



Spatial variations in beak structure to identify potentially geographic populations of *Dosidicus gigas* in the Eastern Pacific Ocean



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ABSTRACT

We explored an approach to using morphological variables of squid body and beaks to identify different geographic populations for *Dosidicus gigas*. We tested this approach using a total of seventeen morphological variables of body and beaks measured for 1490 squids sampled outside the exclusive economic zone (EEZ) waters off Ecuador, Peru and Chile. Linear regression analysis showed significant and positive relationships between beak morphometric variables and mantle lengths. All measured beak variables were significantly different among the three regions ($p < 0.001$), with samples from the areas off Chile and Ecuador having the largest and smallest beaks, respectively. The morphometrics of squid beaks showed a significant sexual dimorphism and were useful for sex determination ($p < 0.001$), although considerable overlaps were found in the scatter-plots. Hard structure (i.e., beaks) variables were shown more effective than soft body in population discrimination, although a stepwise discriminant analysis (SDA) suggested that both the body and beak morphometric variables are useful for the geographic population discrimination. We found that the standardized beak and body variables are more effective in separating *D. gigas* potentially geographic populations than the original variables.

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1. Introduction

The Jumbo flying squid, *Dosidicus gigas* (d'Orbigny, 1835), is an endemic species generally distributed from 40°N to 45°S in the coastal and pelagic waters of Eastern Pacific Ocean (Nigmatullin et al., 2001). High abundance was found in the waters from southern region of the California Current system to northern area of the Humboldt Current system. It supports some of the most important regional fisheries (Morales-Bojórquez et al., 2001; Keyl et al., 2008; Roper et al., 2010). A large scale international fishery was developed by Asian countries off the EEZ waters since the early 1990s (Taipei et al., 2001; Ichii et al., 2002; Liu et al., 2010). China first targeted the squid in 2001 off the Peruvian EEZ (Ye and Chen, 2007), and fishing grounds have since been expanded to Chilean, Costa Rican and Ecuadorian EEZs (Liu et al., 2010; Chen et al., 2013).

Understanding the population structure and connectivity of marine animals is critical for studying their population dynamics and developing effective conservation and sustainable management strategies (Thorrold et al., 2001; Gillanders, 2002). For *D. gigas*, the intra-specific population structures are complicated and no consensus has been reached by scientists to date. Overall, size-, migratory-, spawning- and molecule-based groups were defined, respectively, in different studies (Clarke and Paliza, 2000; Nigmatullin et al., 2001; Sandoval-Castellanos et al., 2007; Chen et al., 2010).

Several methods have been proposed for population discrimination, ranging from molecular markers (Ibáñez et al., 2011), tagging (Cadrin et al., 2005), nature (e.g. parasite fauna analysis, Shukhgalter and Nigmatullin, 2001; Pardo-Gandarillas et al., 2014) and chemical tags (e.g. trace element and stable isotope analysis, Ruiz-Cooley et al., 2013) to morphometrics and meristics (Cadrin et al., 2005). Morphometric analysis is perhaps the most frequently employed and cost-effective method to study fish geographic variations and identify fish population structure. Multivariate discriminant analysis of the morphological characteristics of cephalopod species, in particular genus *Loligo*, revealed patterns of spatial variation (Pineda et al., 2002; Liao et al., 2010), which

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Table 1
Summary information of sampled *D. gigas*.

Geographic population	Sampling date	Coordination	Sampled vessel	ML (mm)	N
Ecuador	Apr. to May, 2012	114°00′–120°00′W, 5°00′S–3°00′N	Ning Tai 1	206–457	488
Peru	Sep. 2008 to Feb. 2009 Jul. to Oct. 2009	82°05′–85°30′W, 10°32′–13°32′S 81°57′–84°29′W, 10°59′–11°17′S	New Century 52 Feng Hui 16	209–499 218–516	193 387
Chile	May 2008, Apr. to May 2010 Apr. to Jun. 2010	75°00′–79°30′W, 20°00′–24°00′S 75°03′–77°50′W, 24°50′–29°25′S 75°05′–79°21′W, 24°04′–28°56′S	Zhe Yuanyu 807 Feng Hui 16 Xin Jili 8	327–485 370–488 355–530	226 47 149

allowed for the identification of population structure based on body morphology. Because cephalopods show the high plasticity of morphology, morphometric studies of hard structures such as inner shell, statolith and beaks have been particularly useful for population discrimination (Pierce et al., 1994; Neige and Boletzky 1997; Vega et al., 2002; Doubleday et al., 2009).

Beaks of the Jumbo flying squid occur frequently in the stomach of sperm whales and other predators, suggesting that the squid play a vital role in the ecosystems (Ruiz-Cooley et al., 2006). Beak sizes, shapes and pigmentations were firstly described in the 1980s (Wolff, 1982, 1984), and several recent studies were focused on analyzing microstructure of beaks and estimating squid trophic positions (Ruiz-Cooley et al., 2006; Miserez et al., 2007). The jumbo flying squid, widely distributed in the Eastern Pacific Ocean, has a complex intraspecific population structure. However, studies attempting to identify its geographic structures have been limited (Liu et al., 2013a).

In this study, the morphometric variables of *D. gigas* beaks and body collected along the EEZ waters off Ecuador, Peru and Chile in the Eastern Pacific Ocean were analyzed. We quantified morphology of beaks (hard structure) and body (soft tissues) to evaluate if these morphological variables can be used to separate different geographic populations. The effectiveness of using the beaks and body in distinguishing geographic populations was evaluated. This study can provide an alternative approach to identifying *D. gigas* stock structure.

2. Materials and methods

Samples of *D. gigas* used in this study were collected randomly from the catch by the Chinese jigging vessels in 2008, 2009, 2010 and 2012 from three different geographic areas, waters off EEZs of Ecuador (488 individuals with 335 females and 153 males), Peru (580 individuals with 467 females and 113 males) and Chile (422 individuals with 294 females and 128 males) in the Eastern Pacific Ocean (Table 1, Fig. 1). We referred the *D. gigas* of these three areas as three geographic populations in this study. Frozen squids were defrosted in the lab and beaks were extracted from buccal mass. Sex was identified and maturity stages were determined by visual evaluation according to an approach defined by Lipinski and Underhill (1995). Following body morphological measurements were recorded to the nearest 1 mm: dorsal mantle length (ML), mantle width (MW), fin length (FL), fin width (FW), head width (HW), tentacle length (TL), and tentacular club length (CL) (Fig. 2). The following beak morphometric variables were measured with digital calipers to 0.01 mm: upper hood length (UHL), upper crest length (UCL), upper rostrum length (URL), upper lateral wall length (ULWL), upper wing length (UWL), lower hood length (LHL), lower crest length (LCL), lower rostrum length (LRL), lower lateral wall length (LLWL), and lower wing length (LWL) (Fig. 2).

A simple linear regression was used to describe the relationship between the log transformed beak variables and the logarithmic ML. An analysis of variance (ANOVA) and a multivariate analysis of variance (MANOVA) were conducted to evaluate spatial variability of beak morphological variables. Both principal component analysis

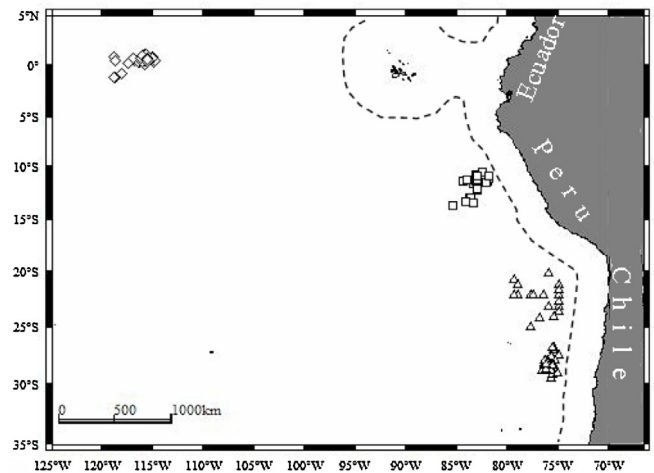


Fig. 1. Sampling locations for *D. gigas* outside EEZ (broken line) waters off Ecuador (diamond), Peru (rectangular) and Chile (triangle) in the Eastern Pacific Ocean.

(PCA) and stepwise discriminant analysis (SDA) were used to examine the variation of beak morphology between females and males. Both body and beak morphometric variables were used to discriminate samples from the three geographic populations using SDA. In

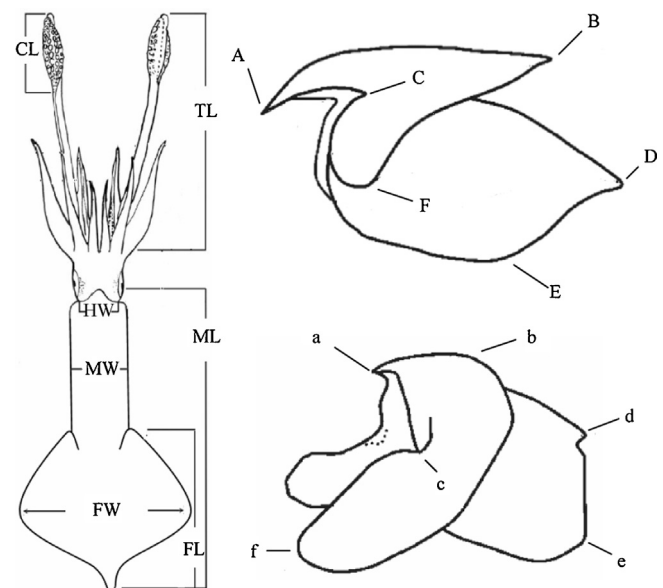


Fig. 2. Schematic diagram showing the body and beak morphometric variables measured for population discrimination. Left panel: ML dorsal mantle length, MW mantle width, FL fin length, FW fin width, HW head width, TL tentacle length, CL tentacular club length. Right panel: (A–B) is UHL upper hood length, (A–C) is UCL upper crest length, (A–D) is URL upper rostrum length, (A–E) is ULWL upper lateral wall length, (A–F) is UWL upper wing length, (a–b) LHL is lower hood length, (a–c) LCL lower crest length, (a–d) is LRL lower rostrum length, (a–e) is LLWL lower lateral wall length, (a–f) is LWL lower wing length.

Table 2The percentages of correct sex classification and values of Wilks' λ .

	Ecuador		Peru		Chile	
	Female	Male	Female	Male	Female	Male
Female	60.6%	39.4%	47.8%	52.2%	62.2%	37.8%
Male	26.8%	73.2%	27.4%	72.6%	34.4%	65.6%
Final	64.5%		52.6%		63.3%	
Wilks' λ	0.840		0.976		0.902	

order to remove the impacts of sizes, SDA was done with standardized beak morphometric variables to identify the variables that can be used to effectively identify samples from the three geographic populations (Chen et al., 2012a). The UHL was chosen as the independent variable to standardize the other variables of beaks (Chen et al., 2012a). The data were described by the following allometric model:

$$\ln(y) = \ln(a) + b \ln(\text{UHL}) + \varepsilon \quad \varepsilon \sim N(0, \sigma^2) \quad (1)$$

where y is the value of the other morphometric variables of beaks except for UHL, a and b are the parameters to be estimated and σ^2 is the variance for the normally distributed unexplained errors ε .

The value of standardized morphometric variables can be estimated from the following formula derived from model (1):

$$\varepsilon = \ln\left(\frac{y}{a\text{UHL}^b}\right) \quad (2)$$

The standardized morphometric variables were represented by adding a lower case letter "s" after each variable, i.e. UCLs, URLs, ULWLs, UWLs, LHLs, LCLs, LRLs, LLWLs and LWLs.

Mean scores and 95% confidence ellipses on the first two functions in the SDA were calculated. Jackknife reclassification procedure, also referred to leave-one-out cross-validation, was used to determine rates of successful classification of squid from different geographic populations. The 95% confidence ellipses were calculated with R 2.13.1, and other statistical analyses were performed with the statistical analysis package SPSS V15.0.

3. Results

3.1. Sexual dimorphism and geographic variation in beak sizes

The regressions coefficients of the log-transformed beak morphometric variables with $\ln(\text{ML})$ indicated significant positive allometric growth relative to ML in the three regions ($p < 0.001$). Beak morphometric variables for samples from Ecuador, Peru and Chile in the SDA showed that the final correct cross-validated classification rates were from 52.6% to 64.5% with the total Wilks' λ values ranging from 0.976 to 0.840 ($p < 0.001$) (Table 2). This indicates that there was a significant difference between the sexes, although PCA scatter-plots showed considerable overlaps between females and males (Fig. 3).

All the beak morphometric variables measured in this study were significantly different among the three geographic populations (ANOVA: $p < 0.001$). Samples from the area off Chile had the largest, while those from the area off Ecuador had the smallest beaks (Table 3). Thus, samples from the three different geographic populations could be identified based on the difference using each of measured variables.

3.2. Discriminant analysis

Five body morphological variables (MW, FL, HW, TL and CL) were included in the discriminant analysis, and the results indicated that FL, HW, and TL contributed to the most of the variations according to the value of canonical coefficients (Table 4) and decreases of the

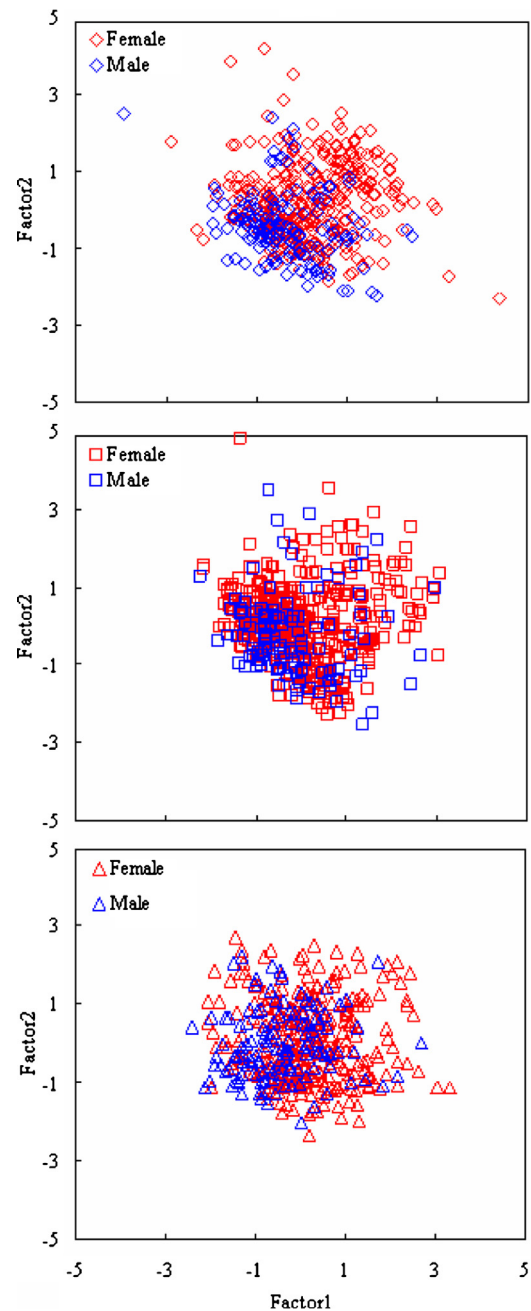


Fig. 3. Factorial scores of principal component analysis made with beaks morphometric variables of female and male squid outside the EEZ waters off Ecuador (diamond), Peru (rectangular) and Chile (triangle).

Wilks' λ from 0.563 to 0.403 (Table 5). Squids from the three geographic populations could be separated from each other by the first two canonical functions, which explained 63.7% and 36.3% of the variations, respectively, in the SDA of the original body morphometric variables (Fig. 4). The overall cross-validated classification rate was 77.3% with 76.6% for Ecuador, 74.8% for Peru and 81.5% for Chile (Table 5).

The SDA revealed that nine beaks morphometric variables (UCL, UWL, LLWL, LHL, ULWL, LCL, URL, LWL and UHL) were effective for population discrimination. Canonical function 1 explained 98.0% variations of the total variability in data (Fig. 5). Wilks' λ decreased from 0.166 to 0.153 when the first three variables, UCL, UWL and LLWL, were included (Table 6), which contributed the most variation to the values of canonical coefficients (Table 4). Samples from

Table 3Beak morphometric variables of *D. gigas* in the EEZ waters off Ecuador, Peru and Chile.

Variables	Ecuador	Peru	Chile	<i>p</i>
	Mean ± Std (mm)			
UHL	9.14 ± 1.99	21.98 ± 4.83	28.64 ± 3.20	<0.001
UCL	11.38 ± 2.44	27.10 ± 5.94	35.52 ± 3.72	<0.001
URL	3.16 ± 0.76	7.95 ± 1.80	10.26 ± 1.33	<0.001
ULWL	9.99 ± 2.11	23.19 ± 5.06	29.49 ± 3.20	<0.001
UWL	2.52 ± 0.53	6.43 ± 1.49	7.46 ± 0.95	<0.001
LHL	2.35 ± 0.49	6.31 ± 1.39	7.59 ± 1.08	<0.001
LCL	5.26 ± 1.01	13.03 ± 2.88	16.71 ± 1.93	<0.001
LRL	3.00 ± 0.60	7.47 ± 1.71	9.42 ± 1.16	<0.001
LLWL	8.60 ± 1.76	20.00 ± 4.31	26.04 ± 2.88	<0.001
LWL	4.60 ± 0.94	10.55 ± 2.25	13.52 ± 1.59	<0.001

Table 4Standardized canonical discriminant function (DF) coefficients for Function1 and Function2 for each morphometric variables used in the discriminant function analysis for *D. gigas* of the three geographic populations. Coefficients represent the relative contributions of variables to each DF.

body	DF1	DF2	Beaks	DF1	DF2	Standardized beaks	DF1	DF2
MW	−0.249	−0.544	UCL	0.167	−1.313	UCLs	−4.592	0.416
FL	1.277	−0.100	UWL	0.691	1.332	URLs	−0.164	−1.719
HW	−0.140	1.510	LLWL	0.187	0.770	ULWLs	0.262	−1.936
TL	0.805	−0.702	LHL	−0.944	−0.438	UWLs	1.183	−0.085
CL	−0.845	0.187	ULWL	−0.087	1.209	LHLs	1.969	−1.604
			LCL	0.151	0.786	LCLs	0.532	3.285
			URL	0.418	−0.204	LRLs	0.550	2.538
			LWL	0.240	−2.715	LWLs	0.548	−0.579
			UHL	0.199	0.879			

Table 5

Summary of stepwise discriminant analysis showing the order of variables to entry for the three geographic populations, and a classification matrix with percentages of correctly classified individuals based on body morphometric variables.

Sep no.	Variable	F to enter	Wilk's λ	F statistic	df 1	df 2
1	FL	577.846	0.563	577.846	2	1487
2	HW	293.509	0.403	426.900	4	2972
3	TL	73.372	0.367	322.011	6	2970
4	CL	60.194	0.340	265.700	8	2968
5	MW	22.603	0.329	220.116	10	2966
Region	Correct (%)	Number of specimens classified				
		Ecuador	Peru	Chile		
Ecuador	76.6	374	56	58		
Peru	74.8	77	434	69		
Chile	81.5	48	30	344		
Total	77.3	499	520	471		

Table 6

Summary of stepwise discriminant analysis showing the order of variables to entry for the three geographic populations, and a classification matrix with percentages of correctly classified individuals based on beak morphometric variables.

Sep no.	Variable	F to enter	Wilk's λ	F statistic	df 1	df 2
1	UCL	3740	0.166	3740	2	1487
2	UWL	37.64	0.158	1127	4	2972
3	LLWL	24.20	0.153	771	6	2970
4	LHL	16.30	0.150	588	8	2968
5	ULWL	11.45	0.147	476	10	2966
6	LCL	10.55	0.145	401	12	2964
7	URL	6.84	0.144	346	14	2962
8	LWL	7.45	0.142	305	16	2960
9	UHL	5.07	0.141	273	18	2958
Region	Correct (%)	Number of specimens classified				
		Ecuador	Peru	Chile		
Ecuador	100.0	488	0	0		
Peru	79.5	11	461	108		
Chile	91.2	0	37	385		
Total	89.5	499	498	493		

Table 7

Summary of stepwise discriminant analysis showing the order of variables to entry for the three geographic populations, and a classification matrix with percentages of correctly classified individuals based on standardized beak morphometric variables.

Sep no.	Variable	F to enter	Wilk's λ	F statistic	df 1	df 2
1	LHLs	21090	0.034	21090	2	1487
2	LCLs	23750	0.001	22374	4	2972
3	UCLs	1778	0.000	27881	6	2970
4	LRLs	305.6	0.000	24900	8	2968
5	URLs	145.4	0.000	21799	10	2966
6	UWLs	108.8	0.000	19456	12	2964
7	ULWLs	31.88	0.000	17025	14	2962
8	LWLs	13.39	0.000	15022	16	2960
Region	% Correct	Number of specimens classified				
		Ecuador	Peru	Chile		
Ecuador	100	488	0	0		
Peru	100	0	580	0		
Chile	100	0	0	422		
Total	100	488	580	422		

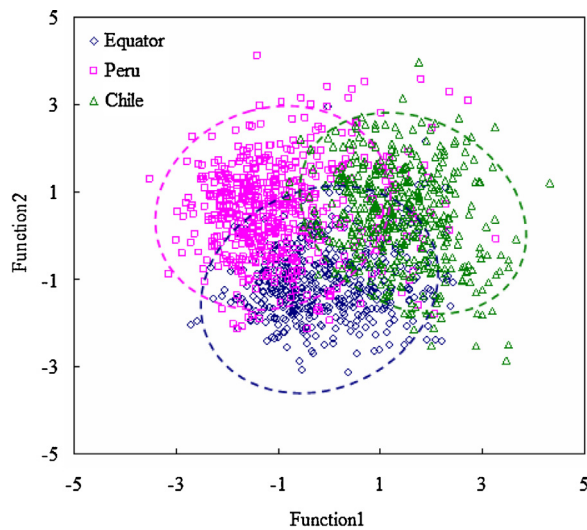


Fig. 4. Canonical discriminant plots of body morphometric variables for samples from the three geographic populations in the Eastern Pacific Ocean. Ellipses represent 95% confidence intervals around the data of each geographic population.

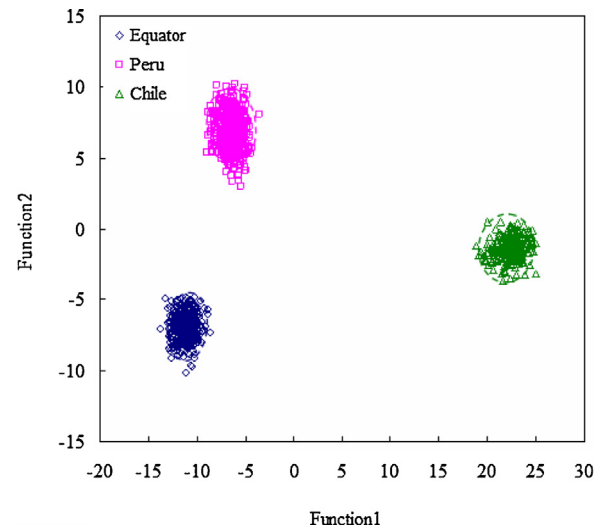


Fig. 6. Canonical discriminant plots of standardized beak morphometric variables of samples from the three geographic populations in the Eastern Pacific Ocean. Ellipses represent 95% confidence intervals around the data of each region.

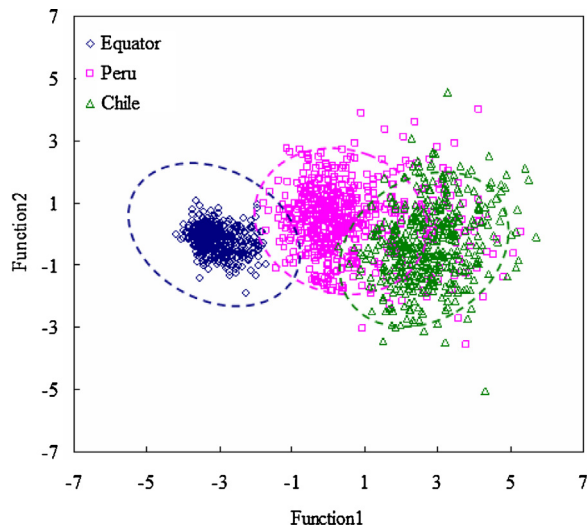


Fig. 5. Canonical discriminant plots of beak morphological variables of samples from the three geographic populations in the Eastern Pacific Ocean. Ellipses represent 95% confidence intervals around the data of each region.

Ecuador were 100% correctly classified, followed by squids from Chile and Peru squids with successful classification rates of 91.2% and 79.5%, respectively. The overall successful classification rate was 89.5% (Table 6). The first two standardized beaks morphometric variables, LHLs and LCLs, contributed to discriminate geographic populations, which explained by canonical coefficients (Table 4) and Wilks' λ (Table 6). Squids from each geographic population were successfully assigned to their respective population with a correct identification rate of 100% (Table 7; Fig. 6).

4. Discussion

Sexual dimorphism in cephalopods occurs in various secondary sexual characters such as body size and morphology (Hanlon and Messenger, 1996). *D. gigas* differed greatly in age structure, size-at-maturity and growth of soft body between females and males (Liu et al., 2013b). Sexual dimorphism in hard structures including statolith, beak and inner shell was investigated for many cephalopods (Bolstad, 2006; Almonacid-Rioseco et al., 2009; Chen et al., 2012b). Beak morphometrics were thought to be useful for squid sex determination (Mercer et al., 1980). *D. gigas* from the waters of Ecuador, Peru and Chile showed significant sexual differences ($p < 0.001$)

in beak morphometric variables with validated classification rates more than 60% (Table 3), although considerable overlaps existed in the PCA scatter-plots (Fig. 3). The result is in accordance with that for the Chilean waters where the average sex misclassification rate of the squid was about 30% (Chen et al., 2012a). Similarly, sexual dimorphism in beaks was also found in other ommastrephids such as *Ommastrephes bartramii* and *Illex argentine*s (Chen et al., 2012a).

The jumbo flying squid is a species with complex intra-specific population structure widely distributed in the Eastern Pacific Ocean. Generally, it was divided into three populations based on the size of adult individuals (Nigmatullin et al., 2001): a small-sized group (140–340 mm and 130–260 mm for females and males, respectively) occurring mainly in the equatorial waters; a medium-sized group (280–600 mm and 240–420 mm, for females and males, respectively) distributed over the whole range of the species; and a large-sized group (550–650 to 1000–1200 mm and >400–500 mm, for females and males, respectively) only inhabiting the northern and southern extremes of its ranges. However, other studies have grouped *D. gigas* into just two populations being the ‘northern’ and ‘southern’ populations based on their migration patterns (Nesis, 1983; Clarke and Paliza, 2000), which were later verified by Sandoval-Castellanos et al. (2007) and Staaf et al. (2010) using a molecular method. Most recently, spatial differences in trace elements deposited in statolith were considered to be a useful tool for identifying *D. gigas* natal origins (Liu et al., 2013a). In contrast, a range of geographic populations of the squid from the Eastern Pacific Ocean were clearly discriminated by numerous morphometric variables in our study, as was done for *Illex* species in the Atlantic Ocean (Martínez et al., 2002).

Most previous morphometric studies for identifying population structure were based on body morphology (Bembo et al., 1996; Saborido-Rey and Nedreaas, 2000). However, it is difficult to quantify morphometric variables of soft-bodied animals such as gastropods and cephalopods (De Wolf et al., 1998; Martínez et al., 2002). Thus, multivariate analyses based on morphometric variables of hard structures are more desirable for studying intra- and inter-specific variations (Neige and Boletzky 1997; Martínez et al., 2002; Chen et al., 2012a). Beaks are one of a few hard structures of cephalopods with high resistance to erosion, making them ideal for identifying species and population structure. Pineda et al. (2002) compared morphometric difference in beaks of two *Loligo* species. Martínez et al. (2002) indicated that multivariate discriminant analysis of beak characteristics had a high rate of correct classification of three *Illex* species throughout the Atlantic Ocean.

Beaks, in several studies, were partially used for cephalopod population discrimination together with other hard structures or molecular methods (Vega et al., 2002; Kassahn et al., 2003; Doubleday et al., 2009). Vega et al. (2002) showed significant differences in morphometric characteristics of *L. gahi* beaks among three geographic populations. Kassahn et al. (2003) indicated a complex population structure in *Sepia apama* by using molecular and morphological analyses of cuttlebones and beaks. Doubleday et al. (2009) successfully revealed a complex population structure in *O. maorum* in south-east Australia and New Zealand using microsatellite DNA markers and morphometric data of stylet and beaks. Li et al. (2010) indicated that there were two stocks of *O. bartarmii* in the northwest Pacific Ocean based on the analysis of beak morphology. In our study, all of the beak morphometric variables for *D. gigas* were significantly different among the three regions showing each of the measured variables could be used for population identification. However, SDA revealed that UCL, UWL and LLWL contributed the most of the variations in the population discrimination. Significant variations in standardized beak morphometric variables (ANOVA: $p < 0.001$) indirectly suggest that regional differences in beak sizes were not likely to result from sampling biases and that

the population structure of *D. gigas* in the eastern Pacific Ocean might be rather complicated with multiple geographic and local populations.

We found higher successful cross-validated classification rates when beak morphological variables were included in SDA (89.5%) compared to body morphological variables (77.3%). Similarly, this was also found by Martínez et al. (2002) in identifying genus *Illex* species and population based on morphometric differences of body and beaks. While similar reclassification percentage was found between body-(80.2%) and beak-dependent discriminations (83.3%) for species identifications, beaks were proven to be more accurate than soft body for population discrimination. For instance, beak-dependent reclassification rate (83.0%) was significantly higher than the body-dependent rate (72.3%) for the separation of *I. coindetii* populations (Martínez et al., 2002). Interestingly, this difference had been also found in *L. gahi* from Peruvian waters, southern Chilean waters and waters around the Falkland Islands (Vega et al., 2002). To remove possible allometric effects caused by size differences in the morphological analyses, beak morphometric variables are usually standardized (Vega et al., 2002; Lefkaditou and Bekas, 2004; Li et al., 2010; Chen et al., 2012a). In this paper, residuals from the regression of each beak morphometric variables on UHL were used in the discriminant analysis, and the results show that all of the individuals were successfully assigned to their respective geographic populations, indicating that standardized data are more effective than original data for the separation of *D. gigas* geographic populations. This study also finds that if standardized body morphometric variables were used in the discriminant analysis, the correct reclassification rate was also 100%. Thus, standardized soft body structures can also perform as well as hard tissues in the separation of squid populations.

Environmental variability was thought to be responsible for morphometric variations of different geographic populations in the growth of soft and hard tissues intra-specifically (Arkhipkin, 1996; Neige and Boletzky, 1997), which was also observed in *D. gigas* (Yi et al., 2012; Liu et al., 2013b). The range expansion of *D. gigas* always correlated well with environment change and food variation (Argüelles et al., 2012; Ruiz-Cooley et al., 2013; Stewart et al., 2014). Therefore, geographic differentiation of morphometric variables for *D. gigas* seems to reflect the effects of environmental variability, as previously revealed in cuttlefish and Octopus (Kassahn et al., 2003; Doubleday et al., 2009). However, many studies have demonstrated that jumbo squid are characterized by high life history plasticity over time (Argüelles et al., 2008; Keyl et al., 2011; Hoving et al., 2013), which was also documented in a wide range of literature for other species (Arkhipkin et al., 2000; Pecl and Jackson, 2008; Ichii et al., 2009). Thus, if high plasticity of the squid correlate well with nonstationary beak morphology invariants, we at the very least should consider in future analyses possible misleading results arising using beak morphology to characterize population origins or structure.

In summary, beak morphometric variables of *D. gigas* have significant and positive relationships with mantle length. The samples from the area off Chile had the largest beaks, while those off Ecuador had the smallest beaks. Significant dimorphism in beak sizes shows that the morphometrics of beaks are useful for determining *D. gigas* sex. Significant differences in original and standardized beak morphometric variables suggest that the geographic variation of *D. gigas* beak sizes could be used for the identification of geographic populations. Although both jumbo flying squid body and beak morphometric variables are useful for geographic population discrimination with hard structure being more effective than soft body, standardized soft and hard tissue morphologic variables perform equally well in the successful identification of the three geographic populations in this study.

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