching 50 to 205 thousand tones during 2002 to 2008 (Liu et al., 2011).

Early studies of age and growth of *D*. *gigas* were based on length frequency analysis (Nesis, 1970; Ehrhardt et al., 1983), which is criticized for potential errors (Jackson, 1994; Yatsu et al., 1997). Statolith was considered as one of most effective body hard parts to study age and growth of squid (Jackson, 1994). The age and growth of *D*. *gigas* from different geographic waters was studied using statolith microstructure analysis. These studies suggest that *D*.

gigas is a short lived species with longevity about 1-2 year (Arkhipkin and Murzov, 1986; Masuda et al., 1998; Argüelles et al., 2001; Markaida et al., 2004; Mejía-Rebollo et al., 2008, Chen et al., 2011). The population structure of *D*. *gigas* is complicated. Within the rage of its spatial distribution, two migratory-based and three size-based groups were identified by Nigmatullin et al. (2001) and Clarke and Paliza (2000), respectively.

The reproduction of *D*. *gigas* was studied off the Peruvian coast (Nesis, 1970; Tafur et al., 2001), in the Gulf of California (Markaida and Sosa-Nishizaki, 2001; Markaida, 2006), in the eastern central Pacific (Koronkiewicz, 1988), and off Chile coast (Ibáñez and Cubillos, 2007) and EEZ waters of Chile (Liu et al., 2010). The squid is a monocyclic species spawning 10-14 batches with fecundity up to 32 million eggs (Nigmatullin and Markaida, 2009). At least four potential spawning grounds were identified based on the presence of mature squid, rhynchoteuthion paralarvae, egg mass and even occurrence of mating events, which is the vicinity region of the Costa Rica Dome, the Gulf of California in north hemisphere, and tropical waters off the coasts of northern Peru and central Chile in south hemisphere (Anderson and Rodhouse, 2001; Tafur et al., 2001; Staaf et al., 2008; Chen et al., 2013).

A number of studies were done on its age, maturation and population structures of the Humboldt squid throughout its ranges, especially in the Gulf of California and Costal waters of Peru (Ehrhardt et al., 1983; Markaida and Sosa-Nishizaki, 2001; Morales-Bojórquez et al., 2001; Tafur et al., 2001; Argüelles et al., 2001; 2008), but few studies were focused on the squid off Peruvian EEZ (Ye and Chen, 2007). In this study, we determined ages of *D*. *gigas* off the Peruvian EEZ waters using statolith microstructure analysis and studied maturation and population structure of the squid.

2. Materials and methods

2.1. Squid collection and ageing

During 2008 to 2010, a total of 2534 *D. gigas* (1985 females, 497 males and 52 unsexed) were sampled randomly off the Peruvian EEZ by the Chinese fishing fleet using method of jigging (Fig.1; Table 1). The sampled squids were frozen on the vessels immediately. They were defrosted in the lab, and dorsal mantle length (ML) and body weight (BW) were recorded to the nearest 1 mm and 1 g, respectively. Sex was identified and maturity stages were evaluated with naked eye following Lipinski and Underhill (1995): stages I and II (immature), III (maturing), IV (mature) and V (spent).

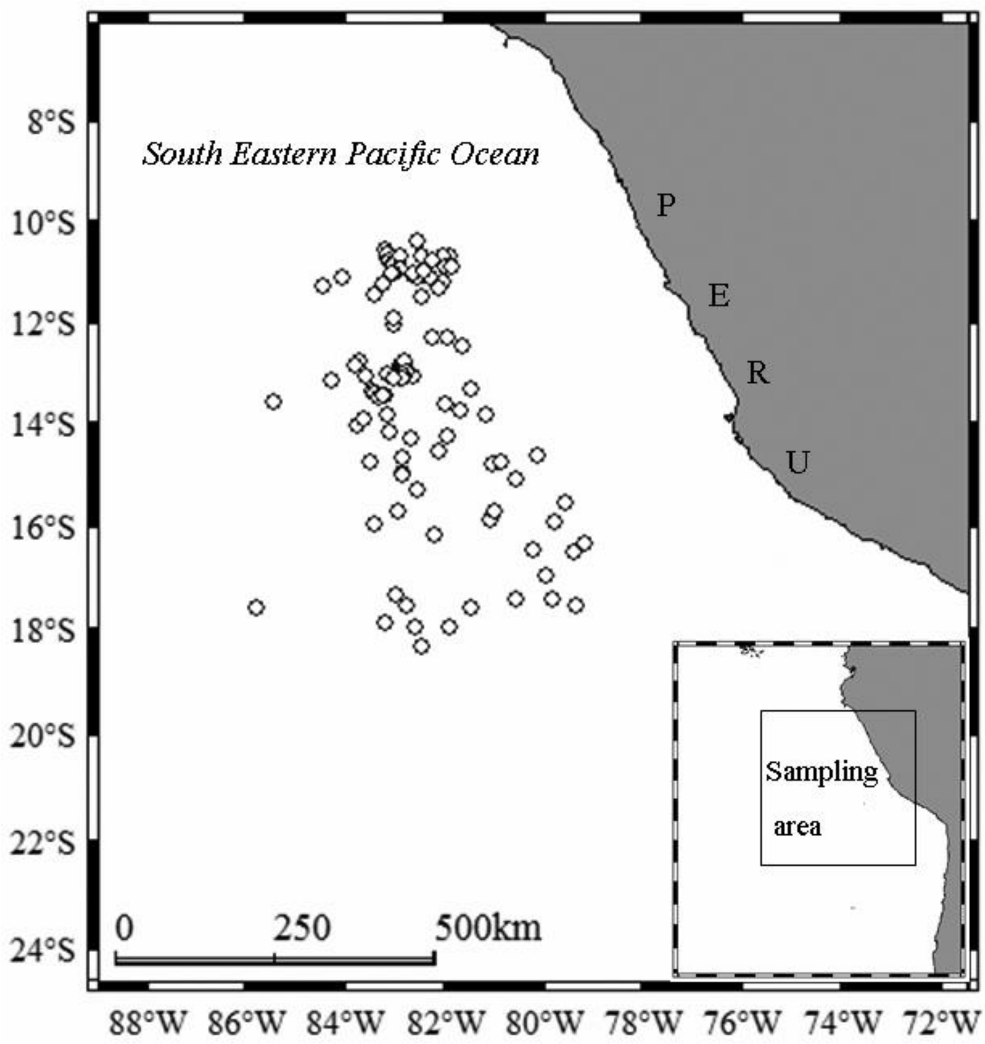


Figure 1. Sampling locations of D. gigas off Peruvian EEZ.

Table 1. Summary information of sampled squid off the Peruvian EEZ.

Vessel	Sample Location	Sample date	N	Mantle length(mm)
New century 52	82°48′-83°37′W 12°43′-15°55′S	Jan to Feb 2008	381	211-705
Zhe Yuanyu 807	82°05′-85°30′W 10°32′-13°32′S	Sep 2008 to Feb 2009	356	209-733
Feng Hui 16	79°30′-89°00′W 10°20′-18°00′S	Jul to Aug 2009	387	159-415
Zhe Yuanyu 807	79°22′-88°48′W 10°21′-18°16′S	Sep 2009 to Oct 2010	1094	209-1149
XinJili 8	79°12′-85°51′W 16°18′-17°32′S	6 Apr and 29 Jun 2010	16	272-494
Feng Hui 16	79°22′-83°11′W 10°52′-17°29′S	May 2010 to Nov 2010	300	178-913

The statoliths were extracted from the head, washed and stored in the centrifugal tube with 90% alcohol for further processing. Only left statolith if not damaged, was prepared for age determination. The standard ageing methodology of a statolith was used in this study (Dawe and Natsukari, 1991). The number of increments was accepted when the two independent counts differed less than 10% of the mean (Yatsu et al., 1997). Hatching date was back-calculated based on the time of capture, assuming that growth increments were formed daily because periodic deposition of increments for many other squids of Ommastrephidae have been confirmed (Nakamura and Sakurai, 1991; Uozumi and Ohara, 1993).

2.2. Data analysis

We analyzed ML frequency distribution of mature adult squids (maturity stages Ⅲ, Ⅳand V) to identify possible populations of different MLs according to the criteria outlined by (Nigmatullin et al., 2001), and different spawning cohorts were also identified based on the back-calculated hatching dates. The sample stations at which no less than 50% females were mature were considered as potential spawning grounds after Tafur et al. (2001). Distribution of size-based populations and mature females were mapped.

Linear, power, exponential, logarithmic and logistic curves were fitted to age-ML and age-BW data of different hatching groups. The model with the highest coefficient of determination (R^2) and smallest coefficient of variance (CV) and Akaike information criterion (AIC) were selected to describe growth (Arkhipkin et al., 2000; Chen et al., 2011). Sexual dimorphism of growth curves was evaluated using ANCOVA.

To estimate size and age at first maturity, changes in the proportion of mature squid with ML or age were fitted to a logistic equation described below using the least square method:

$$p_i = \frac{1}{1 + e^{-r(x_i - x_{50\%})}}$$

where p_i is the proportion of mature individuals in ML or age class x_i, r is the intercept and $x_{50\%}$ is the size or age at first maturity, which were estimated in the regression analysis.

We used F test to compare the difference of these logistic curves between different sexes and between different hatching cohorts (Chen et al., 1992; Arkhipkin et al., 2000). The F test statistic can be calculated as:

$$F = \frac{\dfrac{RSS_{\mathrm{p}} - \sum RSS_i}{DF_{\mathrm{p}} - \sum DF_i}}{\dfrac{\sum RSS_i}{\sum DF_i}} = \frac{\dfrac{RSS_{\mathrm{p}} - \sum RSS_i}{(m+1)(k-1)}}{\dfrac{\sum RSS_i}{\sum_{i=1}^{k} n_i - k(m+1)}}$$

where RSS_{p} is the pooled residual sum of squares, RSS_i is the residual sum of squares for each group, DF_{p} is the pooled degree of freedom, DF_i is the degree of freedom for each group, m is the number of variables to estimate, k is the number of compared regressions, and n_i is sample size of each group.

3. Results

3.1. *Age*

A total of 1535 *D*. *gigas* statoliths were considered to have valid ages based on the criteria described including 1207 females, 286 males and 42 unsexed individuals. The ages ranged from 144 to 633 days olds. The dominant ages for females and males were between 181 and 300 days old consisting of 76.5% and 80.4% of the total samples for females and makes, respectively (Fig. 2). The youngest sampled female was 144 days old with 178 mm ML and 187 g BW, and the oldest was 633 days old with 1118 mm ML and 54500 g BW. The youngest sampled males was 162 days old with 218 mm ML and 253 g BW, and the oldest was 574 days old with 1033 mm ML and 33500 g BW. Ages of mature females ranged from 184 to 633 days old, and males from 162 to 574 (Fig. 3).

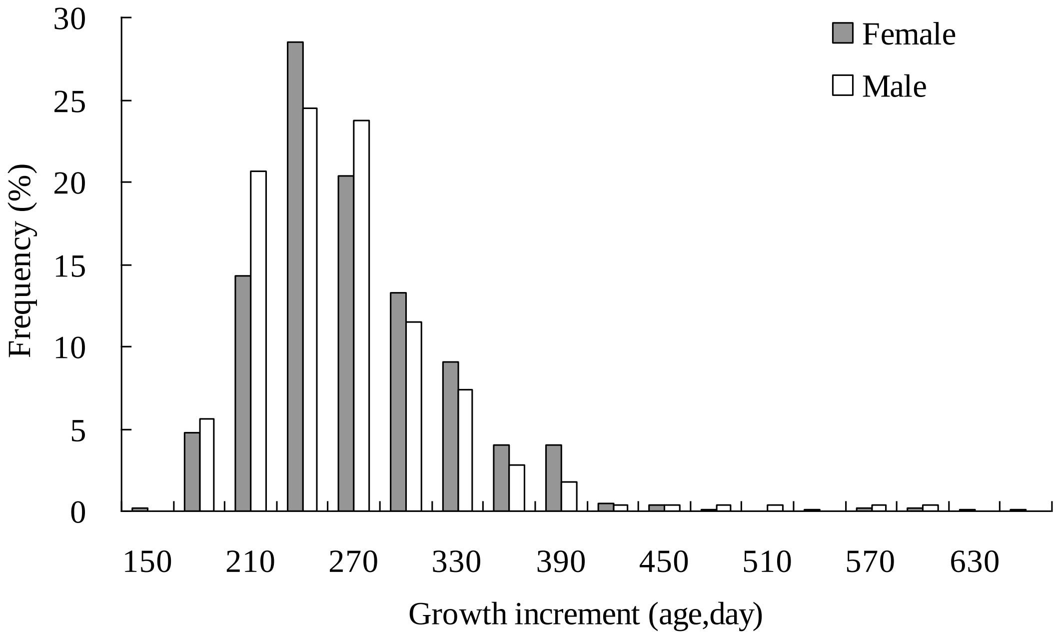


Figure 2. Frequency distribution of ages for D. gigas off the Peruvian EEZ.

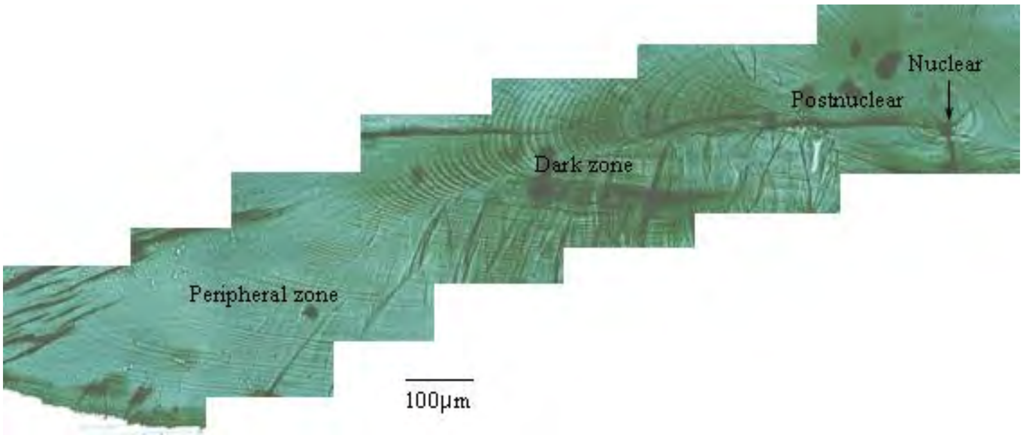


Figure 3 Light micrograph of *D. gigas* statolith off Peruvian EEZ

3.2 *Maturity and hatching*

Mature female widely occurred in the study area, putative spawning area dominantly located near 11°S on the basis of stations where at least 50% females were mature (Fig. 4). Sampled squids hatched during 22nd January 2008 to 22nd April 2010 with most hatching occurring between December and May, especially from January to March (Fig.5). Therefore, *D*. *gigas* could be separated into austral summer-autumn and winter-spring hatching cohorts. Higher percentages of mature females were observed between September and January, which is before the prevailed hatching timing (Fig. 5).

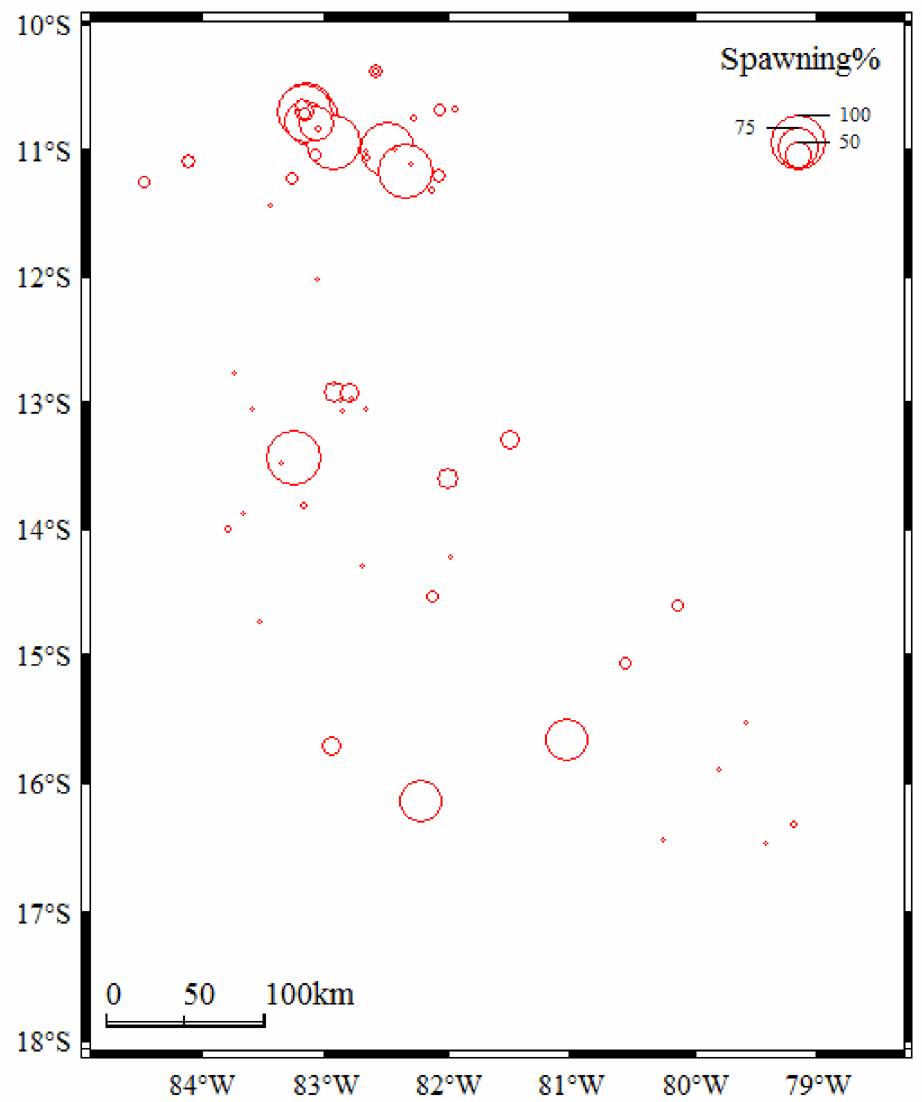


Figure 4. Spatial distribution of matured female D. gigas off the Peruvian EEZ.

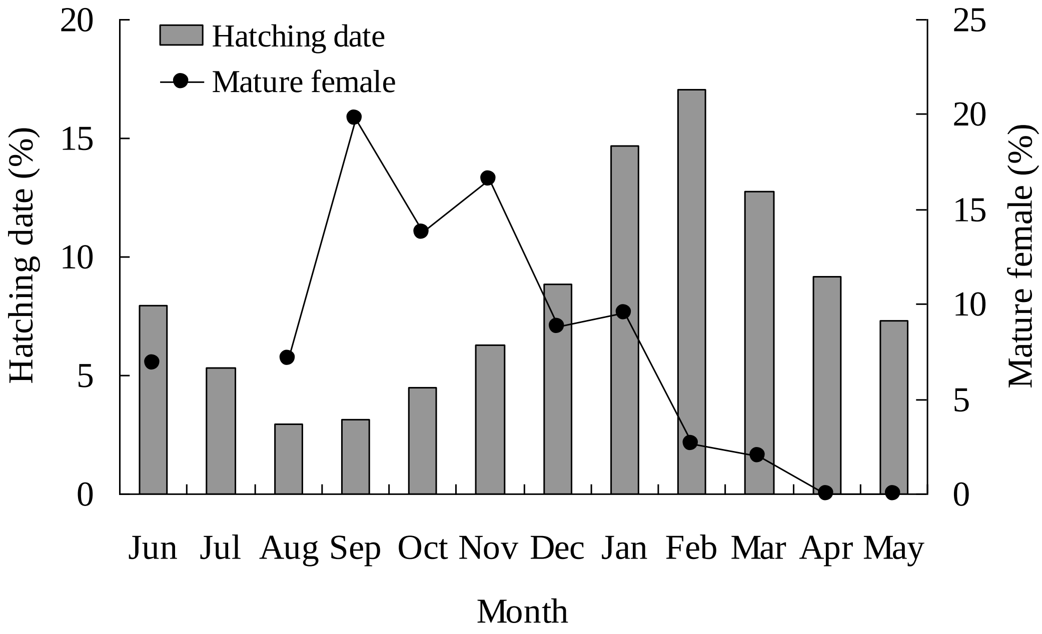
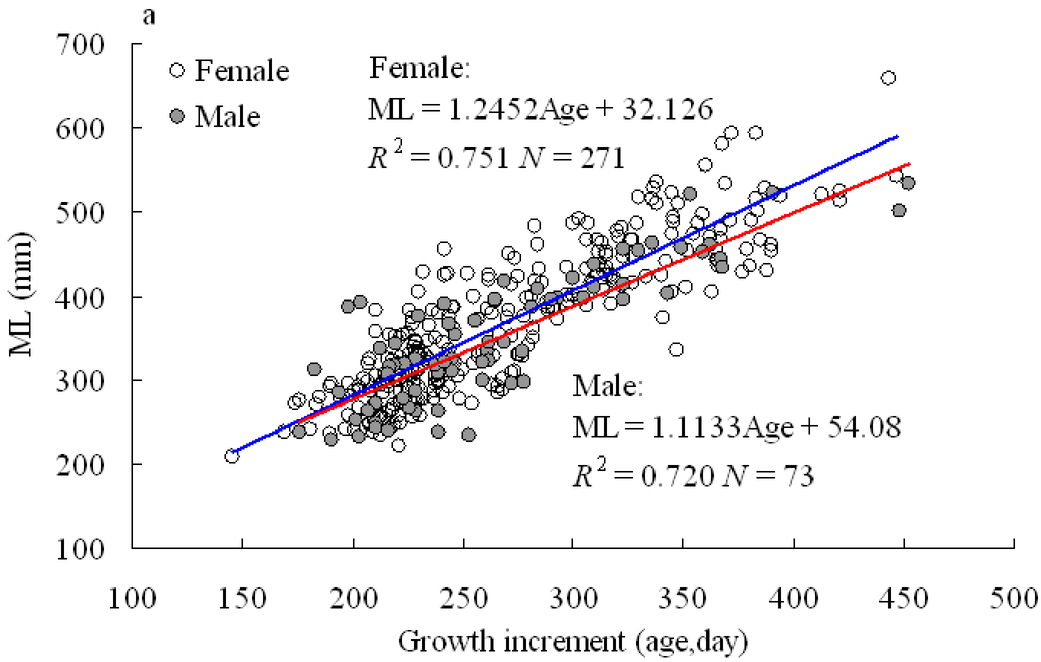


Figure 5. Frequency distribution of back-calculated hatching dates for D. gigas off the Peruvian EEZ.

3.3 *Growth model*

The ML-age data of winter-spring hatching cohort were best described by linear models, and ANCOVA showed significant differences between females and males (ANCOVA, $F_{1,340}$=5.744, P=0.017<0.05, Fig. 6a). The ML-age data of summer-autumn hatching cohort were best fitted by exponential curves, but no significant differences were found between females and males (ANCOVA, $F_{1,854}$=2.366, P=0.124 > 0.05, Fig. 6b)



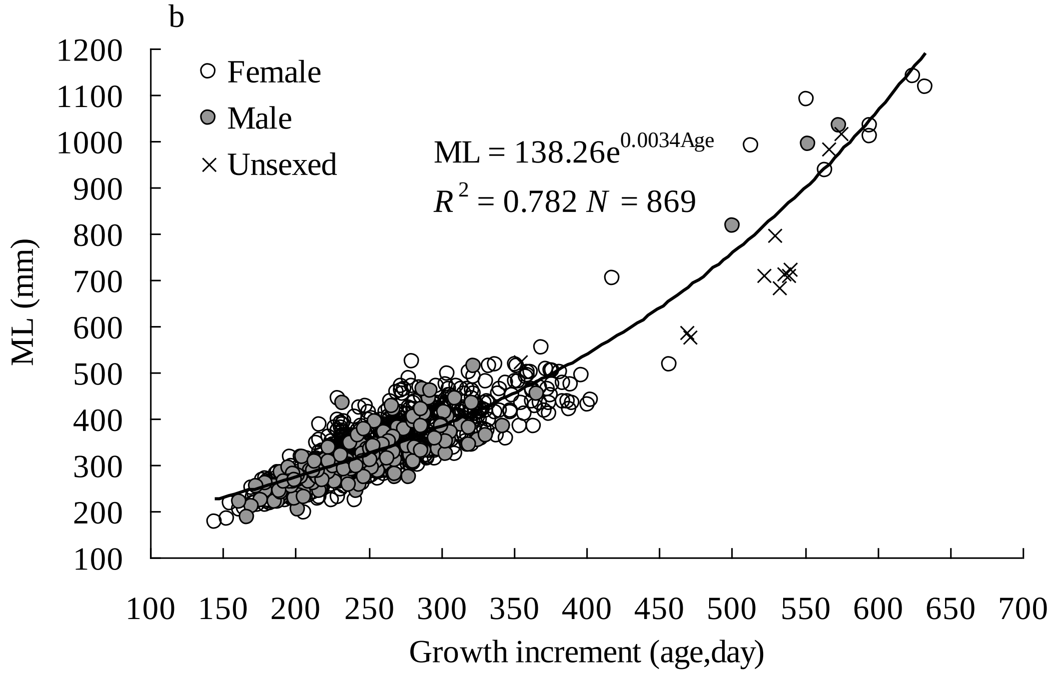
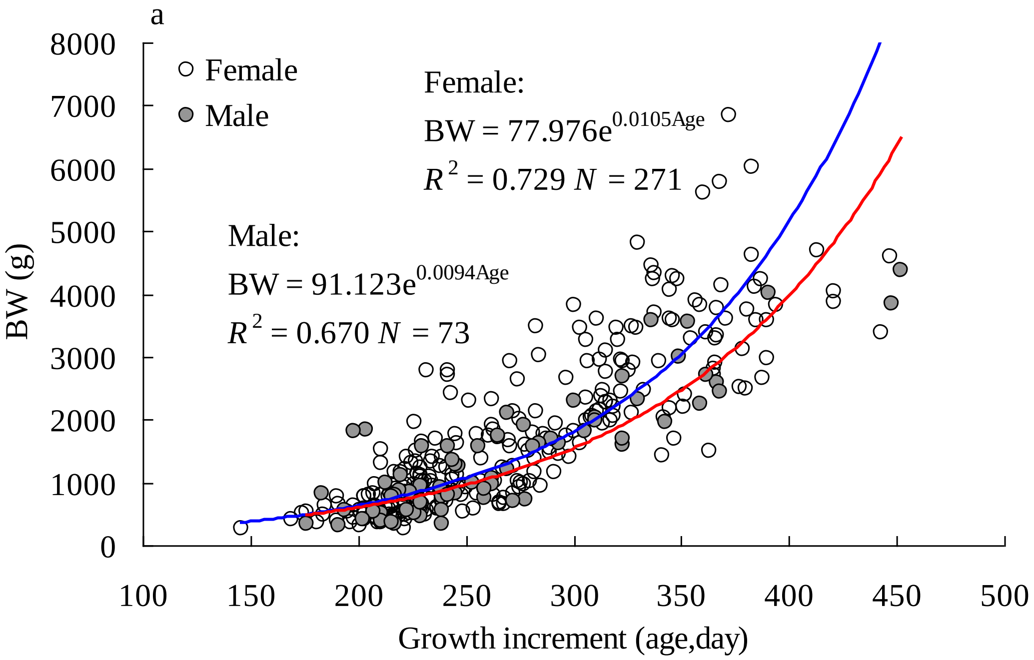


Figure 6. Relationship between age and ML of winter-spring (A) and summer-autumn (B) hatching D. gigas off the Peruvian EEZ. Blue and red lines represent female and male respectively.

The BW-age data of winter-spring hatching cohort were best fitted by exponential curves, and ANCOVA showed significant differences between females and males (ANCOVA, $F_{1,340}$=8.824, P=0.003<0.05, Fig. 7a). The BW-age data of summer-autumn hatching cohort were best fitted by exponential curves, but no significant differences were found between females and males (ANCOVA, $F_{1,854}$=2.237, P=0.135 > 0.05, Fig. 7b).



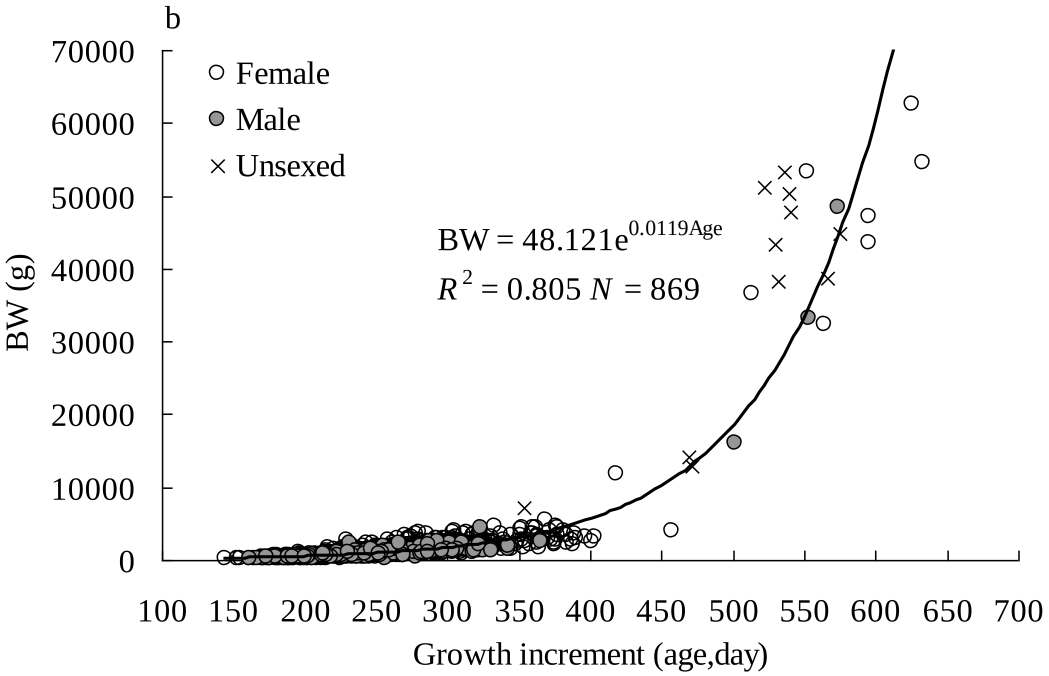


Figure 7. Relationship between age and BW of winter-spring (A) and summer-autumn (B) hatching D. gigas off the Peruvian EEZ. Blue and red lines

represent female and male respectively.

3.4 *Size and age at first maturity*

Significant differences were found in size and age at first maturity between the winter-spring and summer-autumn hatching cohorts (*F* test $P<0.05$, Table 2) except for age at first maturity for males (*F* test $P>0.05$, Table 2). For the winter-spring hatching cohort, size and age at first maturity were 544 mm ML and 419 days old for females, and 552 mm ML and 451 days for males (Table 2). For the summer-autumn hatching cohort, size and age at first maturity were 497 mm ML and 387 days old for females, and 556 mm ML and 420 days for males (Table 2). Size and age at first maturity of females were higher than those of males, except for size at first maturity data for the winter-spring cohort (Table 2).

Table 2. Size (ML, mm) and age (days) at maturity data fitted to logistic model by sex and hatching cohorts.

	Estimate		Standard error		R^2	RSS	RMS
	R	X_{50}	*R*	X_{50}			
Size at maturity for females (testing between hatching groups differences $F_{3,25}=4.86$, p=0.0085*)							
WS	0.0179	544	0.0016	4.98	0.991	94	14
SA	0.0390	552	0.0078	5.60	0.990	747	42
pooled	0.0236	544	0.0027	5.30	0.979	1168	47
Size at maturity for males (testing between hatching groups differences $F_{3,13}=7.02$, p=0.0073*)							
WS	0.0450	497	0.0311	15.67	0.716	1915	383
SA	0.0073	556	0.0020	47.25	0.921	1086	136
pooled	0.0124	501	0.0042	26.42	0.776	4352	290
Age at maturity for females (testing between hatching groups differences $F_{3,13}=2.93$, p=0.0047*)							
WS	0.0176	419	0.0015	4.64	0.987	44	9
SA	0.0303	446	0.0070	9.12	0.980	549	69
pooled	0.0188	445	0.0034	10.12	0.938	1233	95
Age at maturity for males (testing between hatching groups differences $F_{3,9}=0.32$, p=0.8121)							
WS	0.0279	387	0.0107	15.46	0.872	1112	223
SA	0.0151	420	0.0100	73.28	0.678	2948	737
pooled	0.0373	396	0.0185	16.62	0.813	4347	483

WS: winter-spring hatching cohort, SA summer-autumn hatching cohort, RSS: residual sum of squares, RMS: residual mean square, *: significant at $P<0.05$

3.6 *Size structure of adult squids*

The ML distribution of 213 adult females and 116 males from a total of 2534 *D. gigas* was plotted in Fig.2. Adult females ML ranged from 234 to 1149 mm with dominant ML of 350-550 mm, and adult males ML varied between 129 to 1001 mm with dominant ML of 250-400 mm (Fig. 8). Overall, size structures of *D. gigas* for adult females and males were characterized by the two size-based groups: a medium-sized group with ML less than 550 mm and 400 mm and a large-sized group with ML more than 550 mm and 400mm, for female and males respectively (Fig. 8).

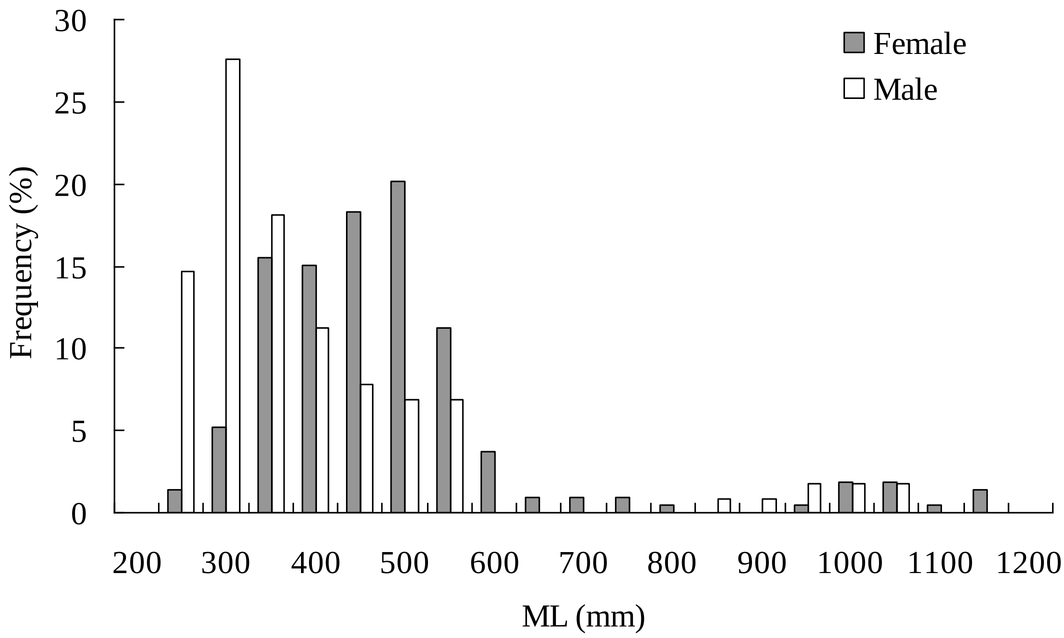


Figure 8. Frequency distribution of mantle length for adult D. gigas off the Peruvian EEZ.

Medium-sized group existed in the whole study area, while large female group occurred in the north part of 14°S and large male group was distributed southward to 16°S with the concentration between 10°S and 12°S (Fig. 9a, b).

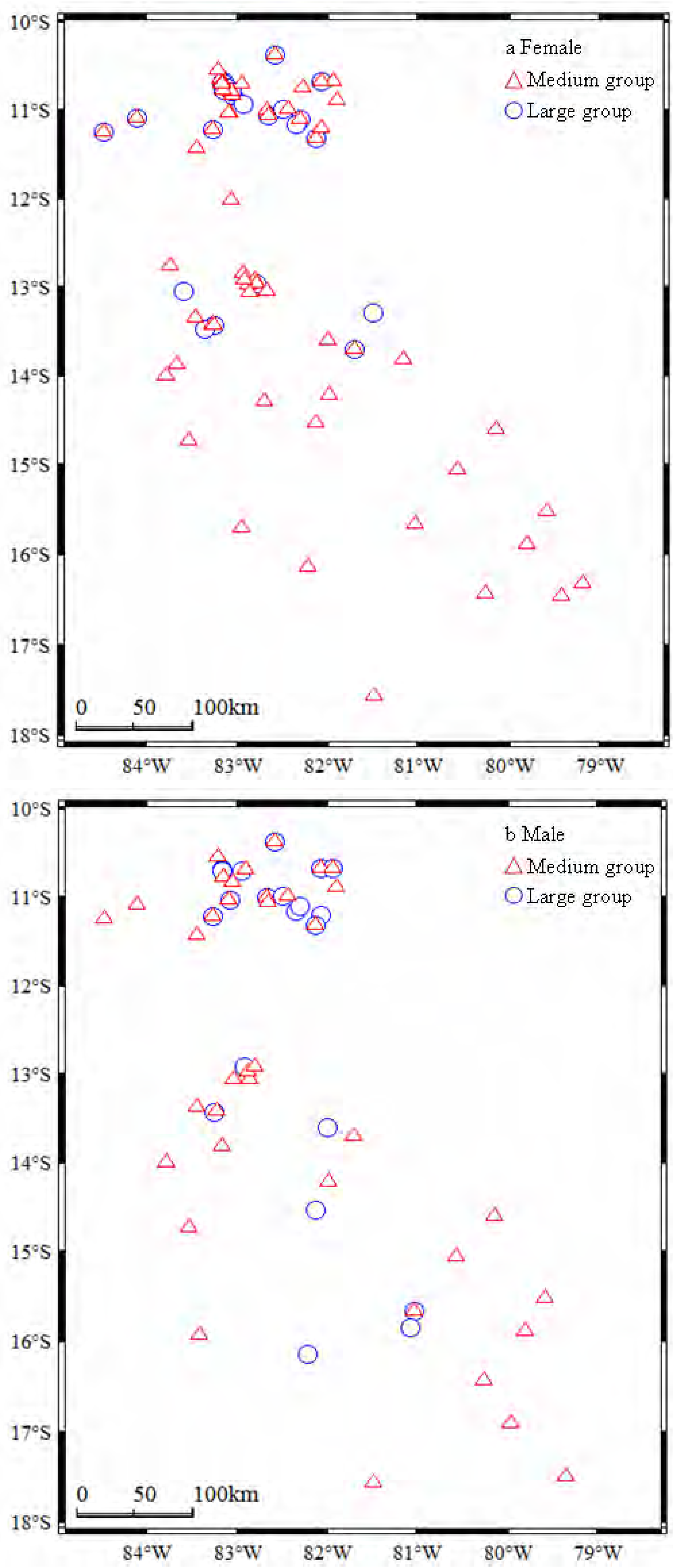


Figure 9. Spatial distributions of medium group and large group of D. gigas for females (A) and males (B) off the Peruvian EEZ.

4. Conclusion

We conclude that the age of the Humboldt squid off the Peruvian EEZ estimated with statoliths microstructure analysis was no more than 2-year old. The squid spawned throughout the year and back-calculated hatching dates were from 22nd January 2008 to 22nd April 2010 with a hatching peak between January and March. There were at least a medium-sized and a large-size based groups in the study area. Moreover, two hatching groups of winter-spring and summer-autumn cohorts were separated on the basis of back-calculated hatching dates. The vicinity waters of 11°S off Peruvian EEZ was considered as a potential spawning ground because more than 50% females sampled in this area were mature. Size and age at maturity differed significantly between the two hatching cohorts, except for age at first maturity for males. Age-ML and BW-ML data of winter-spring cohort were best described by linear and exponential models, respectively, while for summer-autumn cohort both Age-ML and BW-ML data were best described by exponential models. Humboldt squid is a species whose abundance and population structure are susceptible to change with spatio-temporal environmental fluctuations (Anderson and Rodhouse, 2001; Waluda et al., 2006; Argüelles et al., 2008; Keyl et al., 2008). We suggest that much wider size range and more extensive temporal and spatial coverage in sampling are needed in future to further improve our knowledge of the squid off the Peruvian EEZ that had not been well studied.

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