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POPULATION DYNAMICS OF JUMBO SQUID *DOSIDICUS GIGAS* IN PACIFIC ECUADORIAN WATERS

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ABSTRACT Population dynamic studies of *Dosidicus gigas* have not been reported in Ecuadorian waters. The number of cohorts in the population and reproductive features such as sex ratio, seasonal changes in maturity stages, and size at first maturity are unknown. This knowledge is crucial in the study area, because it can provide fishery management support to Ecuadorian stakeholders. Biological data from 2013 (March–December) and 2014 (January–December) in Ecuadorian waters were analyzed. Biological sampling per month was carried out during every year in different coastal waters off of Ecuador. The biological findings indicated the presence of three size groups in the Ecuadorian squid stock, which estimated to be individuals less than 50 cm mantle length (ML). The monthly size groups changed between one and three size groups in 2013 and 2014. The ML at first maturity for females of jumbo squid estimated in 2013 was $L_{50\%} = 32.4$ cm ML, and $L_{50\%} = 35.5$ cm ML in 2014. For both fishing seasons, the ML–mantle weight relationship estimated for jumbo squid presented isometric growth, and the sex ratio for *D. gigas* showed that females were more abundant than males. This study found that the ML structure of jumbo squid, the number of size groups, and ML at first maturity are different from that previously estimated in traditional fishing areas of *D. gigas* in the eastern Pacific Ocean.

KEY WORDS: jumbo squid, mantle length structure, size groups, mantle length at first maturity, *Dosidicus gigas*

INTRODUCTION

The jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) is an important fishery in countries such as Mexico, Costa Rica, Peru, and Chile (Morales-Bojórquez et al. 2001, Zúñiga et al. 2008, Tafur et al. 2010, Ibañez et al. 2015). According to Arkhipkin et al. (2015), world cephalopod landings has increased from 3.5 to 4 million t by the increase in jumbo squid landings; consequently, in Latin America, *D. gigas* is the most important squid fishery (Markaida & Gilly 2016). In this increased capture, the international fishing fleet of China has participated by harvesting jumbo squid off the exclusive economic zone delimited by Chilean, Peruvian, and Costa Rican waters (Chen et al. 2011, 2013, Liu et al. 2013). The international fishing fleet from Japan has also harvested jumbo squid off the exclusive economic zone of Ecuadorian waters. The availability of jumbo squid has increased in the eastern Pacific Ocean since the species has changed its distribution range in the region, and its presence has been observed from Gulf of Alaska to Chile (Cosgrove 2005, Wing 2006, Zeidberg & Robison 2007), promoting incentives and possible profits by harvesting jumbo squid.

Since 1999 in Ecuadorian waters, jumbo squid has been caught as bycatch by trammel net and gill-netting methods and used as bait for the billfish fishery; however, in 2014 the fishery objective changed, and jumbo squid are now considered for human consumption. Thus, new management rules for fishing jumbo squid were approved by the Ecuadorian government, assuming passive management. Since 2014, fishing effort has been controlled by just allowing 36 fishing licenses. These licenses are distributed 30 for the artisanal fleet and six for commercial fishing vessels (Morales-Bojórquez & Pacheco-Bedoya 2016). The spatial distribution of jumbo squid off Ecuadorian waters has been recorded by the artisanal fishery fleet and the industrial fishery of Japan. In this region, the spatial availability of jumbo squid shows a gradient from north to south; in the northern region, the abundance of jumbo squid is scarce, although its presence has been observed in Manabí (Bahía de Manta) and Esmeraldas (border with Colombia) (Fig. 1). Conversely, the species is mainly available in the Gulf of Guayaquil, and high densities have been observed in Santa Elena, although the species is also abundant in coastal waters bordering with Peru (Fig. 1). Additionally, the species is also distributed in the Galapagos Islands; however, its availability in this insular area is unknown.

In Ecuador, the jumbo squid fishery began in 2014, hence the biological and fishery-dependent data are limited, and the species is poorly known. Nonetheless, there is research data available since 1979 identifying and taxonomically classifying squid off Ecuadorian waters and the most abundant species identified at the time were *Dosidicus gigas*, *Sthenoteuthis oualaniensis* (Lesson, 1830), and *Ommastrephes bartramii* (Lesueur, 1821). Later fisheries research surveys such as those in 1992, 1993, and 1995 in waters off the Ecuadorian coast and Galapagos Islands showed that *D. gigas* is mainly distributed off the southern coasts of Ecuador bordering with Peru. Recently, new biological data have provided information clarifying the trophic relationship of jumbo squid and its ecological role in Ecuadorian waters. Rosas-Luis and Chompoy-Salazar (2016) analyzed the diet composition of jumbo squid, and found that it was mainly composed of fish (*Lampanyctus* sp. and *Myctophum* sp.) and squids (cannibalism), whereas that *D. gigas* was the main prey for the swordfish *Xiphias gladius* (Linnaeus, 1758) and the second most important prey for the mako shark *Isurus oxyrinchus* (Rafinesque, 1809) (Rosas-Luis et al. 2016).

Population dynamic studies of jumbo squid have not been previously reported in Ecuadorian waters. The number of cohorts in the population and reproductive features such as sex ratio, seasonal changes in maturity stages, and size at first

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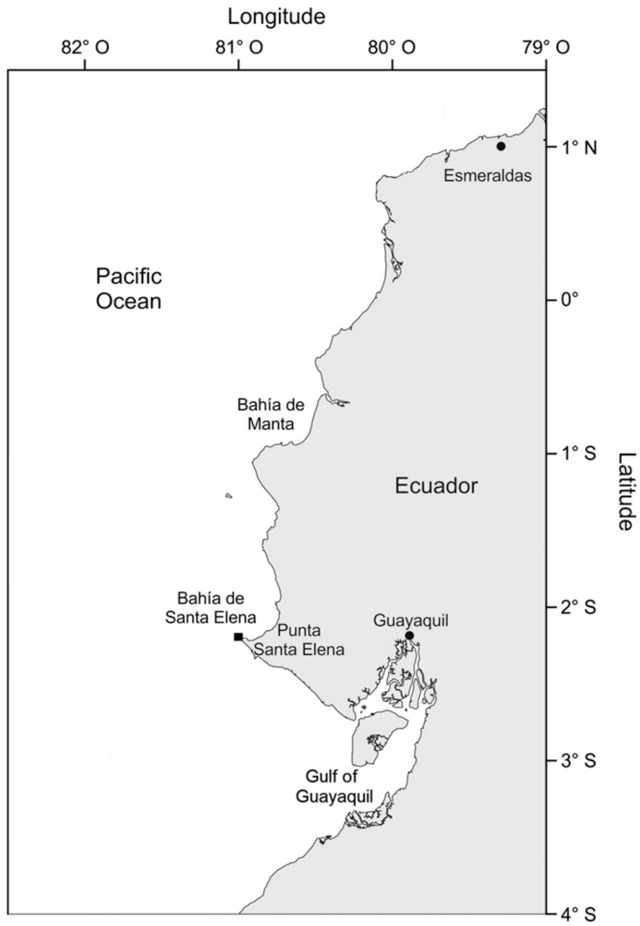

Figure 1. Study area of jumbo squid *Dosidicus gigas* in Ecuador.

maturity are unknown. This knowledge is crucial in the study area, especially because the jumbo squid is being promoted as a new fishery for human consumption. The biological information is necessary to provide fishery management support to Ecuadorian stakeholders (Morales-Bojórquez & Pacheco-Bedoya 2016). Coincidently, jumbo squid has the highest abundance in the southern region of Ecuador and northern zone of Peru, and there is a possibility that both coastal states could be sharing the same stock. Therefore, this species may be classified as a highly migratory and transboundary stock (straddling stock) (Maguire et al. 2006, Russell & VanderZwaag 2010). Thus, effective management of this jumbo squid fishery could be complicated, considering that the population in the Ecuadorian Pacific could show a metapopulation structure. Given the importance of the jumbo squid population in the region, this study evaluates changes in the mantle length (ML) structure, sex ratio, and size at first maturity of jumbo squid off Ecuadorian waters. This information may help to establish sustainable fishing guidelines, and basic biological parameters useful for subsequent stock assessment of jumbo squid.

MATERIALS AND METHODS

Biological Data

Biological data from 2013 (March–December) and 2014 (January–December) fishing seasons in Ecuadorian waters were analyzed. Biological sampling per month was carried out during each fishing season in different areas off Ecuador, mainly Esmeraldas, Bahía de Manta, Bahía de Santa Elena, Punta Santa Elena, and Gulf of Guayaquil (Fig. 1). Random samples of jumbo squid in commercial catches were selected to record individual ML (±0.1 cm) and mantle weight (MW) (±0.1 kg). The maturity stages and sex of *Dosidicus gigas* were determined by visually assessing its internal organs (morphochromatic properties of fresh gonads) by following the four-point maturity scale developed for jumbo squid by Nesis (1983) and modified by Tafur and Rabí (1997). The maturity scale could not be applied to juveniles because their sexual characteristics were not distinguishable by the macroscopical maturity scale used in *D. gigas* according to Tafur and Rabí (1997). It was described for females as (1) immature (stage 1): short and translucid nidamental gland and transparent ovary; (2) maturation (stage 2): cream nidamental glands and granulated ovary; (3) mature (stage 3): larger nidamental glands (20%–50% of the mantle cavity) and ovary full of eggs, yellow colored; and (4) spawned (stage 4): flaccid and reduced nidamental glands and oviduct with some eggs. The maturity scale for males was (1) immature (stage 1): transparent testis and thin and transparent spermatophoric organ; (2) maturation (stage 2): cream testis and spermatophoric sac with some white particles; and (3) mature (stage 3): spermatophoric sac full of spermatophores and white and bigger testis; in this maturity stage were also included squid with spermatophoric sac flaccid with some sperm residuals, although spermatophoric sac flaccid were not observed in the monthly samples from 2013 and 2014 fishing seasons.

Statistical Analysis

To estimate the relationship between ML and MW, the power equation $MW = \alpha \times ML^{\beta}$ was used for each fishing season, where α is the average condition factor and β is the coefficient of allometry, indicating isometric growth when equal to three and allometric growth when significantly different from three (Esmaeili & Ebrahimi 2006, Aguirre-Villaseñor et al. 2008). The estimated value of β was analyzed with Student's *t*-test (Sokal & Rohlf 1995, Zar 1999) to determine whether growth was isometric or allometric. Sex ratio data were calculated monthly as the number of females divided by the sum of males and females, and the data were categorized by a 2-cm ML class. To determine whether the sex ratio can be regarded as 1:1, a Chi-square hypothesis test was carried out (χ^2, $\alpha = 0.05$) (Sokal & Rohlf 1995).

Mantle Length at First Maturity

The ML at sexual maturity of jumbo squid was estimated by using a logistic model proposed by Brouwer and Griffits (2005):

$$P_i = \frac{1}{1 + \exp^{(L_i - \delta)/\gamma}}, \qquad (1)$$

where P_i is the estimated proportion of female mature squid in ML class i (2-cm ML class), sampled during the 2013 and 2014 fishing seasons, L_i is the ML of size-class i, δ is the ML at which 50% of the female squid are sexually mature, and γ is a rate parameter related to the speed of size change from nonreproductive to reproductive status (Fontoura et al. 2009). The function was fitted by a nonlinear least squares (minimization criteria) using Newton's algorithm (Neter et al. 1996). The Monte Carlo resampling method was applied to generate 2,000 data sets for the maturity function, which allowed us to estimate confidence intervals (CI) for the ML at which 50% of the female squid were sexually mature (Haddon 2001).

Number of Size Groups

The number of size groups of *Dosidicus gigas* was estimated monthly and annually for the 2013 and 2014 fishing seasons. The size groups were estimated based on modal progression analyses, assuming that the ML (cm) frequency distributions may be fitted to normal probability density function (NPDF). To statistically determine the observed modes, a multimodal analysis was done using the next probabilistic function:

$$P\{x_i|n, p_1, p_2, ..., p_k\} = n! \prod_{i=1}^{k} \frac{p_i^{x_i}}{x_i!}, \quad (2)$$

where P is the probability, x_i is the number of times an event type i occurs in n samples, and p_i is the separate probability of each one of the type k events possible. The main assumption for the parameter estimation is that the size distribution for each mean ML (cm) or mode can be analyzed with an NPDF to determine that each mode corresponds to a different size group in the jumbo squid population. Under this condition, the estimations of the relative expected proportions of each ML category $f(x)_{\mathrm{ML}}$ was described using the NPDF as follows:

$$f(x)_{\mathrm{ML}} = \left[\frac{1}{\sigma_{\mathrm{ML}}\sqrt{2\pi}} \times e^{\frac{-(\mathrm{ML_o}-\mu_{\mathrm{ML}})^2}{2\sigma^2_{\mathrm{ML}}}}\right] \times \lambda_i, \quad (3)$$

where μ_{ML} and σ_{ML} are the mean and standard deviation of the ML (cm) from each size group and the subscript ML refers to mantle length, the mantle length observed was denoted as $\mathrm{ML_o}$. In this NPDF, the λ_i value represents a penalty function to force the predicted number of observations of each mode, thus stabilizing the solution during the optimization process. To estimate the expected frequencies and the model parameters, it is necessary to compare the estimated and expected values with the negative logarithmic likelihood based on multinomial distribution $-\ln L\{L|\mu_{\mathrm{ML}}, \sigma_{\mathrm{ML}}, \lambda_i, N_{1:n}\}$ as follows (Haddon 2001, Aguirre-Villaseñor et al. 2006):

$$-\ln L\{L|\mu_{\mathrm{ML}}, \sigma_{\mathrm{ML}}, \lambda_i, N_{1:n}\} = -\sum_{i=1}^{\delta} L_i \ln\left(\frac{\hat{L}_i}{\sum \hat{L}_i}\right) + \sum_{m=1}^{n} \left(N_m - \hat{N}_m\right)^2, \quad (4)$$

where L_i is the observed frequency of individuals in the length class i,$\hat{L}_i$ is the expected frequency of individuals in the ML class i, N_m is the total frequency of individuals observed for all ML classes, and $\hat{N}_m$ represents the total frequency of individuals estimated for all ML classes.

The initial values for each size group was made based on inspection of the ML frequency data, using as criterion *a priori* knowledge of the seasonality of recruitment of jumbo squid distributed in the northern region in Peruvian waters (Keyl et al. 2011). The model parameters were estimated when the negative log-likelihood function was minimized with a nonlinear fit using Newton's algorithm (Neter et al. 1996). The CI for each size group was estimated based on a Student's t-test (Madrid-Vera et al. 2007). Previous analyses of the ML frequency distributions of jumbo squid caught in Ecuadorian waters showed lack in statistical convergence when more than four size groups were estimated; however, for three or less size groups, the statistical convergence was robust and stable. The number of size groups was selected based on the Akaike Information Criterion (AIC), which was used to define if the statistical fit could be improved by adding a new size group, increasing the number of size groups from one to three in the ML frequency distributions monthly and annually observed. The best statistical fit was selected based on the smallest AIC estimated (Montgomery et al. 2010). The AIC was expressed as:

$$\mathrm{AIC} = (2 \times -\ln L) + (2 \times \theta_i), \quad (5)$$

where $-\ln L$ is the negative log-likelihood estimated in eq. 4, and θ_i represents the number of parameters for each size group estimated (Haddon 2001).

RESULTS

The squid sampled in Ecuadorian waters were individuals that were less than 50 cm ML, the smallest squid sampled was 12 cm ML, and individuals less than 24 cm ML are frequently caught for the artisanal fishery. The MW for the fishing seasons 2013 and 2014 varied from 0.1 to 2.7 kg. The annual ML–MW relationships of jumbo squid during 2013 showed an isometric growth ($\beta = 2.92$, CI between 2.87 and 2.98; Student's t-test, $P < 0.05$). For 2014, the annual ML–MW relationships was similar, the species also showed an isometric growth (β = 2.87, CI

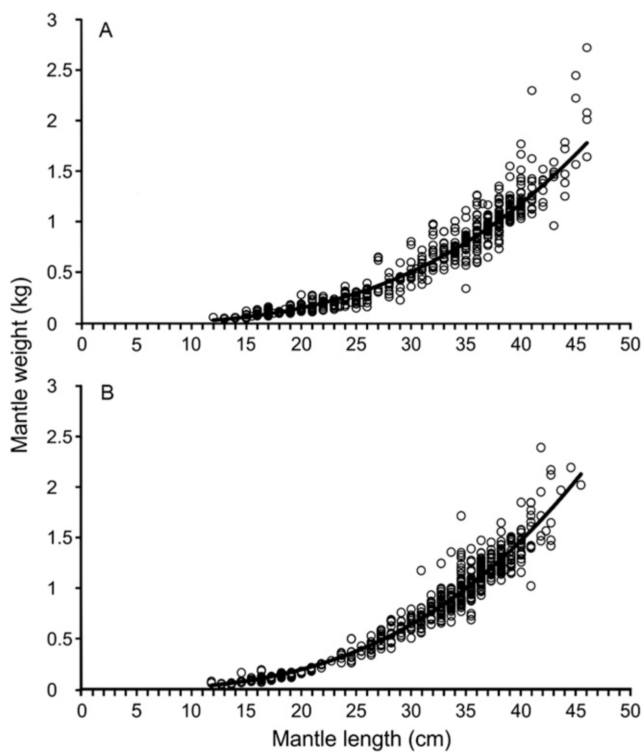

Figure 2. The ML–MW relationship for *Dosidicus gigas* caught during the 2013 (A) and 2014 (B) fishing seasons.

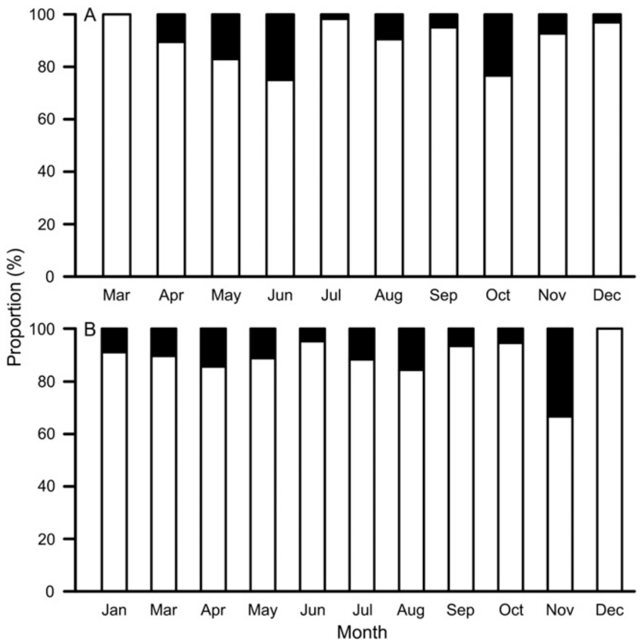

Figure 3. Monthly sex ratios for *Dosidicus gigas* in Ecuadorian waters in 2013 (A) and 2014 (B). White bars show female proportion, and black bars denote male proportion.

between 2.82 and 2.91; Student's *t*-test, $P < 0.05$). For both periods significant statistical differences were not estimated, consequently $\beta = 3$ (Fig. 2A, B). The power equation for the 2013 fishing season was expressed as $MW = 0.000024 \times ML^{2.92} (R^2 = 0.95)$; similar values were estimated for 2014, the mathematical function was $MW = 0.000028 \times ML^{2.87} (R^2 = 0.97)$

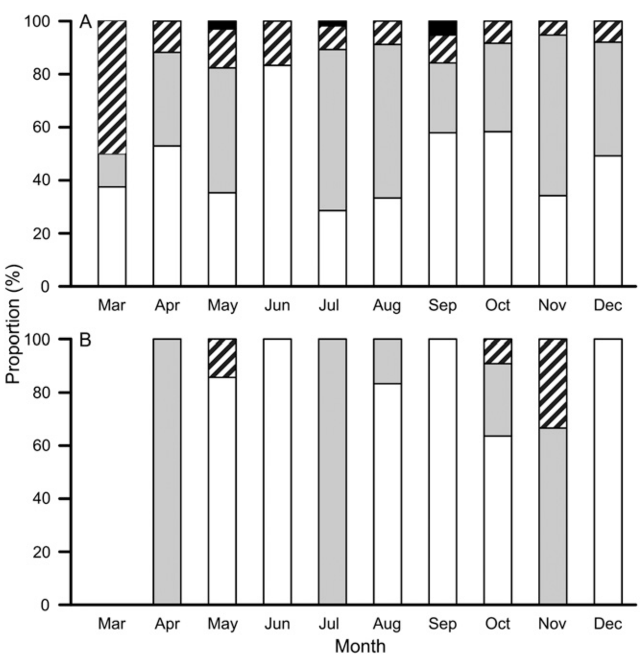

Figure 4. Monthly proportions of maturity stages for females (A), and males (B) of *Dosidicus gigas* in Ecuadorian waters in 2013. Immature (white), maturing (gray), mature (diagonal lines), and spawning/spent (black).

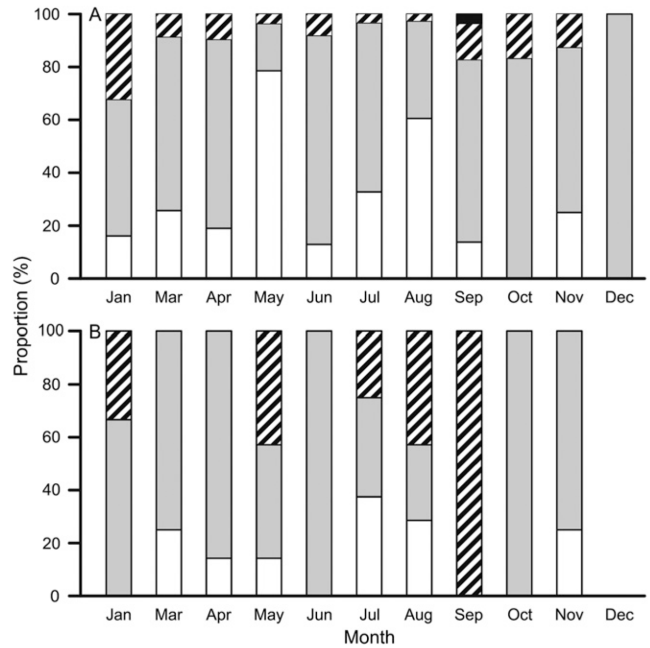

Figure 5. Monthly proportions of maturity stages for females (A), and males (B) of *Dosidicus gigas* in Ecuadorian waters in 2014. Immature (white), maturing (gray), mature (diagonal lines), and spawning/spent (black).

Estimates of the sex ratio showed that females were more abundant than males in 2013 and 2014 (χ^2, $P < 0.05$) (Fig. 3A, B). This pattern in the sex ratio showed that in Ecuadorian waters, females were predominant in the population. The maximum abundance of males was almost 30% (November

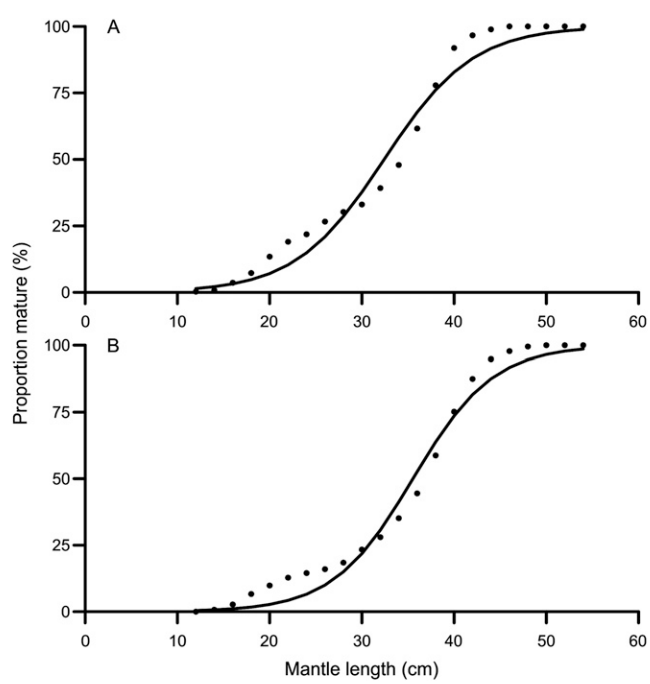

Figure 6. The ML at first maturity of jumbo squid *Dosidicus gigas* estimated by the logistic model in 2013 (A) and 2014 (B).

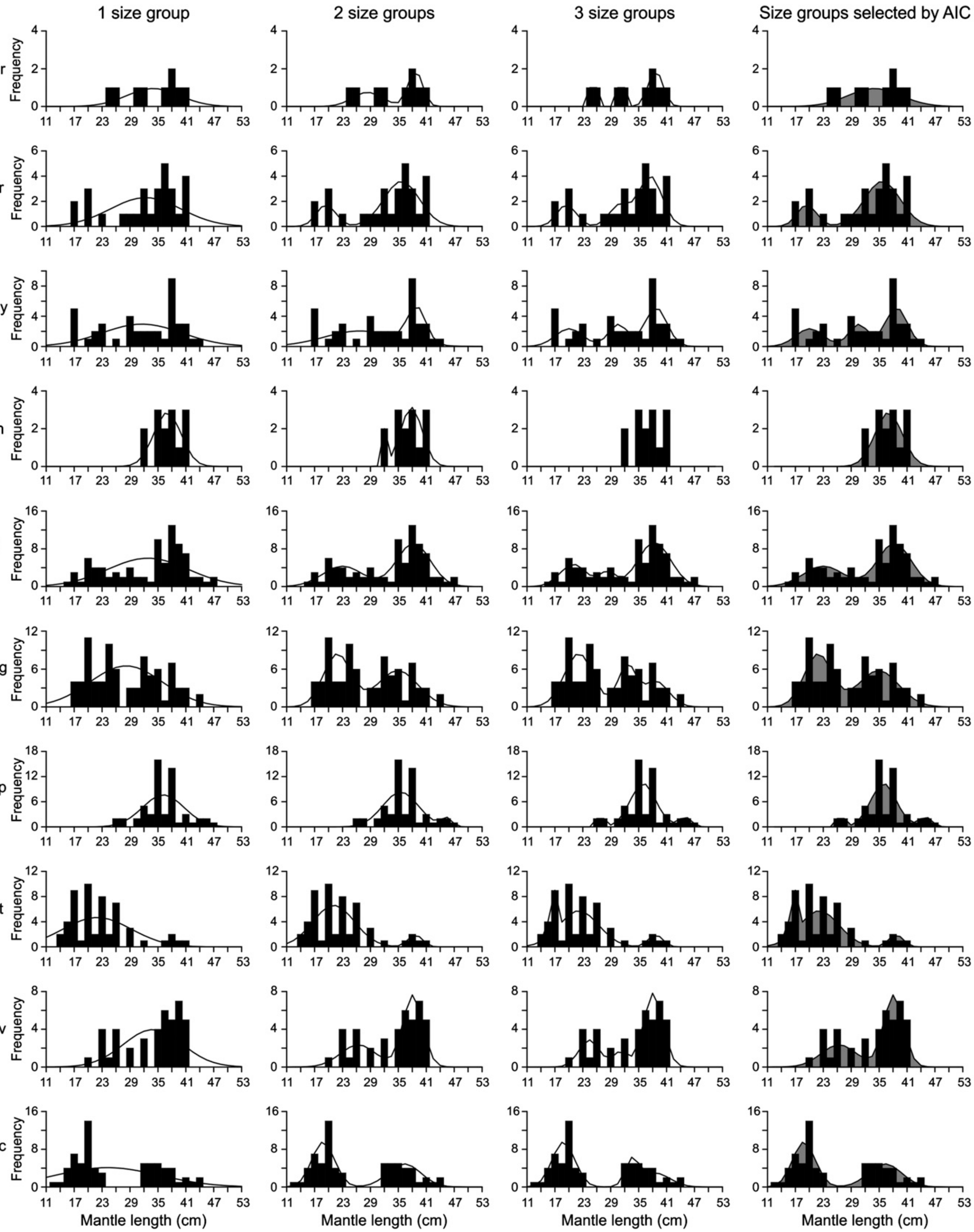

Figure 7. Monthly ML frequency distributions observed (bars) and estimated (lines) for *Dosidicus gigas* during the fishing season 2013. For June, the negative log likelihood function showed lack in convergence when more than two size groups were estimated, consequently, fitted model (line) was not showed. The fourth column shows the best fit (shaded area) to the ML frequency distribution data (black bars).

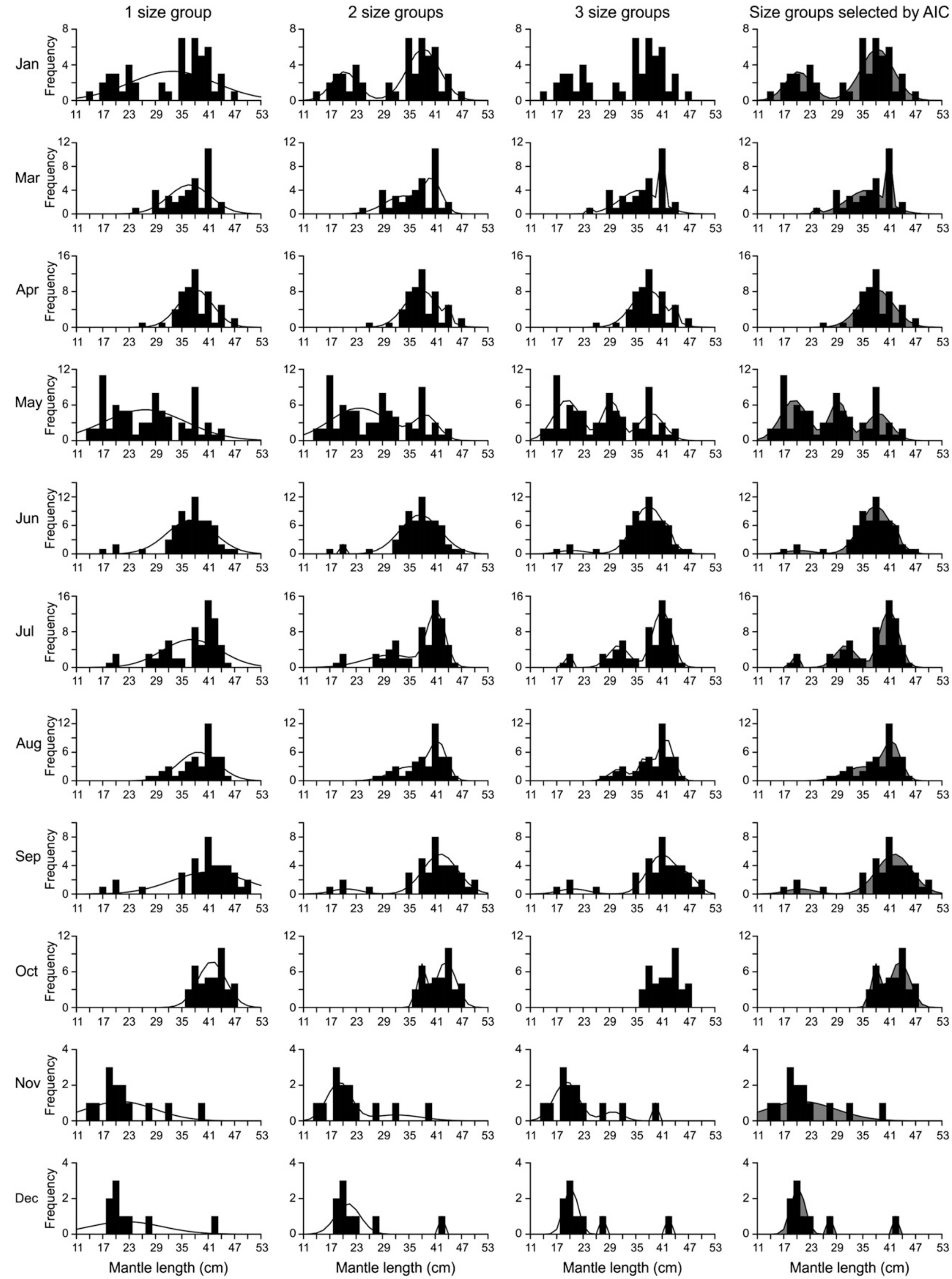

Figure 8. Monthly ML frequency distributions observed (bars) and estimated (lines) for *Dosidicus gigas* during the 2014 fishing season. For January and October, the negative log likelihood function showed lack in convergence when more than two size groups were estimated, consequently, fitted models (lines) were not shown. The fourth column shows the best fit (shaded area) to the ML frequency distribution data (black bars).

TABLE 1.

Number of monthly size groups estimated using multinomial density function applied to ML (cm) frequency distribution of jumbo squid *Dosidicus gigas* in Ecuadorian waters in 2013.

		OF	θ_i	AIC
March	One size group	24.715	3	55.430*
	Two size groups	21.902	6	55.804
	Three size groups	18.921	9	55.841
April	One size group	87.517	3	181.035
	Two size groups	79.193	6	170.386*
	Three size groups	78.253	9	174.506
May	One size group	130.625	3	267.249
	Two size groups	123.394	6	258.789
	Three size groups	120.173	9	258.346*
June	One size group	29.212	3	64.424*
	Two size groups	27.497	6	66.995
	Three size groups	*LC*	*LC*	*LC*
July	One size group	267.946	3	541.891
	Two size groups	252.501	6	517.002*
	Three size groups	250.653	9	519.305
August	One size group	253.675	3	513.351
	Two size groups	243.190	6	498.381*
	Three size groups	241.460	9	500.919
September	One size group	142.996	3	291.992
	Two size groups	141.073	6	294.146
	Three size groups	135.928	9	289.857*
October	One size group	154.097	3	314.193
	Two size groups	145.084	6	302.167
	Three size groups	141.781	9	301.561*
November	One size group	119.822	3	245.643
	Two size groups	107.548	6	227.095*
	Three size groups	106.126	9	230.252
December	One size group	214.969	3	435.939
	Two size groups	186.689	6	385.377*
	Three size groups	183.897	9	385.794

OF is the estimated value of the objective function, θ_i is the number of parameters estimated using nonlinear optimization of OF.
Asterisk (*) denotes the smaller AIC. For June, the negative log likelihood function showed a lack in convergence (*LC*) when more than two size groups were estimated.

2014), and the absence of males was observed during March and December 2013 and December 2014. There was frequent presence of females with monthly sex ratio greater than 70% in Ecuadorian waters.

The monthly proportions of maturity stages for females sampled in 2013 showed than they were mainly in maturation and mature stages, spawned females were observed during May–September with proportions less than 10%, and the greater percentage of immature females was observed in June (Fig. 4A). Conversely, the males in the same fishing season were predominately immature with proportions greater than 60% for May, June, August, September, October, and December (Fig. 4B). The males showed high reproductive activity in April, July, and November, and moderate in August and October, and individuals that were active for reproduction (prevalence of maturation and mature stages) were observed in these months. For 2014, the females showed an increase in reproductive activity, the maturation and mature stages were greater than 65% during January–April, June–July, and September–December, and only during September spawned females were found (Fig. 5A). The predominance of immature females was observed in May and August. Similar pattern was observed for males in this fishing season; the monthly predominance of maturing and mature males was greater than 60%, organisms not active for reproduction (immature) were partially found during March–May, July–August, and November, their frequencies were less than 38% (Fig. 5B).

The ML at first maturity ($ML_{50\%}$) for females changed from 2013 to 2014, it increased from 32.41 (CI = 30.95–33.86, $P < 0.05$) to 35.54 cm $ML_{50\%}$ (CI = 34.55–36.53, $P < 0.05$), respectively. The variation observed in the parameter related to the speed of size change from nonreproductive to reproductive status (γ) from 2012 to 2014 was from 4.82 (CI = 4.22–5.41, $P < 0.05$) to 4.34 (CI = 3.76–4.91, $P < 0.05$), respectively (Fig. 6A, B). The mathematical functions showed the estimated proportion of female mature squid in ML class i for each fishing season was expressed as follows:

$$P_{i,2013} = \frac{1}{1 + \exp^{(ML_i - 32.41)/4.82}},$$

$$P_{i,2014} = \frac{1}{1 + \exp^{(ML_i - 35.54)/4.34}}.$$

The monthly ML frequency distributions of jumbo squid in each fishing season (2013, 2014) showed that the size structure

TABLE 2.

Number of monthly size groups estimated using multinomial density function applied to ML (cm) frequency distribution of jumbo squid *Dosidicus gigas* in Ecuadorian waters in 2014.

		OF	θ_i	AIC
January	One size group	165.742	3	337.485
	Two size groups	148.930	6	309.861*
	Three size groups	LC	LC	LC
March	One size group	100.319	3	206.638
	Two size groups	96.660	6	205.321
	Three size groups	92.075	9	202.150*
April	One size group	129.836	3	265.673*
	Two size groups	128.712	6	269.424
	Three size groups	128.711	9	275.423
May	One size group	243.310	3	492.621
	Two size groups	238.718	6	489.437
	Three size groups	230.627	9	479.254*
June	One size group	175.587	3	357.174
	Two size groups	168.303	6	348.607
	Three size groups	161.202	9	340.404*
July	One size group	198.401	3	402.803
	Two size groups	179.129	6	370.258
	Three size groups	169.346	9	356.693*
August	One size group	112.723	3	231.446
	Two size groups	106.878	6	225.757*
	Three size groups	105.116	9	228.232
September	One size group	121.829	3	249.658
	Two size groups	109.742	6	231.485*
	Three size groups	109.285	9	236.571
October	One size group	88.738	3	183.476
	Two size groups	84.555	6	181.110*
	Three size groups	LC	LC	LC
November	One size group	37.254	3	80.509*
	Two size groups	34.377	6	80.754
	Three size groups	32.270	9	82.541
December	One size group	26.475	3	58.950
	Two size groups	19.429	6	50.859
	Three size groups	16.014	9	50.028*

OF is the estimated value of the objective function, θ_i is the number of parameters estimated using nonlinear optimization of OF.
Asterisk (*) denotes the smaller AIC. For January and October, the negative log likelihood function showed a lack in convergence (LC) when more than two size groups were estimated.

changes between one size group and three size groups in the population (Figs. 7, 8; Tables 1, 2). In 2013, there was dominance of two size groups, although three size groups were estimated in May, September, and October, whereas for March and June only the presence of one size group was estimated (Fig. 7). In this fishing season, when ML frequency distribution from June was analyzed, only one and two size groups were estimated. The estimation of three size groups was not possible, given that the optimization process did not converge. For 2014, a similar pattern in the number of size groups was found, the dominance of three size groups was evident, mainly from January to July; conversely, the presence of one group size was only observed in April and November (Fig. 8). For this fishing season, a lack in statistical convergence occurred when more than two size groups were estimated for January and October, the ML frequency data were noninformative of three size groups in these months. The number of size groups and their temporal variability was selected based on AIC applied to the monthly ML frequency distribution of *Dosidicus gigas*. Outputs for both fishing seasons are shown in Tables 3 and 4 where parameter values and CI ($P < 0.05$) are shown. When the annual ML frequency distributions were analyzed for both fishing seasons, the presence of three size groups were estimated, although the size groups two and three were overlapped (Fig. 9), the AIC identified the presence of three modal values (Table 5). The CI and parameters estimated for each annual size group are shown in Table 6.

DISCUSSION

The annual ML–MW relationship estimated for jumbo squid in Ecuadorian waters in 2013 and 2014 showed an isometric growth for both periods. The ML data for these years were individuals less than 50 cm ML in comparison with Peruvian, Chilean, and Mexican waters where the squid are larger (from 25 to 90 cm ML). For example, for Chilean waters, ML–total weight relationship showed that β parameter varied between 3.4 and 3.5 showing an allometric growth (Chong et al. 2005). Afterwards, Ibañez and Cubillos (2007) estimated β values between 3.1 and 3.2 for oceanic and coastal areas,

TABLE 3.

Number of size groups estimated using multinomial analysis applied to monthly ML (cm) frequency distributions of *Dosidicus gigas* for fishing season 2013 in Ecuador waters.

		Mean (cm)	σ_i	λ_i	Minimum (cm)	Maximum (cm)
March	Size group one	34.004	34.001	13.505	30.302	37.706
April	Size group one	19.48.2	2.056	8.947	18.733	20.230
	Size group two	35.697	3.832	34.552	34.302	37.092
May	Size group one	20.053	2.943	17.382	19.163	20.943
	Size group two	30.575	2.070	15.161	29.948	31.201
	Size group three	38.708	2.348	30.462	37.997	39.418
June	Size group one	37.035	32.306	20.999	35.503	38.567
July	Size group one	23.013	4.302	46.479	22.104	23.922
	Size group two	38.291	3.575	82.587	37.536	39.047
August	Size group one	21.858	2.980	62.779	21.221	22.495
	Size group two	34.881	4.362	63.223	33.948	35.813
September	Size group one	26.742	0.504	7.417	26.611	28.873
	Size group two	35.948	2.754	71.710	35.233	36.663
	Size group three	44.975	1.362	7.955	44.621	45.328
October	Size group one	16.391	0.465	17.186	16.267	16.516
	Size group two	22.158	4.214	60.716	21.034	23.282
	Size group three	38.608	1.527	7.478	38.201	39.016
November	Size group one	26.359	3.800	22.409	25.210	27.508
	Size group two	37.464	2.124	40.590	37.464	38.749
December	Size group one	18.843	2.439	58.499	18.264	19.423
	Size group two	36.290	3.544	43.510	35.447	37.132

Values of mean ML (cm), standard deviation (σ_i), proportion (λ_i), and CI ($P < 0.05$) for each size group are shown.

respectively. Unfortunately, they did not report if β parameter explains isometric or allometric growth. In contrast, the variation of β parameter for Peruvian waters was reported between 2.8 and 3.4 (Bazzino 2014). For Mexican waters the β parameter has varied between allometric and isometric growth with values from 1.7 to 3.5 (Hernández-Herrera et al. 1998, Nevárez-Martínez et al. 2006, 2010, Morales-Bojórquez & Nevárez-Martínez 2010, Velázquez-Abunader et al. 2012, Bazzino 2014, Zepeda-Benitez et al. 2014).

According to Froese (2006), biological information such as growth rate, body morphology, and/or lipid content may be inferred from β parameter, and its variation along the eastern Pacific Ocean have not shown evidence of isometric growth for *Dosidicus gigas*. In Humboldt and California current systems, the species has an allometric growth, it may explain two different conditions: (1) the squid grows faster in ML than in weight ($\beta < 3$ means negative allometric) and (2) the squid grows faster in weight than in ML ($\beta > 3$ is called positive allometric). There are no patterns in the changes of β in the eastern Pacific Ocean, for the northern or southern hemisphere the variability in this parameter depends on several factors, e.g., availability of prey (including type and amount of them), and environmental conditions. These affect ML structure and individual growth between years and geographic areas. Nonetheless, in the eastern Pacific Ocean there is a tendency toward slightly positive allometric growth (Bazzino 2014), except in Ecuadorian waters where an isometric growth has been observed for jumbo squid.

Sex ratio for *Dosidicus gigas* in Ecuadorian waters showed that females were more abundant than males in 2013 and 2014. Similar results were reported for Peruvian waters where the sex ratio was 7.3:1 (Rubio & Salazar 1992) and 2.5:1 (Ye & Chen 2007), respectively. This condition was also observed in Chilean waters in 1993 and 1994 (Chong et al. 2005); the sex ratio varied from 3:1 to 9:1. New data obtained for oceanic and coastal Chilean waters in 2003 and 2004 showed that the maximum dominance of females was 4.5:1 (Ibañez & Cubillos 2007). For Mexican Pacific, the sex ratio estimates varied from 1.7:1 (Bazzino et al. 2007), 2.3:1 (Markaida 2006), 4:1 (Díaz-Uribe et al. 2006), 4.9:1 (Markaida & Sosa-Nishizaki 2001), and 14.3:1 (Hernández-Herrera et al. 1996). The high frequency of squid females seems to be a common feature in the eastern Pacific Ocean.

In Ecuadorian waters, it was not possible to define a reproductive period for jumbo squid. The species showed reproductive activity during several months, and a peak associated to reproduction was not clear. Similar results have been documented in the Humboldt and California Current Systems. In Peruvian waters, Tafur et al. (2010) found reproduction peaks occurring at the end of the year based on time series (1991 to 2007) of maturity stages for jumbo squid. They also reported that the reproductive peaks of males are generally wider than those of the females, although this pattern in the reproductive period was unclear for several years. Additionally, the influence of the El Niño and La Niña events temporality modified the peaks. For Chilean waters, in 2003 and 2004, the frequency of sex maturity stages in oceanic waters showed dominance of males and females in maturing and mature stages. Similar pattern was observed in coastal waters, although the presence of immature females was also observed (Ibañez & Cubillos 2007). In Mexico, Hernández-Herrera et al. (1998) reported a spawning season for jumbo squid in the Gulf of California from February to May 1996; during this period, the frequency of active females to the reproduction was greater than 90%. In 1996 and 1997, Markaida and Sosa-Nishizaki (2001) reported that approximately 50% of the females were mature,

TABLE 4.

Number of size groups estimated using multinomial analysis applied to monthly ML (cm) frequency distributions of *Dosidicus gigas* for fishing season 2014 in Ecuador waters.

		Mean (cm)	σ_i	λ_i	Minimum (cm)	Maximum (cm)
January	Size group one	20.389	2.965	24.037	19.583	21.195
	Size group two	38.294	3.690	53.969	37.291	39.297
March	Size group one	24.725	0.341	0.907	24.618	24.832
	Size group two	35.823	4.400	43.676	34.441	37.204
	Size group three	41.042	0.248	5.690	40.964	41.120
April	Size group one	38.109	37.5	82.501	37.092	39.126
May	Size group one	19.327	3.057	52.640	18.649	20.006
	Size group two	29.359	1.821	32.355	28.955	29.763
	Size group three	38.575	2.768	32.075	37.961	39.189
June	Size group one	20.534	3.181	5.780	19.760	21.307
	Size group two	37.904	3.486	88.849	37.057	38.752
	Size group three	41.975	0.390	4.178	41.880	42.070
July	Size group one	19.422	0.484	7.488	19.308	19.537
	Size group two	31.110	2.264	28.226	30.576	31.644
	Size group three	41.001	2.038	69.275	40.520	41.482
August	Size group one	34.958	4.001	29.331	33.789	36.127
	Size group two	41.576	1.899	38.168	41.021	42.131
September	Size group one	20.735	3.278	5.994	19.731	21.738
	Size group two	42.152	3.940	55.594	40.946	43.358
October	Size group one	37.984	1.051	18.513	37.662	38.305
	Size group two	43.503	2.156	42.983	42.842	44.163
November	Size group one	20.967	19.925	21.322	16.706	25.228
December	Size group one	19.573	2.734	116.56	19.335	19.811
	Size group two	30.090	2.664	96.152	29.858	30.322
	Size group three	39.657	39.657	547.83	39.342	39.972

Values of mean ML (cm), standard deviation (σ_i), proportion (λ_i), and CI ($P < 0.05$) for each size group are shown.

and no spent squid were found, concluding that mature females and the changes in monthly distributions of maturity stages did not show a particular reproductive period. Similar pattern was observed for male squid, they were available for reproduction all year round.

The variations of ML at first maturity for females of jumbo squid estimated in 2013 and 2014 in Ecuadorian waters (32.4 and 35.5 cm ML) were similar to those estimated for southern locations. Tafur and Rabí (1997) reported a value of 32.2 cm ML at first maturity for off Peruvian coasts females of jumbo squid. Afterwards, Ye and Chen (2007) reported values of 32.7 cm ML. Comparatively, in central-south Chile the estimates of ML at first maturity were higher, 71.0 (Ibañez & Cubillos 2007), 76.3 (Ulloa et al. 2006), and 89.0 cm ML (González & Chong 2006). Finally, the variation in ML at first maturity for Gulf of California and Pacific Ocean coasts off Baja California Peninsula, Mexico, showed values of 42.0 (Hernández-Herrera et al. 1996), 42.0 and 60.0 (Markaida & Sosa-Nishizaki 2001),

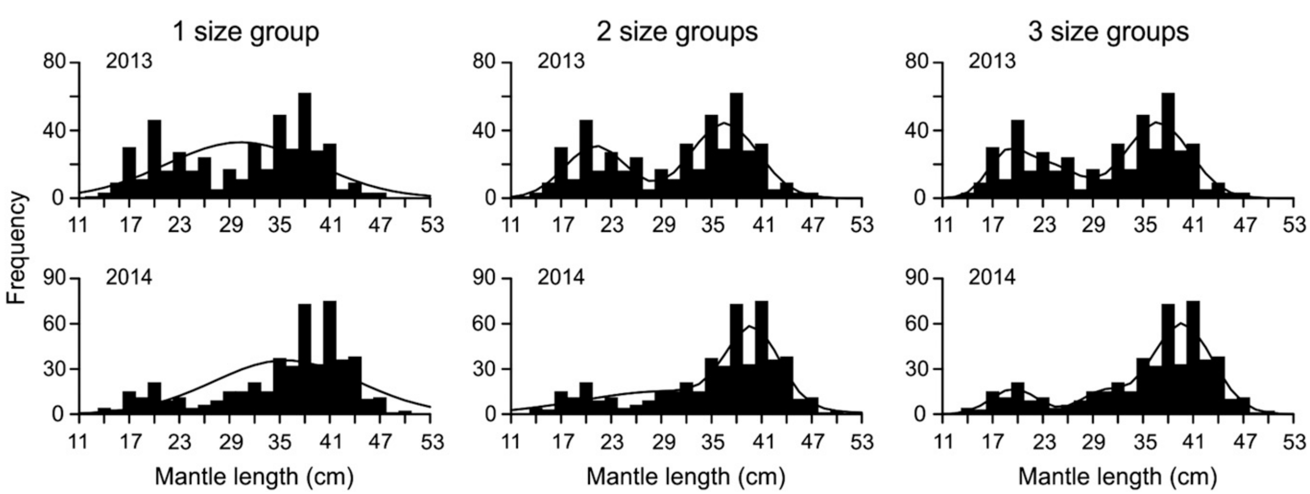

Figure 9. Annual ML frequency distributions observed (bars) and estimated (lines) for *Dosidicus gigas* during fishing seasons 2013 and 2014.

TABLE 5.

Number of annual size groups estimated using multinomial density function applied to ML (cm) frequency distribution of jumbo squid *Dosidicus gigas* in Ecuadorian waters.

		OF	θ_i	AIC
2013	One size group	1520.160	3	3046.320
	Two size groups	1440.973	6	2893.946
	Three size groups	1437.292	9	2892.584*
2014	One size group	1569.269	3	3144.539
	Two size groups	1485.652	6	2983.304
	Three size groups	1462.914	9	2943.829*

OF is the estimated value of the objective function, θ_i is the number of parameters estimated using nonlinear optimization of OF.
Asterisk (*) denotes the smaller AIC.

31.0 and 45.8 (Markaida 2006), 74.0 (Díaz-Uribe et al. 2006), and between 77.0 and 69.0 cm ML (Bazzino et al. 2007). These variations in ML at first maturity along the eastern Pacific Ocean show that small females are located in Ecuadorian and Peruvian waters, and larger females are distributed in the southern region, mainly in the central-south Pacific off Chilean coasts. For Mexican waters a high variability in ML at first maturity was observed, it has changed from 31.0 to 77.0 cm ML, the presence of small or large females has been attributed to environmental effects associated with El Niño and La Niña events (Markaida 2006). Until now such pattern of change in the length at first maturity of jumbo squid along the eastern Pacific has not been explained.

In Ecuadorian waters between one and three size groups were estimated monthly, and annual length frequency distribution analysis for fishing seasons 2013 and 2014 showed the presence of three size groups, which estimated to be individuals less than 50 cm ML. Thus, it is unsurprising that previous studies on annual or monthly ML structure of *Dosidicus gigas*, along the eastern Pacific Ocean show high variability in the number of size groups. In the Humboldt Current System, the species has had incursions in Ecuador coastal zones from Peruvian waters (Morales-Bojórquez & Pacheco-Bedoya 2016), nonetheless the dynamics of the ML structure is different. For example, for Ecuador the number of size groups is less than those estimated for Peru. Comparatively, Argüelles et al. (2001) estimated two size groups off the Peruvian waters in 1992, a size group characterized by small individuals (10–49 cm ML), and a size group of larger squid (52–110 cm ML). Subsequently, Keyl et al. (2011) analyzed ML frequency distribution of *Dosidicus gigas* from 1991 to 2007 (ML ranged from 27.3 to 102.4 cm), and reported that the number of size groups per year fluctuated between zero and six. The time series showed that size groups varied in four different time periods: (1) from 1990 to 1994 the number of size groups varied between one and six; (2) from 1995 to 1999 the number of size groups estimated diminished to two or less size groups, including the absence of identifiable cohort in 1999; (3) from 2000 to 2004 the number of size groups increased, varying between one and six; and (4) from 2005 to 2006 the monthly size groups showed a constant decrement from three to zero size groups. Thus, the number of size groups recruiting to the Peruvian fishery per year is not constant, and they are highly variable, including failures in recruitment denoted by absence of size groups. Similar variation in size group presence was also reported in the central Gulf of California Mexico. During 1980 to 1981, Ehrhardt et al. (1983) reported five size groups of *Dosidicus gigas*. After this study, Hernández-Herrera et al. (1998) analyzed ML frequency distribution of jumbo squid between April 1996 and May 1997; based on modal progression analysis, they found one cohort of *D. gigas* in the region. Subsequently, Nevárez-Martínez et al. (2006, 2010), and Velázquez-Abunader et al. (2012) showed that the size groups in the Gulf of California can vary between one and three, although the presence of two size groups was predominant in the study area.

Chong et al. (2005) based on the data from research cruises off of coastal areas of Chile, specifically Coquimbo, Valparaiso, and Talcahuano, found two cohorts in July 1993 and January 1994. The first cohorts grouped individuals less than 44 cm ML, and the second cohort was represented by specimens between 76

TABLE 6.

Number of size groups estimated using multinomial analysis applied to annual ML (cm) frequency distributions of *Dosidicus gigas* in Ecuador waters.

		Mean (cm)	σ_i	λ_i	Minimum (cm)	Maximum (cm)
2013	Size group one	18.569	2.296	127.217	18.364	18.773
	Size group two	23.712	3.521	171.536	23.399	24.026
	Size group three	36.783	3.815	428.771	36.444	37.123
2014	Size group one	19.573	2.734	116.567	19.335	19.811
	Size group two	30.090	2.664	96.152	29.858	30.322
	Size group three	39.657	3.619	547.853	39.342	39.972

Values of mean ML (cm), standard deviation (σ_i), proportion (λ_i), and CI ($P < 0.05$) for each size group are shown.

and 98 cm ML. According to Ibañez and Cubillos (2007), for Chilean waters the ML frequency distribution observed in 2003 and 2004 showed differences between seasons and fishing areas (oceanic and coastal waters). For both areas, the ML frequency distribution varied from 20 to 95 cm ML, and the presence of two size groups in the region was reported. So, a multimodal ML distribution is assumed in the region as consequence of an apparent migratory pattern of jumbo squid from oceanic to coastal areas, and *vice versa*. Ibañez et al. (2015) explained that off of the coast of Coquimbo, two size groups from 45 to 55 and 65 to 100 cm ML were identified during 2003–2011. In this period, for the Talcahuano region two size groups from 25 to 45 cm ML, and 65 to 100 cm ML were also reported. Recent information based on qualitative descriptions rather than quantitative analysis of ML data showed that ML range of *Dosidicus gigas* caught in the Peruvian exclusive economic zones for females varied from 17.8 to 111.8 cm ML, whereas that for males the ML ranged from 21.8 to 103.3 cm ML (Bilin et al. 2013). Meanwhile, Chen et al. (2014) reported the variations of ML of jumbo squid off Costa Rica Dome, they found that the males ranged from 21.1 to 35.5 cm, and within this range the abundance of individuals was of 72.5%. Similarly, for females a 73.8% of abundance was observed within ML ranging from 26.0 to 36.0 cm.

Comparison of the variability in number of size groups in association with their ML (quantitatively estimated) showed singular features for different areas in the eastern Pacific Ocean. The influence of environmental conditions (Markaida 2006), type and availability of prey (Rosas-Luis & Chompoy-Salazar 2016), and specific population dynamics by region may strongly change the ML structure of the squid stocks, varying the number of size groups and recruitment patterns (Morales-Bojórquez & Nevárez-Martínez 2010). Thus, the generalization of the intraspecies structure of *Dosidicus gigas* along the eastern Pacific Ocean as proposed by Nigmatullin et al. (2001) could not be a plausible hypothesis. They suggested the presence of three groups on the basis of ML: one small-sized group with male and female ML varying from 13 to 26 cm and 14 to 34 cm, respectively; a medium-sized group of males and females with ML from 24 to 42 cm and 28 to 60 cm, respectively; and a third group with individuals from 50 to 120 cm ML, where they noted that in this last group the females were larger than males. This assumption was based on a causal and theoretical generalization on the biology of jumbo squid. The biology related to the intraspecies structure of jumbo squid must be analyzed regionally, and characterized according to its particular population dynamics.

CONCLUDING REMARKS

The jumbo squid population distributed in Ecuadorian waters has particular biological features not previously reported for them along the eastern Pacific Ocean. The ML structure of 2013 and 2014 were characterized for ML less than 50 cm ML, and the presence of three annual size groups that were monthly changing between one and three size groups. In the study area, it was not possible to define a reproductive period for jumbo squid, the species showed reproductive activity during several months, but peak reproductive event associated to a certain time period was not clear. The ML at first maturity for females of jumbo squid in 2013 and 2014 was 32.4 and 35.5 cm ML, respectively. These estimates are between the smaller ML at first maturity observed in the eastern Pacific Ocean. The females were more abundant than males during the study period, and based on ML–MW relationship the species showed isometric growth for both periods.

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