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Inter-annual variability in trophic patterns of jumbo squid (*Dosidicus gigas*) off the exclusive economic zone of Peru, implications from stable isotope values in gladius



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ABSTRACT

The jumbo squid *Dosidicus gigas* plays an important role in marine food webs in the eastern Pacific Ocean, as not only a voracious predator but also a valuable prey source. In this study, the proostracum (a morphological part of the gladius) from 45 samples were selected over three years and were serially sampled based on growth information obtained from the statolith. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along the proostracum were used to reconstruct the feeding variations of *D. gigas* and to evaluate the potential effects of 2009–10 El Niño event on the variability of their trophic patterns. The results show a strong variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along the proostracum for all the squid; changes that could be determined by temporal variation of foraging as well as migration among regions with distinct baselines. An El Niño event could decrease the variation of trophic patterns of squid through compressing the space and time for foraging and migration. These results support our general hypothesis that a time-based consecutive sampling of the gladius can back-calculate an ontogenetic shift and the possible migration patterns of squids more precisely and comprehensively and suggest that the isotopic values of *D. gigas* might be influenced much more by their migration behavior.

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1. Introduction

The jumbo squid, *Dosidicus gigas*, is found from California (47°N) to Chile (37°S) within the eastern Pacific Ocean, extending to the west and reaching 125–140°W at the equator. A dramatic expansion in its range has been documented in both hemispheres since the 1997–1998 El Niño event (Nigmatullin et al., 2001; Ruiz-Cooley et al., 2013). *D. gigas* is one of the main target species of commercial fisheries and the annual catch exceeded 950,000 tons in 2012 (FAO, 2014). As a pelagic cephalopod, *D. gigas* plays a vital role in the marine ecosystems of the eastern Pacific Ocean, not only as a voracious predator but also as a valuable source of prey (Ruiz-Cooley et al., 2006; Field et al., 2007; Rosas-Luis et al., 2008; Alegre et al., 2014). Knowledge of their trophic dynamics is fundamental for understanding the community structures and ecosystem functions

of the eastern Pacific Ocean. The economic and ecological role of *D. gigas*, its foraging strategies, migration patterns and population structure have drawn much interest recently, though knowledge of their whole life history remains limited (Markaida, 2006; Robinson et al., 2013).

In recent years, the stable isotopes (^{13}C and ^{15}N) have increasingly proved to be efficient intrinsic markers for investigating the trophic ecology of cephalopods (Cherel and Hobson, 2005; Ruiz-Cooley et al., 2010, 2011; Argüelles et al., 2012). This technique is based on the fact, that as predators consume prey, the carbon and nitrogen stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) of those predators fractionate systematically throughout the food web. Specifically, the change in $\delta^{13}\text{C}$ values of the predator are conservative (0–1‰), relative to the prey consumed, allowing identification of basal productivity or foraging locations while $\delta^{15}\text{N}$ values show a stepwise enrichment from prey to predators (2–5‰), providing a method to quantify trophic position (Post, 2002). Thus, the stable isotope composition of a predator's tissue is a reflection of its diet and environment for a certain period of time. A squid's gladius is a continuously growing, metabolically inert tissue that

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reflects the diet of the squid at the time of tissue synthesis, providing a continuous time series of diet and environment (Carlisle et al., 2015). Serial sampling of this accretionary structure for stable isotope analysis (SIA) is a convincing approach that can be used to study changes in diet and habitat use throughout the entire life history of an individual squid (Ruiz-Cooley et al., 2010, 2013; Lorrain et al., 2011). However, within marine ecosystems, differences in oceanographic and biogeochemical processes can cause strong temporal and spatial variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of primary production at the base of the food web (Rau et al., 1989; Somes et al., 2010). Relative to less productive oceanic waters, higher $\delta^{13}\text{C}$ values are found in productive nearshore regions, such as upwelling zones off Peru, because of the preferential uptake of ^{12}C by phytoplankton during photosynthesis (Kline 1999; Perry et al., 1999; Argüelles et al., 2012). A similar gradient in $\delta^{13}\text{C}$ values is also observed between latitudes, with high-latitude pelagic ecosystems typically having much lower $\delta^{13}\text{C}$ values than pelagic ecosystems at lower latitude (Rau et al., 1989). The spatial heterogeneity of $\delta^{15}\text{N}$ values is more complex for different sources of nutrient (i.e. nitrate, ammonium and N_2) and their corresponding biogeochemical cycling (i.e. N_2 fixation and denitrification) (Montoya, 2007; Somes et al., 2010). N_2 fixation drives waters with lower $\delta^{15}\text{N}$ baseline values, since the inputs (dissolved N_2) is near 0‰ and $\delta^{15}\text{N}$ values shows little variations during the biological uptake by phytoplankton (Montoya, 2007). In contrast, denitrification preferentially removes ^{15}N -depleted NO_3^- and leaves the ^{15}N -enriched residual nitrate (Voss et al., 2001). These differences will affect the baseline species and propagate up the food web (McMahon et al., 2013). *D. gigas* is a highly mobile species and its broad distribution may cross areas with strong gradients in biogeographic and biogeochemical characteristics and these gradient-driven isotopic differences will be preserved in the squid's tissues (Ruiz-Cooley et al., 2010, 2013; Lorrain et al., 2011).

Previous studies using jumbo squid gladius isotopic data, Ruiz-Cooley et al. (2010) observed strong evidence of geographic variation of *D. gigas* in the eastern Pacific Ocean. Lorrain et al. (2011) reported a large inter-individual variability in dietary and movement patterns. However, these studies did not consider time indeterminacy since the gladii were cut into several equidistant sections, and the time period represented by each section was unknown, which may have difficulty in accurately revealing the historical events occurring in the lifetime of *D. gigas*. Besides, little attention has been paid to the variation of gladius growth in these studies although the seasonal and bathymetric growth variability of gladius have often been observed (Perez et al., 2006; Schroeder and Perez, 2013).

In the present study, we incorporated statolith-derived age information with stable isotope data along the proostracum to (1) explore the feasibility of using a time-based continuous sampling method to back-calculate ontogenetic shift and possible migration patterns and (2) investigate potential temporal differences in trophic patterns of jumbo squid off the Exclusive Economic Zone (EEZ) of Peru under 2009–10 El Niño event.

2. Materials and methods

2.1. Squid sampling and age determination

Jumbo squids were randomly sampled from catches by commercial jigging vessels operating during 2009, 2013 and 2014 off the Peruvian EEZ (Fig. 1). All sampled specimens were frozen whole on board immediately, then defrosted in the laboratory. Mantle length (ML) and body weight (BW) were recorded to the nearest 1 mm and 1 g, respectively. Age was determined by counting the number of growth increments in the statolith (Perez et al., 2006;

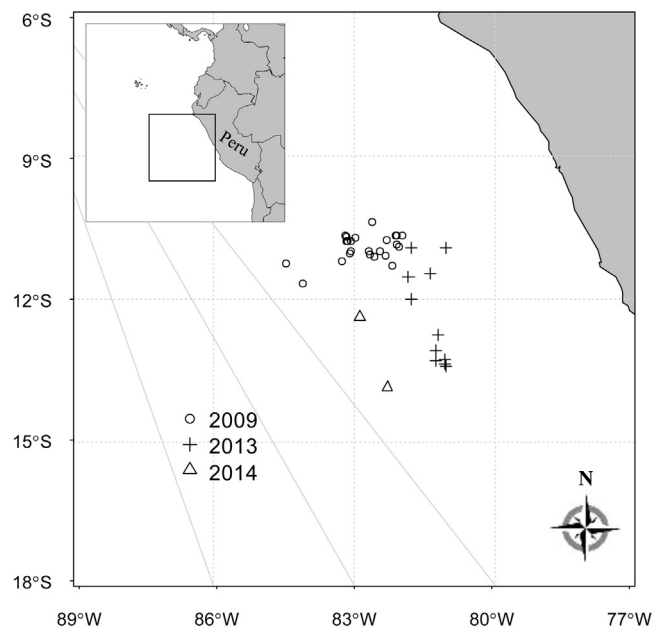


Fig. 1. Sampling locations of *Dosidicus gigas* off the Peruvian EEZ.

Arkhipkin et al., 2014). The number of increments was assessed by comparing three independent counts when the deviation was less than 10% of the mean (Jackson, 1994). The approximate hatching date was back-calculated using the difference between age and sampling date. A total of 290 individuals from the summer/autumn hatching cohort were selected.

The gladius of *D. gigas* consists of 3 morphological parts: rostrum, conus and proostracum (Bizikov, 1991). In this study, part of the proostracum was used while the other two parts were excluded for stable isotope analysis. The gladius was extracted from the back of the mantle cavity and cleaned in ultrasonic cleaner for 5 min to remove residual soft tissue with distilled water. The proostracum length (PL) was measured to the nearest 1 mm. Based on the growth equations of the proostracum (detailed information of the growth equations can be seen in statistical analysis), sections were cut consecutively every ten days with acetone washed fine scissors following the 'V' shape of the growth lines (Fig. 2). All sections were rinsed again with distilled water, freeze-dried at -55°C for ≥ 24 h, and homogenized into a fine powder using a Mixer mill MM440 (Retsch, Haan, Germany) prior to SIA.

2.2. Stable isotope analysis

A total of 45 individuals with a similar sampling date were selected for SIA. Detailed information of the samples is summarized in Table 1. 1.5 mg powder of each proostracum section was pooled using a 0.3 mg tin capsule and analyzed using an IsoPrime 100 isotope ratio mass spectrometer (IsoPrime Corporation, Cheshire, UK) and Vario Macro Elemental Analyser (Elementar Analysensysteme GmbH, Hanau, Germany). To calibrate the system and compensate for drift, international reference materials (USGS 24 (-16.049‰ v PDB), USGS 26 (53.7‰ v N_2) and a laboratory reference (protein, -26.98‰ v PDB and 5.96‰ v N_2)) were analyzed after every ten samples in triplicate, meanwhile a blank sample was run to clear off residual gases. Isotopic compositions of samples were expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using the equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N , R_{sample} and R_{standard} are the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ of the sample and the standard,

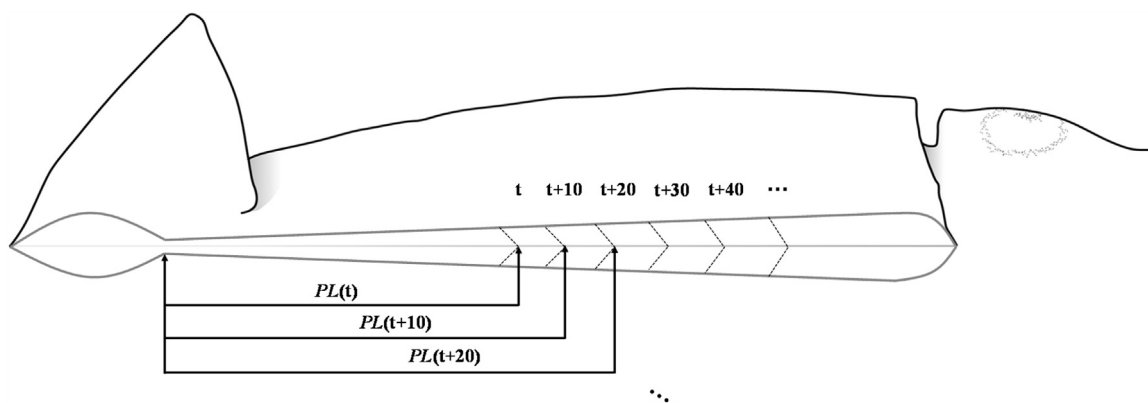


Fig. 2. Schematic figure of *D. gigas* gladius (adapted from Lorrain et al., 2011).

Table 1
Morphometry of gladius proostracum.

Year	Sex	N	ML/cm				PL/cm				Age/d	
			Max	Min	Mean	SD	Max	Min	Mean	SD	Max	Min
2009	F	101	52.0	22.0	35.4	6.5	37.4	17.2	26.4	5.1	413	176
	M	23	46.3	26.3	34.3	6.5	35.0	17.6	24.9	5.1	349	162
2010	F	13	41.2	20.7	29.8	5.8	37.0	16.2	23.5	5.5	288	165
	M	4	26.1	24.0	25.3	5.7	20.1	18.4	19.2	4.1	237	180
2013	F	87	38.8	22.2	27.0	3.5	29.0	17.4	21.0	2.3	273	126
	M	51	39.6	21.8	25.8	3.7	30.1	17.2	20.3	2.4	220	138

respectively. Analytical errors of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were approximately 0.05‰ and 0.06‰, respectively. Stable isotope analysis was conducted in the stable isotope laboratory of Shanghai Ocean University.

2.3. El Niño event indicator

We used the Oceanic Niño Index (ONI, based on a 3 month running mean of ERSST.v4 Sea surface temperature (SST) anomalies in the Niño 3.4 region (170°W to 120°W, 5°N to 5°S)) to predict the El Niño event (Huang et al., 2015). An El Niño event would have ONI values exceeding +0.5 °C for at least 5 consecutive months (Hoving et al., 2013; Fig. 3). The 2009–10 El Niño is known to be a strong Central-Pacific El Niño event (Lee and McPhaden, 2010). In order to determine the variation in the trophic dynamic of jumbo squid influenced by the 2009–10 El Niño event, two stages were considered: (i) stage 1 El Niño year, (individuals from 2009); (ii) stage 2 non-El Niño years (individuals from 2013 and 2014).

2.4. Statistical analysis

The relationship between PL and age was determined using linear regression analysis. Four growth function models (Linear, Exponential, Power and Logistic) were tested. We used the Akaike Information Criterion (AIC) (Akaike, 1974) for model selection. The AIC was obtained from the following equation:

$$\text{AIC} = -2 \times \ln(Z) + 2k + 2k \times (k + 1) / (n - k - 1)$$

where k equals the number of parameters, n equals the number of samples and Z equals the minimum residual sum of squares. The model with the lowest AIC value and largest R^2 (coefficient of determination) is considered to be the best model, but models within two AIC units of the lowest model perform as best model fits, those within four to seven units indicate considerably less support and models >10 units are considered to have no support (Logan et al., 2008).

Since each section recorded a ten-day period of squid growth, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each section may explain the niches of jumbo squid during the 10 days. Furthermore, the isotopic values of sections were grouped by the same time period and linear regression analysis was used to evaluate the relationship between the grouped isotopic values and age.

We used standard ellipse corrected area (SEA_C) to determine the isotopic niche width and overlap among different age-classes (Jackson et al., 2011; Carlisle et al., 2015). The SEA_C was proposed as a metric that was less sensitive to sample size and a much more robust method to estimate isotopic niche (Jackson et al., 2011). All statistical analyses were performed using R.

3. Results

3.1. Relationship between proostracum growth and age

The length data of 279 proostraca were collected (201 Female, 78 Male, ML 22–52 cm, Table 2) after 11 proostraca were ruptured during the extraction process. Assuming a deposit of one increment per day in the statolith (Arkhipkin et al., 2014), the estimated life span of the sampled squid ranged from 126 to 413 days old (Table 2). A high correlation was found between PL and age ($F_{1,556} = 13.46$, $p < 0.001$). Among the four models tested, the logistic model

$$PL = \frac{749.389}{1 + e^{-0.005(t-395.244)}}$$

performed the best fit with the lowest AIC and the highest R^2 values (Table 3). Since the minimum age in this study was 126 d, the proostraca were cut in succession starting from the position of 130 d (Table 2).

3.2. Trophic variations

A total of 45 individuals (14, 19 and 12 sampled from year 2009, 2013 and 2014, respectively) with a similar sampling date were selected for stable isotope analysis (Table 1, Fig. 4). 396 gladius

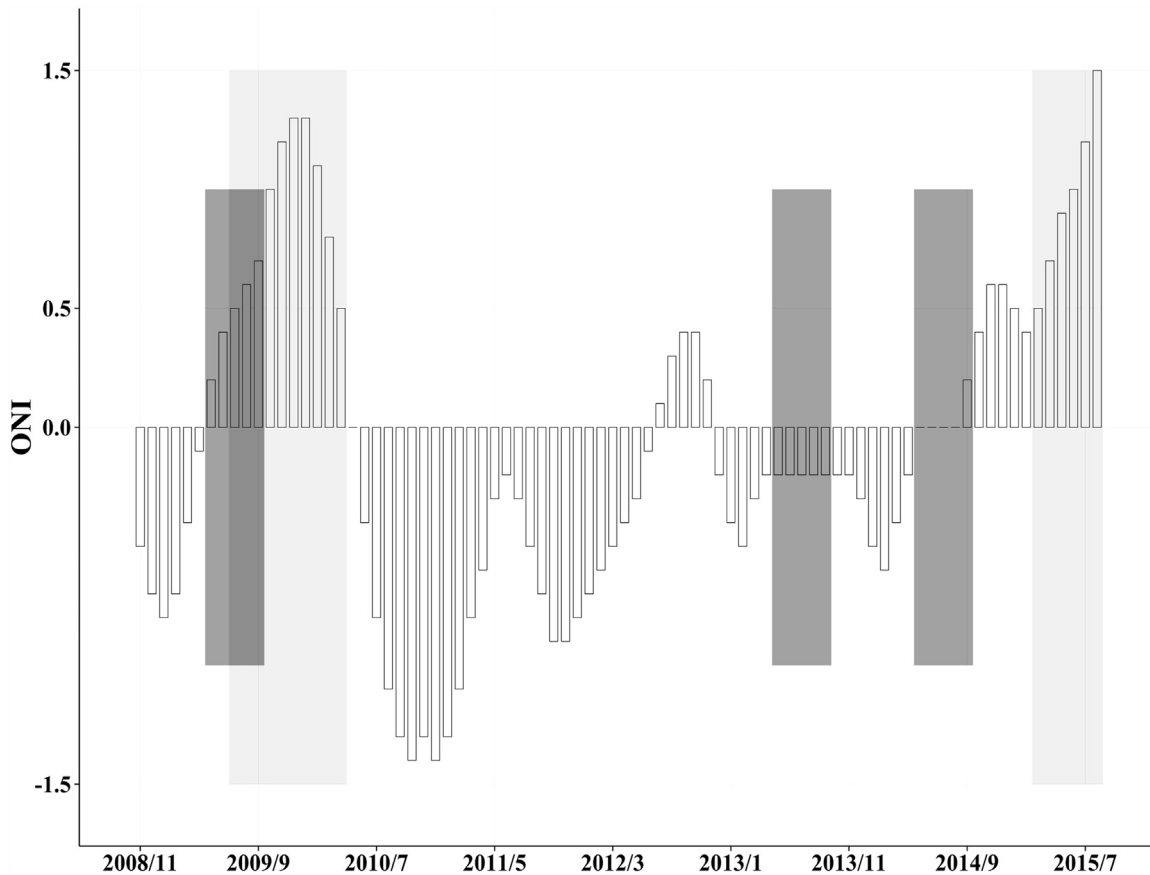


Fig. 3. Schematic illustration of the periods of stable isotope analysis (black shadow) in this study during different stages of El Niño events (gray shadow). ONIs were derived using the data from NOAA climate prediction center (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml).

Table 2

List of the selected models and diagnostic statistics for the relationship between proostracum length (PL) and age (t) of *D. gigas* off the EEZ of Peru.

Number	Model	Fitted function	R ²	AIC
1	$PL_t = a + bt$	$PL_t = 72.789 + 0.739t$	0.691	2308.345
2	$PL_t = ae^{bt}$	$PL_t = 121.629e^{0.003t}$	0.692	2307.865
3	$PL_t = at^b$	$PL_t = 5.350t^{0.703}$	0.685	2312.465
4	$PL_t = \frac{PL_{\infty}}{1+e^{-k(t-t_0)}}$	$PL_t = \frac{749.389}{1+e^{-0.005(t-395.244)}}$	0.693	2307.414

*The experimental results in this study cannot adopt the model to fit function.

sections were obtained with a maximum of 14 in one proostracum. Each section would represent a ten-day period of proostracum growing length. A significant difference in section $\delta^{15}N$ values were detected between the three years (ANOVA, $F_{2,397} = 7.49, p < 0.001$). No significant difference was observed between 2013 and 2014 individuals (t-test, $F_{1,236} = 0.15, p > 0.05$). However, the $\delta^{13}C$ values of individuals collected in both years were significantly lower than those of squid sampled in 2009 (t-test, $F_{1,398} = 37.10, p < 0.001$) (Table 4).

The variability in foraging habits was exhibited at population level by grouping the isotopic data of the proostracum sections of individuals from the same year and representing the same age period. For 2013 squid, both mean isotopic values of the grouped sections showed a significantly decreasing trend through time/age (Fig. 5, the trend of $\delta^{13}C$ values (C_{2013}): $R^2 = 0.33, F_{1,10} = 6.70, p < 0.05$, the trend of $\delta^{15}N$ values (N_{2013}): $R^2 = 0.93, F_{1,10} = 84.36, p < 0.01$). The same pattern was observed by 2014 individuals (C_{2014} : $R^2 = 0.81, F_{1,10} = 47.08, p < 0.01, N_{2014}$: $R^2 = 0.94, F_{1,10} = 17.31, p < 0.01$). However, small variations were observed in both $\delta^{13}C$ and $\delta^{15}N$ profiles of 2009 specimens (C_{2009} and N_{2009} , respectively) ($F_{1,12} = 0.08, p > 0.50, F_{1,12} = 4.50, p > 0.05$, respec-

tively). There were strong decreases in both $\delta^{13}C$ and $\delta^{15}N$ values of individuals from 2013 and 2014, starting approximately from Day 200 (Fig. 5).

3.3. Isotopic niche

The SEA_C of 2009 individuals (2.30‰²) was lowest compared with that of 2013 (3.59‰²) and 2014 squid (4.60‰²) (Fig. 6). A relatively high degree of overlap were observed between 2013 and 2014 (76.32%), 2014 and 2009 (77.39%), while overlaps between 2013 and 2009 (52.61%) was relatively small.

4. Discussion

In this study, a total of 45 proostraca were cut consecutively, based on the age data obtained from the statolith. Furthermore, the potential impacts of El Niño events on the trophic patterns of *D. gigas* were investigated using the isotopic data along the proostracum. Our results found strong individual-specific variation in stable carbon and nitrogen isotope values of this highly migratory species.

Table 3
Biological parameters of *D. gigas* sampled for stable isotope analysis.

Serial Number	Sampling location	Body mass(g)	Mantle length (cm)	Sampling date	Age (d)	Hatching date
G1	82°40'W, 11°03'S	950.6	32.3	2009/09/28	278	2008/12/24
G2	82°05'W, 10°39'S	1260.3	34.9	2009/09/08	273	2008/12/09
G3	82°05'W, 10°39'S	1678.0	36.0	2009/09/08	251	2008/12/31
G4	82°05'W, 10°39'S	2185.0	39.9	2009/09/08	274	2008/12/08
G5	82°36'W, 10°21'S	1208.0	33.8	2009/09/06	248	2009/01/01
G6	82°36'W, 10°21'S	889.8	30.4	2009/09/06	213	2009/02/05
G7	82°36'W, 10°21'S	1365.6	35.1	2009/09/06	270	2008/12/10
G8	82°36'W, 10°21'S	1034.9	32.4	2009/09/06	237	2009/01/12
G9	83°17'W, 11°12'S	974.6	31.7	2009/09/13	237	2009/01/19
G10	83°12'W, 10°38'S	1486.5	36.9	2009/09/22	246	2009/01/19
G11	82°36'W, 10°21'S	1156.9	33.7	2009/09/06	225	2009/01/24
G12	84°29'W, 11°14'S	1448.8	35.6	2009/09/14	260	2008/12/28
G13	83°11'W, 10°40'S	1803.0	38.2	2009/09/21	279	2008/12/16
G14	82°04'W, 10°49'S	927.8	30.4	2009/09/21	240	2009/01/24
G15	81°21'W, 11°27'S	987.1	33.4	2013/08/25	258	2012/12/10
G16	81°00'W, 13°25'S	483.6	26.0	2013/09/03	195	2013/02/20
G17	81°00'W, 13°25'S	410.5	24.9	2013/09/03	181	2013/03/06
G18	81°45'W, 10°54'S	496.3	26.6	2013/08/18	190	2013/02/09
G19	81°13'W, 13°18'S	361.0	23.6	2013/09/11	177	2013/03/18
G20	81°45'W, 12°00'S	719.6	29.4	2013/08/09	208	2013/01/13
G21	81°45'W, 12°00'S	843.0	30.8	2013/08/09	242	2012/12/10
G22	81°01'W, 13°17'S	507.1	26.5	2013/08/30	180	2013/03/03
G23	81°01'W, 13°17'S	515.4	27.0	2013/08/30	195	2013/02/16
G24	81°01'W, 13°17'S	441.0	25.4	2013/08/30	186	2013/02/25
G25	81°11'W, 12°46'S	467.1	26.6	2013/09/19	193	2013/03/10
G26	81°49'W, 11°31'S	1090.8	33.8	2013/09/15	231	2013/01/27
G27	81°49'W, 11°31'S	1229.0	35.4	2013/09/15	251	2013/01/07
G28	81°13'W, 13°06'S	404.0	24.7	2013/08/15	179	2013/02/17
G29	81°13'W, 13°06'S	314.3	22.9	2013/08/15	167	2013/03/01
G30	81°01'W, 13°17'S	540.5	28.1	2013/08/30	169	2013/03/14
G31	81°01'W, 13°17'S	348.0	24.0	2013/08/30	176	2013/03/07
G32	81°45'W, 10°54'S	587.2	28.0	2013/08/18	200	2013/01/30
G33	81°45'W, 10°54'S	324.0	23.3	2013/08/18	165	2013/03/06
G34	82°17'W, 13°53'S	615.0	26.8	2014/08/18	205	2014/01/25
G35	82°17'W, 13°53'S	768.4	26.7	2014/08/18	210	2014/01/20
G36	82°17'W, 13°53'S	864.5	30.2	2014/08/18	240	2013/12/21
G37	82°17'W, 13°53'S	643.1	27.9	2014/08/18	206	2014/01/23
G38	82°53'W, 12°23'S	925.1	28.6	2014/08/21	214	2014/01/19
G39	82°53'W, 12°23'S	819.2	31.4	2014/08/21	250	2013/12/14
G40	82°53'W, 12°23'S	985.5	32.8	2014/08/21	234	2013/12/29
G41	82°53'W, 12°23'S	703.7	29.6	2014/08/21	224	2014/01/9
G42	82°53'W, 12°23'S	705.8	29.5	2014/08/21	240	2013/12/24
G43	82°53'W, 12°23'S	661.2	28.1	2014/08/21	235	2013/12/29
G44	82°53'W, 12°23'S	641.2	29.0	2014/08/21	218	2014/01/15
G45	82°53'W, 12°23'S	811.5	29.1	2014/08/21	229	2014/01/04

4.1. Trophic variation

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values showed variable isotopic shifts along the proostracum for all squid instead of showing consistently increasing or decreasing patterns, and expressed a range of 3.4‰ for $\delta^{13}\text{C}$ values and 9.4‰ for $\delta^{15}\text{N}$ values though the proostracum were cut serially starting from the age of Day 130. Such isotopic variation was similar to previous study on gladius isotopic data of this species in offshore waters of Northern Peru ($\delta^{13}\text{C}$: 2.7‰; $\delta^{15}\text{N}$: 8.2‰, Lorrain et al., 2011). Since the assimilated diet and geographic variation of isotopic baseline were incorporated along the proostracum during growth, the isotopic variability along the proostracum represents a record of the jumbo squid's foraging patterns (Ruiz-Cooley et al., 2010). The isotopic values of each proostracum section would reflect the shifts in *D. gigas* feeding activities for 10 days. Hence, the observed intra-individual isotopic variation may suggest their opportunistic feeding behavior and relatively complex life span (Nigmatullin et al., 2001; Ruiz-Cooley et al., 2010; Lorrain et al., 2011).

Another possible explanation of variation in stable isotopes along the proostracum could be squid moving and foraging in areas with different isotopic baseline values, since this species is expected to be highly migratory as it grows (Nigmatullin et al., 2001). The gradients in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between primary

producers in different geographical locations have been well recognized (Rau et al., 1989; McMahon et al., 2013; Somes et al., 2010). Compared to less productive offshore waters, higher $\delta^{13}\text{C}$ values are associated with high productivity nearshore waters, such as upwelling regions (Graham et al., 2010) and $\delta^{15}\text{N}$ values reflect the regional characteristic of nitrogen metabolism such as nitrogen-fixing or denitrification (Takai et al., 2000; Montoya, 2007). The eastern South Pacific Ocean off Peru has the largest upwelling regions and the most intense shallow oxygen minimum zones (OMZs) in the world (Ruiz-Pino and Paulmier, 2009; Stramma et al., 2012). In upwelling regions, nitrate-rich deep water supplied to the surface and cause increasing phytoplankton productivity and a correspondingly higher $\delta^{13}\text{C}$ value than in non-upwelling oceanic waters, since the preferential uptake of ^{12}C by phytoplankton during photosynthesis (Rau et al., 2001; Echevin et al., 2008). In OMZs, the absence of adequate O_2 facilitates the denitrification activity which preferentially consumes ^{14}N -nitrite and increases the baseline $\delta^{15}\text{N}$ value (Voss et al., 2001). For instance, Lorrain et al. (2011) detected a 5.2‰ $\delta^{15}\text{N}$ baseline difference along a 6° latitudinal gradient. Such baseline isotopic variation along the Peruvian coast can be propagated up the food chain and integrated in jumbo squid (Argüelles et al., 2012).

At population level, based on the results of stomach content analysis, Nigmatullin et al. (2001) revealed a continually change

Table 4

The summary of isotopic values and C/N mass ratios along the proostracum for all squid.

Serial Number	Number of sections	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)				C/N			
		Mean	SD	Maximum	Minimum	Mean	SD	Maximum	Minimum	Mean	SD	Maximum	Minimum
G1	14	-16.93	0.22	-16.52	-17.20	10.81	0.51	12.03	10.13	3.62	0.02	3.66	3.58
G2	14	-16.96	0.32	-16.40	-17.41	11.29	1.47	13.67	9.27	3.74	0.02	3.76	3.68
G3	11	-16.52	0.21	-16.16	-16.83	11.25	1.47	12.43	9.16	3.69	0.03	3.73	3.65
G4	14	-16.62	0.24	-16.16	-17.19	13.35	1.04	14.50	11.49	3.71	0.03	3.75	3.64
G5	11	-17.37	0.21	-17.09	-17.85	9.52	0.34	9.97	8.99	3.69	0.08	3.80	3.52
G6	9	-17.75	0.34	-17.19	-18.23	7.53	0.73	8.56	6.11	3.70	0.03	3.75	3.64
G7	10	-16.86	0.37	-16.03	-17.23	9.34	1.50	10.96	6.54	3.67	0.06	3.77	3.59
G8	10	-17.62	0.18	-17.35	-17.85	7.18	0.44	7.97	6.56	3.66	0.02	3.69	3.61
G9	12	-16.62	0.29	-15.95	-16.94	11.21	0.94	12.79	10.25	3.65	0.05	3.70	3.54
G10	10	-17.43	1.22	-15.95	-18.57	9.05	1.51	11.48	7.09	3.69	0.04	3.79	3.62
G11	13	-17.05	0.20	-16.72	-17.40	10.68	0.98	12.90	9.84	3.69	0.04	3.74	3.61
G12	11	-17.11	0.21	-16.92	-17.72	10.17	0.55	10.93	9.04	3.67	0.01	3.69	3.66
G13	14	-16.90	0.28	-16.60	-17.44	11.22	0.56	11.91	9.91	3.69	0.04	3.78	3.66
G14	9	-18.03	0.38	-17.54	-18.64	7.93	1.22	9.81	6.51	3.73	0.04	3.78	3.67
G15	12	-16.96	0.67	-15.72	-17.73	9.30	0.84	10.50	8.16	3.72	0.02	3.76	3.68
G16	6	-17.48	0.65	-15.72	-18.97	10.89	0.58	11.69	10.18	3.71	0.01	3.73	3.70
G17	5	-18.24	0.26	-17.93	-18.61	10.09	0.51	10.86	9.51	3.75	0.01	3.76	3.73
G18	6	-17.65	0.11	-17.51	-17.81	10.17	0.10	10.32	10.00	3.71	0.03	3.75	3.69
G19	4	-18.17	0.45	-17.54	-18.50	11.85	0.84	12.94	11.11	3.61	0.02	3.63	3.59
G20	7	-17.53	0.20	-17.31	-17.86	7.76	1.49	9.91	6.26	3.72	0.02	3.74	3.70
G21	11	-17.30	0.26	-16.74	-17.69	12.30	0.92	13.67	10.93	3.75	0.03	3.78	3.72
G22	5	-17.89	0.37	-17.49	-18.45	12.76	0.39	13.33	12.31	3.73	0.04	3.75	3.66
G23	6	-17.81	0.10	-17.65	-17.96	11.28	0.24	11.62	11.01	3.69	0.05	3.71	3.60
G24	5	-17.66	0.16	-17.49	-17.93	11.69	1.03	13.39	10.65	3.65	0.06	3.68	3.55
G25	6	-18.12	0.46	-17.36	-18.54	12.19	0.46	13.06	11.81	3.77	0.05	3.84	3.70
G26	10	-17.38	0.23	-17.08	-17.79	11.32	0.85	12.74	10.38	3.68	0.03	3.72	3.65
G27	12	-17.03	0.68	-16.17	-18.23	10.44	1.78	13.00	8.13	3.65	0.04	3.72	3.61
G28	4	-16.37	0.31	-16.00	-16.71	11.33	0.27	11.57	11.03	3.73	0.05	3.77	3.70
G29	3	-17.42	0.20	-17.19	-17.58	11.55	0.83	12.44	10.78	3.77	0.02	3.78	3.76
G30	3	-17.39	0.44	-17.08	-17.89	12.79	0.62	13.42	12.18	3.68	0.04	3.72	3.65
G31	4	-17.81	0.23	-17.50	-18.07	12.37	0.61	13.27	11.97	3.67	0.05	3.70	3.60
G32	7	-16.64	0.86	-15.82	-17.85	11.06	1.27	12.2	8.65	3.70	0.02	3.72	3.68
G33	3	-17.96	0.16	-17.80	-18.11	8.39	0.60	9.02	7.83	3.73	0.01	3.74	3.72
G34	8	-17.90	0.36	-17.39	-18.36	8.04	0.90	9.29	6.94	3.83	0.06	3.93	3.74
G35	9	-17.90	0.42	-17.17	-18.43	9.91	1.67	12.28	7.94	3.87	0.07	3.99	3.78
G36	10	-16.96	0.29	-16.47	-17.51	10.23	1.44	11.97	7.74	3.93	0.05	4.01	3.86
G37	9	-17.40	0.45	-16.81	-18.15	10.09	2.59	13.37	7.46	3.83	0.04	3.88	3.78
G38	9	-17.89	0.58	-17.13	-19.00	9.21	2.27	12.74	6.46	3.79	0.07	3.93	3.69
G39	11	-17.23	1.07	-15.56	-19.00	8.98	2.07	12.35	6.19	3.75	0.06	3.84	3.63
G40	12	-17.57	0.66	-16.41	-18.57	11.67	3.06	14.37	7.32	3.83	0.05	3.93	3.76
G41	10	-17.12	0.74	-16.09	-18.32	8.11	1.38	10.00	6.53	3.76	0.06	3.84	3.67
G42	9	-17.35	0.67	-15.92	-18.24	9.84	2.55	12.81	6.29	3.84	0.03	3.90	3.79
G43	8	-17.22	0.44	-16.21	-17.76	10.43	2.15	13.49	7.53	3.66	0.15	3.85	3.36
G44	9	-17.51	0.32	-17.03	-17.99	7.68	0.47	8.25	6.75	3.82	0.06	3.94	3.75
G45	11	-17.49	0.62	-16.89	-18.48	11.98	1.58	13.60	8.89	3.89	0.10	4.07	3.77

from low to high trophic level prey during the growth of *D. gigas*. Ruiz-Coolley et al. (2006) also found *D. gigas* in the Gulf of California tended to prey at a higher trophic level during ontogenesis from the SIA results of muscle and beak wing tissues. However, such patterns were not fully reflected by our data. In our study, most individuals from 2013 and 2014 had decreasing but variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along the proostracum, suggesting they were moving from ^{15}N -enrich to ^{15}N -depleted areas, or increasingly feeding on prey from lower trophic levels during the time period studied. It was reported that jumbo squid have adapted to spawning in less productive offshore waters to avoid predation (Argüelles et al., 2012). Such behavior causes the seasonal ontogenetic migration whereby juveniles move from offshore to nearshore in their growing period and large mature individuals move from inshore to offshore for spawning (Nesis, 1983; Nigmatullin et al., 2001). Since the isotopic values along the proostracum in our study started from the age of Day 130, their decreasing patterns (especially from Day 200) might be attributed to their spawning migration. *D. gigas* was reported to start its spawning migration in summer and autumn (Nigmatullin et al., 2001; Keyl et al., 2010) and during the time periods of our study the isotopic values were indeed during autumn and winter time (May to September). Argüelles et al. (2012) revealed an

increasing trend in $\delta^{15}\text{N}$ values of *D. gigas* muscle tissue from north to south in Peru waters with an 8‰ $\delta^{15}\text{N}$ difference from 3° to 18°S, which was similar with the $\delta^{15}\text{N}$ range of 9.4‰ for our samples. Such result was also in agreement with the change of latitude gravity center of the fishing effort of *D. gigas*, moving northwestward off Peru during May to September (Liu et al., 2013). Besides, Alegre et al. (2014) found that the contribution of small mesopelagic fish and Euphausiids to the diet of *D. gigas* increases with the decreasing contribution of cephalopoda during ontogenetic migration in normal years, moving from productive nearshore areas to relatively oligotrophic offshore waters and the mesopelagic fish and Euphausiids generally have a lower trophic level relative to cephalopoda. These studies indeed supported the hypothesis that our samples might migrate from the southeast of the sampling locations (^{15}N -enrich waters) to the spawning ground (^{15}N -depleted waters), and suffered the impact of a decline in trophic level of diet composition.

4.2. Potential impacts of El Niño

There was no discernible trend detected for either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values along the proostracum for the 2009 individuals, suggesting a considerable difference in feeding or habitat use relative to the 2013

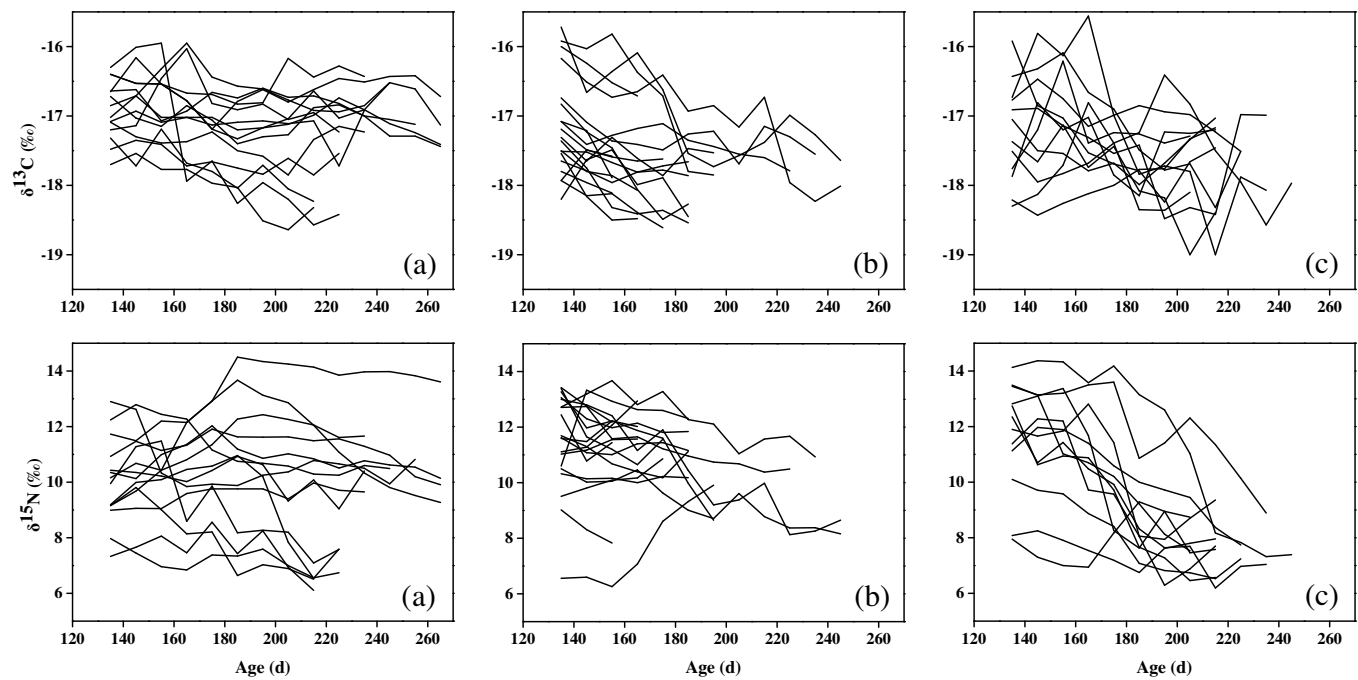


Fig. 4. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along the proostracum of *D. gigas* from 2009 (a), 2013 (b) and 2014 (c).

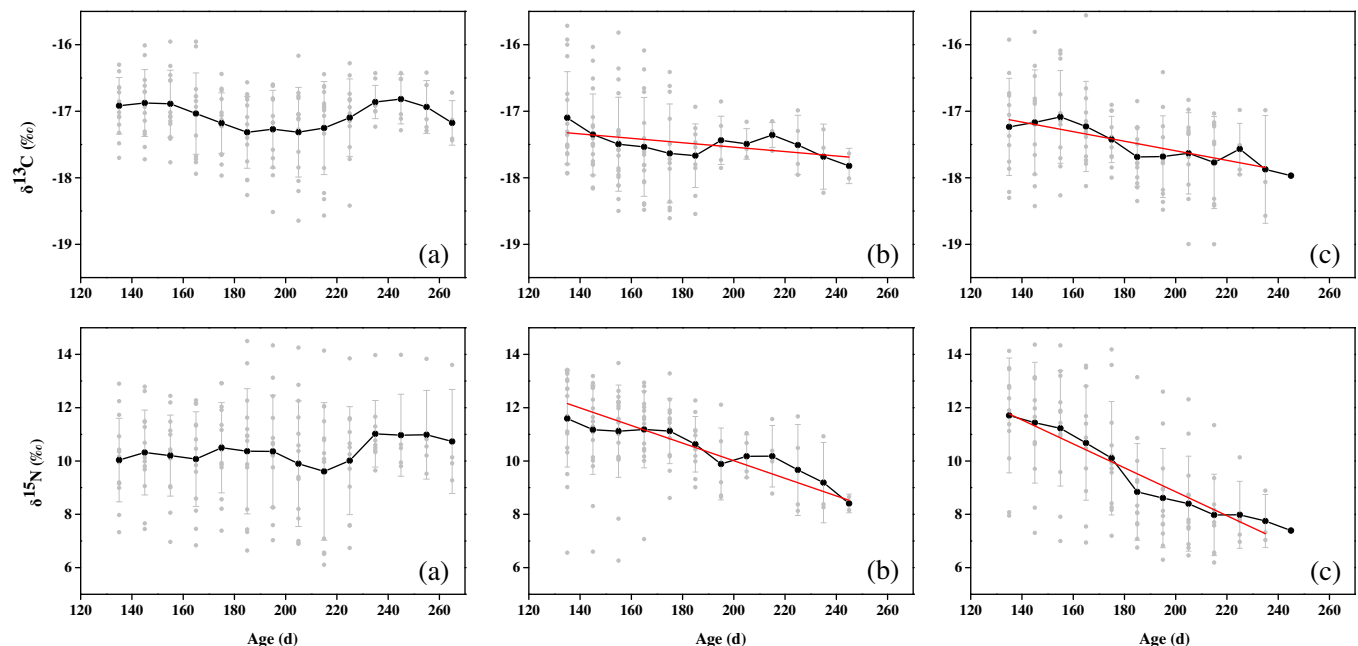


Fig. 5. Ontogenetic time series of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and mean (1SD) values for each ten-day period of 2009 (a), 2013 (b) and 2014 (c). Lines represent significant relationships.

and 2014 squid. In addition, the SEA_C of the 2009 squid yielded the smallest value among the years as well, indicating that *D. gigas* in 2009 had a smaller trophic niche variation compared with the 2013 and 2014 population, with similar body size during the different stages of development of an El Niño event, although there was a relatively high degree of overlap among the samples over three years (Fig. 6). One possible explanation of the difference of 2009 individuals could be the shortened horizontal migration. According to the ONI index, 2009 was known as an El Niño year when the slackening wind trend strengthened the warm water of the equatorial undercurrent southward, pushing the subtropical surface current much closer to the Peruvian coast, which in turn narrowed the nutrient-

enriched cold mixing waters and weakened the coastal upwelling effects (Keyl et al., 2008). Such changes in water mass distributions may lead to diminishing primary production resulting in the depletion of pelagic fish resources which may move to more productive nearshore areas (Ballón et al., 2008; Xu et al., 2013). Changes in environmental condition and food availability might be the decisive factor in directly causing a restriction of horizontal migration area of *D. gigas*. Ichii et al. (2002) observed an increased abundance of jumbo squid close to the coast of the Costa Rica Dome (9°N; 89°W) during El Niño conditions. In addition, indoor experiments revealed that the eggs of *D. gigas* can only successfully develop at water temperatures between 15 and 25 °C as larvae and small-size squid have

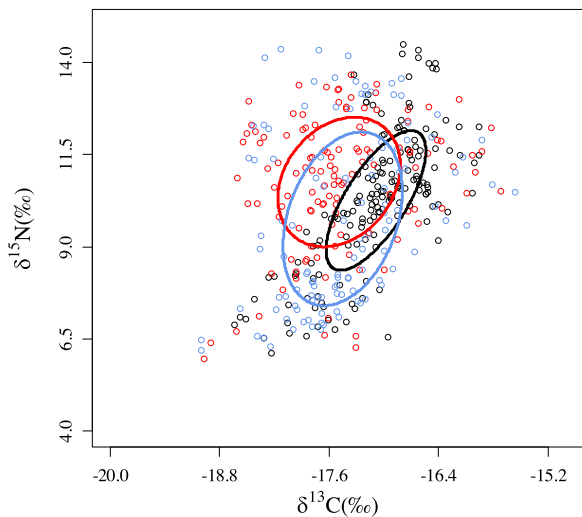


Fig. 6. Bi-plots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along the proostracum. Solid lines enclose the standard ellipse areas (SEAc), showing the isotopic niche of *D. gigas* from 2009 (black), 2013 (red) and 2014 (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a lower thermal tolerance than adult squid (Staaft et al., 2011). Such thermal requirement also raises the hypothesis that during “normal” years, offshore transport of surface water leads to entrainment of planktonic eggs and larvae away from the shelf towards the Central Pacific Ocean where they are dispersed so the cohort develops over a large area. During El Niño conditions, paralarvae are retained near the shelf and the population reaches high densities because of the reduced offshore transport (Anderson and Rodhouse, 2001; Argüelles and Tafur, 2010; Ruiz-Coolley et al., 2013).

Another possible explanation might be the increasing energy cost for vertical migration, since the El Niño events also have a potential impact on their vertical migrations (Zeidberg and Hamner, 2002; Hoving et al., 2013). Seibel (2013) reported that *D. gigas* has adapted to a low dissolved oxygen environment and prefers to inhabit OMZs where denitrification is strong (Stewart et al., 2013). It has been shown that *E. ringens* and *V. lucetia* often comprise an important percentage of the diet of *D. gigas* juveniles and adults (Markaida, 2006; Alegre et al., 2014). However, these fish cannot enter the OMZs since they are not adapted to anoxia (Alegre et al., 2014). The upper OMZs boundary shows a significant deepening which is derived from subsided upwelling in an El Niño occurrence, which may increase the energy demands as *D. gigas* moves up to the surface water to forage (Levin et al., 2002). Moreover, using electronic tags, Gilly et al. (2006) reported a shortened foraging time of *D. gigas* since they will rapidly dive into deep water after excursions into warm near-surface water. Keyl et al. (2008) hypothesized a compressed horizontal foraging area of *D. gigas* in El Niño years due to the alternation of current circulation. Our results here indeed supported this hypothesis that such decline in the trophic niche of space-time scales was reflected by the decreasing SEAc in 2009 (Jackson et al., 2011).

5. Conclusions

In this study, we report here the first results on the isotopic information in jumbo squid gladii with growth information obtained from the statolith to interpret the relationship between individuals' independent isotopic data and historical events which had occurred in their lifetime. As feeding opportunists, it is likely that the isotopic values of *D. gigas* may be influenced much more by their migration behavior that crosses several regions with distinct baseline isotopic values, during which diet switch might occur. Although our age data

started from Day 130, strong inter-individual variation was found and significant differences in sequential isotopic values and isotopic niches during El Niño events were identified. These results would support our general hypothesis that time-based consecutive sampling of gladii can back-calculate the ontogenetic shift and possible migration patterns of squid more precisely and comprehensively. Our results furthermore reinforce the evidence of the *D. gigas* foraging area being influenced by El Niño events and not simply based on fisheries catch data. Future steps are needed to (1) increase the sampling size of each representing year with more small individuals to construct year-specific proostracum growth model and increase their accuracy; (2) shorten the time interval represented by each section, and (3) better discriminate the isotopic variation related to shifting habitat baselines vs. trophic position using amino acid stable isotope analysis. Above all, incorporating age data with biochemical tracers along the proostracum will be a good way to differentiate subpopulations and study the adaption in trophic ecology of squid due to changes in the climate.

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