



# Article Decadal Changes in the Annual Growth of Two Commercial Ommastrephid Species in the Pacific Ocean

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**Abstract:** Neon flying squid *Ommastrephes bartramii* and jumbo flying squid *Dosidicus gigas* are two important commercial ommastrephid species in the Pacific Ocean. As short-lived marine species, squids are highly susceptible to changes in climate and marine environments. According to samples collected from the northwest and southeast Pacific Ocean in different years, we explored the growth characteristics of these two squids in terms of their mantle length (ML) distribution and the relationship between mantle length and body weight (LWR), also considering the relative condition factors ( $K_n$ ), and explored the effects of the El Niño and Southern Oscillation (ENSO) on their growth. The results showed that the ML for *O. bartramii* and *D. gigas* had significant differences among different years and different sexes (p < 0.01), and the size of females was larger than that of males. LWR showed that both squids demonstrated a positive allometric growth pattern (b > 3), and parameters *a* and *b* were influenced by year and sex. Furthermore, there were significant differences in *Kn* in both squids for different years and different sexes (p < 0.01), and their interannual fluctuations were quite significant. In conclusion, the alterations in the marine environment caused by climate change had a significant impact on the growth of *O. bartramii* and *D. gigas* in this study. ENSO events had opposite effects on the growth of both squid species.

**Keywords:** *Ommastrephes bartramii; Dosidicus gigas;* Pacific Ocean; growth; relative condition factor; ENSO

# 1. Introduction

Cephalopods are considered one of the most valuable potential fishery resources in the world's oceans [1]. At present, the commercially developed cephalopods mainly include species of the families Ommastrephidae, Loliginidae, Sepiidae, and Octopodidae, with Ommastrephidae accounting for 51–62% [1–3]. Ommastrephid squids are typical ecological opportunists with a short life cycle, fast growth, complex population structure, and long-distance migration [4–6]. The squid is an important component in the marine ecosystem and occupies an intermediate position in the food web [7]. The squid plays an important role as prey for large fish and marine mammals, and also as a predator that preys on crustaceans, small pelagic fish, and other cephalopods [1,8]. A change in its biomass directly affects the stability of the whole marine ecosystem [1,8,9]. In order to sustainably develop and utilize oceanic squid resources, it is necessary to strengthen basic research on its fishery biology [1,10,11]. At present, two large squid species, neon flying squid *Ommastrephes bartramii* and jumbo flying squid *Dosidicus gigas*, are the primary targets for Chinese squid-jigging fisheries in the Pacific Ocean [6,12].



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**Copyright:** © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). *Ommastrephes bartramii* is a highly migratory oceanic species with distribution mainly in the North Pacific Ocean [13–15]. This species has become an important fishing target since 1974 [14]. Currently, the highest catch country of this species is Mainland China, which began to commercially exploit this species in 1994 [14]. *O. bartramii* can be divided into two segregated populations based on the different spawning peak and geographical location: a winter–spring population (Western population) that is mainly located west of 170° E and an autumn population (Eastern population) occurring east of 170° E, both of which have only about a one-year lifespan [16–19]. The winter–spring population, distributed in the western waters of the North Pacific Ocean, is the main fishing target population for Mainland China, with an annual catch of 37,000–132,000 tons, accounting for 80% of the global total catch of squid in the North Pacific Ocean [20,21].

The largest ommastrephid, *D. gigas*, is widely distributed in the eastern Pacific Ocean [22–24]. The population structure of *D. gigas* is complex [25]. Three groups were defined based on the size of adult males and females: the small group (male: 130–260 mm; female: 140–340 mm), the medium-sized group (male: 240–420 mm; female: 280–600 mm), and the large group (male: >400–500 mm; female: 550–650 mm to 1000–1200 mm) [25–27]. The main fishing grounds are located in the Gulf of California, the waters off the coast of Costa Rica, equatorial waters (5° N–5° S, 95–120° W), and the coastal and oceanic regions off Peru and Chile [6,25,28]. China conducted its first fishery survey of *D. gigas* in the high seas off Peru and Costa Rica in 2001, followed by commercial exploration [14]. In recent years, the most abundant fishing ground is located off the Peru exclusive economic zone waters, and the catch of *D. gigas* accounted for 60–90% of its global total catch [29].

As short-lived marine species, squids are highly susceptible to external factors. Among these factors, changes in marine environment are considered to be the main factor affecting the growth of squid [30–32]. Previous studies found that a warm water temperature results in faster growth, smaller body size, and smaller gonads, while a cold temperature results in slower growth, larger body size, longer lifespan, and larger gonads [31–33]. At the same time, the frequent extreme weather events (such as El Niño and La Niña) in recent years have not only had a great impact on squid resources but have also directly affected squid growth, resulting in a large difference in individual size compared with previous years [15,34,35]. In addition, previous studies have discussed how O. bartramii and D. gigas might experience concurrent fluctuations in catch, abundance, and/or distribution on various temporal scales, and found that they undergo synchronous changes due to climate or environmental changes [6,12,29]. During the warm Pacific decadal oscillation (PDO) phase, the environmental conditions in the western Pacific and eastern Pacific changed in opposite directions, resulting in an increase in suitable habitat for O. bartramii in the western Pacific and a decrease in suitable habitat for *D. gigas* in the eastern Pacific [12,36]. Yu et al. (2021) found that, from September to November, 2006 to 2015, there were interannual variations and synchronous fluctuation, with significantly negative associations in the abundance and distribution of O. bartramii and D. gigas, and they believed that the proportion of favorable sea surface temperature (SST) area conversely shifted due to SST anomaly changes at Niño 3.4 (5° N–5° S and 120–170° W) and Niño 1 + 2 regions (0–10° S and 90–80° W) [6]. In terms of individual growth, however, it is still unclear whether there is a link between the growth changes in these two squid species.

Individual growth patterns are most commonly described by the length–weight relationship (LWR), which is also one of the most important biological parameters in statistical modeling [37,38]. It provides important information for assessing individual population characteristics, understanding life cycles, ontogeny changes, growth, and fishery resource conservation [39,40]. Meanwhile, the relative condition factor, another important biological parameter derived from the LWR, measures the deviation of an individual from the average weight in a given sample in order to assess the suitability of environmental changes for individual growth [38,41–43].

The purpose of this study is to analyze the interannual growth changes in *O. bartramii* and *D. gigas* in the Pacific Ocean. Specifically, the growth characteristics of *O. bartramii* 

and *D. gigas* were studied according to samples collected in the Northwestern and Eastern Pacific Ocean in different years. We analyzed their sex and annual growth differences using a linear mixed-effects model (LMEM), and also explored the effects of climate change and the marine environment on the growth of two species under a decadal time series. This study provides basic information and a scientific basis for a comprehensive understanding of individual growth changes and the responses of the biological characteristics to climate change for two ommastrephid squids in the Pacific Ocean.

#### 2. Materials and Methods

# 2.1. Sampling and Measurement

All samples in this study were collected in the Pacific Ocean by Chinese jigging fishing vessels. A total of 8560 *O. bartramii* samples were collected from 2009 to 2018 in the Northwest Pacific Ocean (38–46° N, 149–164° E), and a total of 5520 *D. gigas* samples were collected from 2008 to 2017 outside the exclusive economic zone waters of Peru (8–19° S, 78–87° W) (Table 1, Figure 1). All samples were immediately frozen at -20 °C on the vessel and transported to the laboratory for subsequent biological analysis in each consecutive year.

 Table 1. Sample size (total number) of Ommastrephes bartramii and Dosidicus gigas among years and sexes.

	Ommastreph	es bartramii	Dosidicus gigas		
Year	Female	Male	Female	Male	
2008	0	0	304	72	
2009	729	703	565	146	
2010	1194	1317	470	114	
2011	324	278	925	343	
2012	301	464	469	217	
2013	247	223	285	167	
2014	150	103	221	142	
2015	529	494	370	257	
2016	362	368	214	135	
2017	287	326	66	38	
2018	116	45	0	0	
Total	4239	4321	3889	1631	

The thawed samples were subjected to biological determination, including mantle length (ML,  $\pm 1$  mm) and body weight (BW,  $\pm 1$  g). According to the approach proposed by Lipinski and Underhill (1995) [44], the sex and maturity stage were visually assessed.

#### 2.2. The Relationship between Mantle Length and Body Weight (LWR)

The relationship between mantle length and body weight can be expressed as follows [41]:

$$BW = aML^b \tag{1}$$

where BW is the body weight of samples (g), ML is the mantle length of samples (mm), *a* is the scaling parameter, and *b* is the allometric growth parameter. Since the variance of BW increases with the increase in ML, the above equation was logarithmically transformed, and the equation becomes:

$$\ln(BW) = \ln(a) + b \times \ln(ML)$$
<sup>(2)</sup>

Simple LWR models are often constructed as single-factor regression models, which have poor ability to model the compound impact of multiple factors (such as geographic, interannual, and sex) [45]. A linear mixed-effect model (LMEM) is a powerful tool that allows for analyzing a wide variety of data structures [46,47]. In addition to the overall



average and random error, the models also contain both fixed effects and random effects [47]. Due to its unique advantages, it has been widely used in many fields [46,48,49].

Figure 1. Sampling area of Ommastrephes bartramii and Dosidicus gigas in the Pacific Ocean.

In this paper, a generalized linear model (GLM) and nine linear mixed-effect models were used to describe the relationship between mantle length and body weight in these two squids. Nine LMEMs take the influence of year (Y.I, Y.S) and/or sex (S.I, S.S) as the random effect of coefficient *a* and/or parameter *b* to explain the relationship between mantle length and body weight [49] (Table 2). The lme4 and nlme packages of R language software were used to complete the construction process of all models [50].

Table 2. Models for length-weight relationship of two ommastrephid species and its fitting effects.

Model	Equation	Log-Transformed	Ommastrephes bartramii		Dosidicus gigas	
	•	0	AIC	RMSE	AIC	RMSE
GLM	$W = a \times L^b$	$\ln(W) = \ln(a) + b \times \ln(L)$	-16,614	0.09165	-9064	0.10641
Y.I	$W = [a \times exp(ReY.I)] \times L^b$	$\ln(W) = [\ln(a) + \text{ReY.I}] + b \times \ln(L)$	-17,044	0.08914	-9429	0.10244
S.I	$W = [a \times exp(ReS.I)] \times L^b$	$\ln(W) = [\ln(a) + \text{ReS.I}] + b \times \ln(L)$	-16,650	0.09132	-9144	0.10538
Y and S.I	$W = [a \times \exp(\text{ReY.I}) \times \exp(\text{ReS.I})] \times L^{b}$	$\ln(W) = [\ln(a) + \text{ReY.I} + \text{ReS.I}] + b \times \ln(L)$	-17,073	0.08887	-9542	0.10119
Y.S	$W = a \times L^{(b + \text{ReY.S})}$	$\ln(W) = \ln(a) + (b + \text{ReY.S}) \times \ln(L)$	-17,018	0.08919	-9408	0.1025
S.S	$W = a \times L^{(b + \text{ReS.S})}$	$\ln(W) = \ln(a) + (b + \text{ReS.S}) \times \ln(L)$	-16,649	0.09132	-9147	0.10535
Y and S.S	$W = a \times L^{(b + \text{ReY.S} + \text{ReS.S})}$	$\ln(W) = \ln(a) + (b + \text{ReY.S} + \text{ReS.S}) \times \ln(L)$	-17,062	0.08893	-9539	0.10121
Y.I and S	$W = [a \times \exp(\text{ReY.I})] \times L^{(b + \text{ReY.S})}$	$\ln(W) = [\ln(a) + \text{ReY.I}] + (b + \text{ReY.S}) \times \ln(L)$	-17,171	0.08823	-9605	0.10033
S.I and S	$W = [a \times \exp(\text{ReS.I})] \times L^{(b + \text{ReS.S})}$	$\ln(W) = [\ln(a) + \text{ReS.I}] + (b + \text{ReS.S}) \times \ln(L)$	-16,646	0.09131	-9163	0.10515
Y and S.I and S	$W = [a \times \exp(\text{ReY.I}) \times \exp(\text{ReS.I})] \times L^{(b + \text{ReY.S} + \text{ReS.S})}$	$ln(W) = [ln(a) + ReY.I + ReS.I] + (b + ReY.S + ReS.S) \times ln(L)$	-17,216	0.08794	-9748	0.09893

Note: The second column shows the abbreviations of models detailed in the third and fourth columns. Y.I: random effects on intercept  $(\ln(a))$  of Years; Y.S: random effects on slope (b) of Years; S.I: random effects on intercept  $(\ln(a))$  of Sex; S.S: random effects on slope (b) of Sex; Y and S.I: random effects on intercept  $(\ln(a))$  of Years and Sex; Y and S.S: random effects on slope (b) of Years and Sex; Y.I and S: random effects on intercept  $(\ln(a))$  and slope (b) of Years; S.I and S: random effects on intercept  $(\ln(a))$  and slope (b) of Years; S.I and S: random effects on intercept  $(\ln(a))$  and slope (b) of Years and Sex; Y.I and S: random effects on intercept  $(\ln(a))$  and slope (b) of Years and Sex.

### 2.3. Model Comparison

Akaike information criterion (AIC) and root mean square error (RMSE) were used to compare the fit of the 10 models. AIC values are widely used to compare the quality of models [51]. We selected the best model with the lowest AIC value. RMSE is a value that

measures how close a predicted value is to the final result [52]. The closer the value is to 0, the smaller the difference between the predicted value of the model and the observed value of the sample—that is, the better the prediction performance.

The AIC was calculated using the following equation:

$$AIC = \frac{2p - 2M}{N}$$
(3)

where *p* is the number of parameters in the model, *N* is the number of samples, and *M* is the likelihood function.

The formula for calculating RMSE is as follows:

RMSE = 
$$\sqrt{\frac{\sum_{i=1}^{N} (f_i - y_i)^2}{N}}$$
 (4)

where  $f_i$  represents the predicted value and  $y_i$  represents the observed value.

# 2.4. Relative Condition Factor

The relative condition factor ( $K_n$ ) was calculated to evaluate the condition factors of two squids.  $K_n$  was determined from the following equation [41,53]:

$$K_n = \frac{W}{W_s} \tag{5}$$

where  $K_n$  is the relative condition factor, W is the observed body weight, and Ws is the calculated weight.

# 2.5. Climatic Index Data

El Niño and La Niña are major climatic events that have a great impact on the growth of marine life in the Pacific Ocean [20,54]. The Niño index (NI) is an indicator that reflects the intensity of El Niño and La Niña events. The monthly SST anomalies (SSTA) in the Niño 3.4 region ( $5^{\circ}$  N– $5^{\circ}$  S and 120–170° W, close to the *O. bartramii* fishing ground) and Niño 1 + 2 region ( $0-10^{\circ}$  S and 90–80° W, close to the *D. gigas* fishing ground) were used as indicators to represent the climate variability in the Northwest and the Southeast Pacific Ocean, respectively [6]. The Oceanic NI data were obtained from the IRI/LDEO Climate Data Library (http://iridl.ldeo.columbia.edu/SOURCES/.Indices/ (accessed on 15 June 2022)).

According to the time of sample collection and the definition of El Niño and La Niña events, El Niño and La Niña events during 2008–2017 are classified (Table 3, Figure 2).

**Table 3.** The classification of the El Niño and La Niña event from 2008 to 2018 according to the time of sample collection and the definition of El Niño and La Niña. All other unclassified years were normal.

Fishing Ground	Anomalous Climate Conditions	Year
Ommastrephes bartramii	El Niño event La Niña event	2009, 2015 2010, 2011
Dosidicus gigas	El Niño event La Niña event	2014, 2015, 2017 2010, 2013, 2017



**Figure 2.** The time series of Niño 3.4 (between  $5^{\circ}$  N and  $5^{\circ}$  S and  $120^{\circ}$  and  $170^{\circ}$  W) index and Niño 1 + 2 (between  $0^{\circ}$  and  $10^{\circ}$  S and  $90^{\circ}$  and  $80^{\circ}$  W) index from 2008 to 2018. Dashed lines of  $\pm$  0.5 are the definition of the El Niño/La Niña event: the NI over 0.5 represents the El Niño event and below -0.5 represents the La Niña event.

#### 3. Results

#### 3.1. Mantle Length Distribution

The mantle length of *O. bartramii* and *D. gigas* showed changing trends over the years. The distribution of *O. bartramii* was generally unimodal. Its ML was larger in 2009 and smaller in 2010, then gradually decreased from 2011 to 2014, and increased after 2015 (Figure 3). The distribution of *D. gigas* was scattered. Its ML was larger in 2009–2010, dominated by small and medium-size groups. Then, the ML gradually decreased from 2012 to 2016 and slightly increased in 2017, dominated by small groups (Figure 4). The ML of females and males was also different in each year. The size of females' was larger than that of males'; the same trend was seen for both species. Two-way analysis of variance (ANOVA) results showed that the ML of both squids showed significant differences by year and sex (p < 0.01).

# 3.2. LWR

Based on the pooled data, a GLM was used to establish the LWR for both *O. bartramii* and *D. gigas* (Figure 5), and the following equations were obtained:

*O. bartramii*:  $BW = 1.0298 \times 10^{-5} ML^{3.1843}$  (*a*: 95%CI = 9.5959 × 10<sup>-6</sup>, 1.1052 × 10<sup>-5</sup>; *b*: 95%CI = 3.1718, 3.1971).

*D. gigas*:  $BW = 1.2425 \times 10^{-5} ML^{3.1412}$  (*a*: 95%CI = 1.1504 × 10<sup>-5</sup>, 1.3420 × 10<sup>-5</sup>; *b*: 95%CI = 3.1277, 3.1547).

The estimated allometric growth parameter *b* for *O*. *bartramii* was slightly larger than the estimated value for *D*. *gigas*, and the value was greater than 3 for both species.

### 3.3. Recommended LWR and Temporal and Sexual Variations in LWR

In this study, a generalized linear model and nine linear mixed-effects models were established to describe the relationship between mantle length and weight for the two ommastrephid species. The results showed that the LMEM (Y and S.I and S) had the smallest AIC and RMSE values (–17,216 and 0.08794, respectively), indicating that a random effect on both intercept and slope of year and sex was the best fit for LWR of *O. bartramii*. The same was true for *D. gigas*, where the AIC was –9748 and the RMSE was 0.09893 (Table 2). According to this selected model, *a* and *b* with fixed effects of *O. bartramii* were estimated at  $1.3295 \times 10^{-5}$  and 3.1395, respectively; and *a* and *b* with fixed effects of *D. gigas* were estimated at  $1.8982 \times 10^{-5}$  and 3.0629, respectively (Table 4, Figure S1). There were significant differences in the LWR of both squids by year and sex (*p* < 0.01).



**Figure 3.** Distribution of mantle length of *O. bartramii* in different years. The boxes show the median and the interquartile range. The black dots are indications of outliers in the data. The red dots show the mean.

Frequency/%





**Figure 4.** Distribution of mantle length of *D. gigas* in different years. The boxes show the median and the interquartile range. The black dots are indications of outliers in the data. The red dots show the mean.



**Figure 5.** The mantle length–weight relationships of *O. bartramii* and *D. gigas* based on the generalized linear model.

	Variables		Fixed Effects		Random Effects				Estimate of Parameter	
Species			ln( <i>a</i> )	b	ln(a)			b		
					Estimate	Confidence Interval	Estimate	Confidence Interval	- (×10 <sup>-5</sup> )	в
Ommastrephes bartramii	Year	2009 2010 2011 2012 2013 2014 2015 2016 2017 2012	-11.2281	3.1395	$\begin{array}{c} 0.5018 \\ -0.3874 \\ -0.7620 \\ 0.7982 \\ -0.1458 \\ -0.4229 \\ -0.6278 \\ -0.0406 \\ 0.1710 \\ 0.0175 \end{array}$	$ \begin{bmatrix} 0.2622, 0.7414 \\ [-0.6083, -0.1677] \\ [-1.0769, -0.4474] \\ [0.4996, 1.0959] \\ [-0.4983, 0.2065] \\ [-0.9091, 0.0623] \\ [-0.8639, -0.3927] \\ [-0.3187, 0.2377] \\ [-0.1675, 0.5106] \\ \end{bmatrix} $	-0.0851 0.0656 0.1331 -0.1391 0.0275 0.0746 0.1121 0.0025 -0.0310	$\begin{bmatrix} -0.1268, -0.0433 \\ [0.0270, 0.1043] \\ [0.0776, 0.1886] \\ [-0.1917, -0.0864] \\ [-0.0355, 0.0905] \\ [-0.0128, 0.1621] \\ [0.0708, 0.1535] \\ [-0.0463, 0.0513] \\ [-0.0906, 0.0283] \\ [-0.0906, 0.0283] \end{bmatrix}$	$\begin{array}{c} 2.1961 \\ 0.9025 \\ 0.6205 \\ 2.9536 \\ 1.1491 \\ 0.8710 \\ 0.7096 \\ 1.2766 \\ 1.5775 \\ 1.5775 \end{array}$	3.0544 3.2050 3.2725 3.0003 3.1670 3.2140 3.2515 3.1420 3.1084
	Sex	F M			-0.0940 0.0940	[-0.2563, 0.0646] [-0.0646, 0.2563]	0.0158 -0.0158	[-0.2495, -0.0711] [-0.0109, 0.0431] [-0.0431, 0.0109]	1.2102 1.4606	3.1553 3.1237
Dosidicus gigas	Year	2008 2009 2010 2011 2012 2013 2014 2015 2016 2017	-10.8720	3.0629	$\begin{array}{c} -0.1811\\ -0.8622\\ -1.0330\\ -0.6823\\ -0.8741\\ 0.6522\\ 1.1261\\ 0.6666\\ 0.2332\\ 0.9545\end{array}$	$\begin{matrix} [-0.5479, 0.1859] \\ [-1.1057, -0.6182] \\ [-1.2639, -0.8018] \\ [-0.9087, -0.4556] \\ [-1.1847, -0.5629] \\ [0.2367, 1.0677] \\ [0.6235, 1.6281] \\ [0.4012, 0.9321] \\ [-0.1436, 0.6101] \\ [0.2488, 1.6590] \end{matrix}$	$\begin{array}{c} 0.0331\\ 0.1469\\ 0.1788\\ 0.1218\\ 0.1574\\ -0.1153\\ -0.1902\\ -0.1158\\ -0.0554\\ -0.1613 \end{array}$	$ \begin{bmatrix} -0.0311, 0.0972 \\ [0.1033, 0.1903 ] \\ [0.1373, 0.2202 ] \\ [0.0804, 0.1632 ] \\ [0.1022, 0.2126 ] \\ [-0.1902, -0.0404 ] \\ [-0.2806, -0.0997 ] \\ [-0.1647, -0.0668 ] \\ [-0.1245, 0.0137 ] \\ [-0.2891, -0.0334 ] \\ \end{bmatrix} $	$\begin{array}{c} 1.5838\\ 0.8016\\ 0.6756\\ 0.9595\\ 0.7921\\ 3.6444\\ 5.8535\\ 3.6972\\ 2.3968\\ 4.9308\end{array}$	3.0960 3.2098 3.2418 3.1847 3.2204 2.9476 2.8727 2.9472 3.0076 2.9016
	Sex	F M			-0.1175 0.1175	[-0.2307, -0.0045] [0.0021, 0.2330]	$0.0240 \\ -0.0240$	[0.0009, 0.0470] [-0.0475, -0.0004]	1.6878 2.1351	3.0869 3.0390

Table 4. Estimates values for parameters a and b in the LMEM (R and Y.I and S).

In terms of different years, the maximum estimated *b* value occurred in 2011 (3.2725) for *O. bartramii*, followed by the estimate (3.2515) in 2015, and it had its minimum value (2.9794) in 2018 (Table 4, Figure S1). For *D. gigas*, the largest estimate of the *b* value was 3.2418 in 2010, followed by the estimate (3.2204) in 2012, and the smallest estimate was 2.8727 in 2014 (Table 4, Figure S1). In terms of sex, the *b* value of females was larger than that of males, whether *O. bartramii* or *D. gigas* (Table 4, Figure S1).

# 3.4. The Relative Condition Factor $(K_n)$

The fluctuations of  $K_n$  values are represented in Figure 6. There were significant differences in  $K_n$  by year and sex (p < 0.01). For *O. bartramii*, The  $K_n$  value of the female ranged from 0.9668 to 1.0276, and the  $K_n$  value of the male ranged from 0.9844 to 1.0375. The  $K_n$  value of females was lower than that of males. The annual variation trend for females and males was roughly the same, showing an upward trend from 2010 to 2012 and a downward trend from 2012 to 2016. In 2010–2011 and 2014–2016, the  $K_n$  value was less than 1. A cross-correlation analysis revealed significantly positive relationships between the Niño 3.4 index and  $K_n$ , and the highest correlation coefficients were 0.5108 for females and 0.4323 for males.



1		١
	A	
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**(B)** 

**Figure 6.** Variation in relative condition factors and Niño index of *O. bartramii* (**A**) and *D. gigas* (**B**). The black dot lines show the relative condition factor equal to 1.0.

As far as *D. gigas* was concerned, the  $K_n$  value of females ranged from 0.9425 to 1.0913, and that of males ranged from 0.9295 to 1.0713. The  $K_n$  value of females was greater than that of males. The annual variation trend in female and male  $K_n$  values was also roughly the same. From 2009 to 2013,  $K_n$  values showed an upward trend, sharply decreased from 2014 to 2016, and were lowest in 2016. With the exception of 2016, the  $K_n$  value of females was greater than 1, while the  $K_n$  value of males was less than 1 in half of the years. A significantly negative cross-correlation was found between Niño 1+2 index and  $K_n$  at a time lag of one year, and the highest correlation coefficients were –0.7134 for females and –0.5613 for males.

#### 4. Discussion

#### 4.1. Body Size of the Two Squids

Short-lived cephalopods are always affected by large-scale climate change and marine environmental changes, resulting in changes in habitat, fishery center of gravity, resource abundance, and spatial distribution [55,56]. As typical phenotypic plastic species, squids tend to make their morphology variable to adapt to the changing environmental conditions they experience, especially as oceanic species [15,32,57]. In this study, the ML group of *O. bartramii* and *D. gigas* was analyzed, and it was found that there were significant differences in ML by year and sex (p < 0.01).

In this study, squid had a larger body size in El Niño years (2009), followed by normal years (2012, 2013, and 2014), and the smallest body size in La Niña years (2010 and 2011). A similar conclusion was also suggested for *Todarodes pacificus* in the East China Sea [58]. Previous studies have suggested that individual body size is closely related to water temperature, with higher water temperatures causing body size to shrink, and lower water temperatures increasing body size [32,33]. In El Niño years, the water temperature in the fishing ground for *O. bartramii* was lower, which made the individual body size increase, while in La Niña years, the water temperature was higher, leading to a decrease in body size [35,54]. From 2015 to 2016, a strong El Niño event occurred in the Pacific Ocean. The water temperature decreased abnormally and the growth rate was slow, which made the body size larger during this period than in the last several years [35,54]. The impact of this phenomenon continued until 2018.

With regard to *D. gigas*, previous studies indicated that the dominant population of this squid off Peru changed dramatically between the 1990s (the small size group) and the early 2000s (mainly large individuals) [27]. In this study, the population structure of *D. gigas* from 2008 to 2017 had small and medium-sized groups dominating in 2008–2010, while small groups dominated in the remaining years. The year 2010 was a La Niña year. At this time, the water temperature off Peru decreased and upwelling increased, which promoted the entry of nutrients into the upper and middle waters, promoting the massive reproduction of phytoplankton, and provided more primary productivity for the squid, resulting in a large body size [59,60]. However, El Niño events occurred for two consecutive years in 2014 and 2015. Previous studies showed that, during the El Niño event, the water temperature in the eastern Pacific Ocean increased abnormally and productivity decreased [59,60]. The higher temperature and lack of food may inhibit the growth of *D. gigas*, making the body size smaller during this period, and the influence of this phenomenon continued until 2017. In addition, previous studies noted that climate change leads to changes in the morphology of cephalopod beaks, which in turn affect individual food intake and ultimately reflect individual body size changes [24,61].

In general, the change in individual size of *O. bartramii* showed an opposite trend to that of *D. gigas*, especially in 2009–2011 and 2014–2016, which may be related to its geographical location. *O. bartramii* and *D. gigas* are located in the northern and southern hemispheres, respectively. ENSO events in the northwest Pacific and the southeast Pacific would show opposite environmental changes, i.e., the water temperature in the Northwest Pacific Ocean would decrease and the water temperature in the Southeast Pacific Ocean would increase during an El Niño year. This phenomenon presented an opposite pattern in

La Niña years [6,54]. In addition, the average ML of female individuals was larger than that of male individuals in each year, and the annual difference in body size of females was greater than that of males. This indicated that female body morphology tends to be more plastic than males', which is consistent with previous studies [15,18,62]. Generally, a female squid grows faster than a male squid due to its high feeding rate, resulting in faster metabolism and gonad growth, as also proved in *Illex* species (*Illex illecebrous* and *Illex argentinus*) [63]. This may be a survival strategy for squid to maintain a certain population scale [15,63].

# 4.2. LWR of Two Squids and Their Sexual and Interannual Variations

The intraspecific variation in LWR is a very important indicator, depending on geographic region, the year or season, population size range, and/or annual variation in environmental conditions [42,53]. Ten models were used to estimate the LWR of two important squid species in the Pacific Ocean. The results indicated that mixed-effects models performed better than the generalized linear model. Substantial sexual and annual variations in growth were revealed for these two squids on different aspects of scales. The allometric growth parameter *b* can be used to explore the growth form in the body proportion, and its interannual change can be used as an indicator of the adaptability of marine organisms to changes in the marine environment [42,46]. In addition, in LWR, parameter *b* can represent the growth pattern of squid (negative allometric, isometric, and positive allometric growth patterns) [64]. In addition, Hile (1936) pointed out that there were obvious differences in the intraspecific growth patterns of squid, with growth parameter *b* ranging from 2.5 to 4.0 [65]. According to the results of LMEM (Y and S.I and S), the *b* values of *O. bartramii* (2.9636–3.2338) and *D. gigas* (2.8488–3.2657) in this study were both within this range.

For *O. bartramii*, the effect of ENSO events on its growth pattern was not obvious. When ENSO events occurred, the growth of O. bartramii was in positive allometric growth mode with little change. However, we found that the *b* value of *O*. *bartramii* in very strong El Niño years (2015) was greater than that in moderate El Niño years (2009). On the contrary, the *b* value in a moderate La Niña year (2011) was higher than that in a strong La Niña year (2010), which suggested that the b value might be negatively correlated with temperature. Higher temperatures with higher productivity lead to an increase in the metabolic rate of squid; the digestion process will speed up and the body will tend to become slender [66]. In addition, studies showed that the Kuroshio Current advected warmer and food-rich waters into the fishing ground of O. bartramii in La Niña years, while in El Niño years, the fishing ground had colder water and lower productivity [35,67]. Abundant food often increased the thickness of the body, which resulted in the *b* value in La Niña years (2010, 2011) being higher than that in moderate El Niño years (2009). So, temperature and food supply are both important factors affecting the interannual variation in squid growth [15,66]. In D. gigas, the ENSO event caused significant differences in the growth relationship in different years. The growth parameter b of D. gigas in La Niña years (2010) was much larger than that in El Niño years (2014 and 2015). The *b* value of the individual in a normal year was somewhere in between. High temperature and low nutrient intake may inhibit the growth and development of squid, while low temperature and high nutrient intake are conducive to growth and development [59,60]. This explains why the *b* value of *D*. *gigas* was low/high during the El Niño/La Niña event in this study. Moreover, the interannual variation of the growth parameter b of D. gigas was greater than that of O. bartramii, and O. bartramii generally exhibited positive allometric growth, while *D. gigas* exhibited negative allometric growth for several years, which may be due to the difference in response of these two squids to ENSO events [35,60]. As mentioned above, when ENSO events occurred, the influence of the changes in temperature and bait abundance in the fishing ground of *D. gigas* on their *b* values was consistent, while

the influence of the changes in temperature and bait abundance in the fishing ground of *D. gigas* on their *b* values was inconsistent.

In addition, this study found that the growth parameter *b* of females was greater than that of males in the two squid species, indicating that females had thicker bodies than males, a phenomenon also seen in *Sepia officinalis* [68] and *Uroteuthis edulis* [69]. Males convert most of the energy ingested into mantle growth, while females convert more of it into the reproductive system, which is reflected in the increase in body weight [70,71]. It can be inferred that the growth differences in cephalopods between different sexes may be related to the development of reproductive organs [15,71].

#### 4.3. Relative Condition Factors of Two Squids

A change in growth pattern reflects changes in the squid body, which can be analyzed by conditional factors [41]. The relative condition factor ( $K_n$ ) is an effective method to compare the relationship between individual weight and length at different stages [41,42,52]. The deviation between the  $K_n$  value and 1 reveals individual feeding condition or the fitness/well-being [41,72]. When  $K_n \ge 1$ , the growth condition of the individual is good, while when  $K_n < 1$ , the growth of the individual is poor compared to the average individual of the same length [43,72].

In this study, the growth status of *O. bartramii* fluctuated dramatically. The  $K_n$  value was relatively low, indicating that the growth condition of *O. bartramii* was poor. The growth condition of females was worse than that of males. We also found that in La Niña years (2010 and 2011) and the super El Niño year (2015), the  $K_n$  value was less than 1, indicating that its growth condition was poor, while in the moderate El Niño year of 2009, its growth condition was good.

For *D. gigas*, the growth condition was relatively good in these years, and the growth condition of females was greater than that of males. Its growth condition fluctuated slightly from 2009 to 2012 and showed an upward trend, but there was a large difference between males and females. Pecl et al. (2004) believed that the female individual had better mantle condition and higher reproductive growth in colder years [73]. Thus, the low water temperature caused by the La Niña event in 2010 may have contributed to this phenomenon. In addition, the  $K_n$  value fell sharply from 2014 to 2015, which might be due to the adverse environmental conditions caused by the El Niño in 2014-2015. Previous studies have shown that the poor growth condition of *D. gigas* in the Gulf of California and Mexican waters in 1998 and 1999 was considered to be caused by the 1997–1998 El Niño event [53]. The  $K_n$  value increased sharply in 2017, which may be related to the weakening of El Niño in 2016 and the La Niña event in the second half of 2017. Overall, the growth condition of O. bartramii was positively correlated with the Niño index, while the growth condition of D. gigas was negatively correlated with the Niño index. We also found that the  $K_n$  value of *D. gigas* showed a low peak and a high peak in 2013 (La Niña year) and 2014 (El Niño year), respectively, and the  $K_n$  of O. bartramii was also at a high peak in some normal years. Therefore, we believe that the growth of squid might not only be regulated by climatic factors but also affected by some other factors. Studies had also shown that many factors affect the individual's growth, including the reproductive cycle, level of gonadal maturity, number and density of predators, food availability, and habitat [42,53,74]. In addition, the relative condition factor is considered as the nutrient conditions of spawners; the survival rate of eggs is also lower when the growth/nutrient condition is poor [71,75–77]. Therefore, we can appropriately adjust the management strategy according to the actual situation. For example, with decreasing trends of  $K_n$ , fishermen can reduce resource development in the next few years to protect resources.

# 5. Conclusions

In this study, we explored the growth characteristics of these two squids by mantle length composition, LWR, and relative condition factors, and a series of life history parameters were obtained, which provided a certain reference value for subsequent study of population dynamics and related fishery management. In addition, the research showed that the growth of *O. bartramii* and *D. gigas* underwent obvious interannual changes, and their change trends were almost opposite, especially during the period of ENSO events. Thus, when ENSO events occur, how the growth of the two squids change with the environmental conditions can be deduced based on the present study, and we can provide different management schemes for the two squids. In addition, we could combine statolith microchemistry and stable isotopes ( $\delta^{13}$ C and  $\delta^{15}$ N) in future research to more accurately determine the habitats they experience at each stage of their life history by speculating on their migration route, so as to carry out profound research into the impact of climate change on their individual growth and migration paths.

**Supplementary Materials:** The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/fishes7050280/s1, Figure S1. Variations of *a* and *b* among years and sexes from the LMEM (Y&S.I&S). (A,B): estimates of parameter *a* and *b* with random effects of both years and sexes. (C): temporal variations of ln(*a*) and *b*. (D): Sexual variations of ln(*a*) and *b*.

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**Institutional Review Board Statement:** The study was conducted according to the guidelines of the Code of Ethics of the University Department of Marine Studies; all specimens obtained from the surveys were already dead.

**Data Availability Statement:** The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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