

Synchronous Variations in Abundance and Distribution of *Ommastrephes bartramii* and *Dosidicus gigas* in the Pacific Ocean

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Abstract An analysis was performed in this study to investigate synchronous fluctuations in abundance and distribution of *Ommastrephes bartramii* in the Northwest Pacific Ocean and *Dosidicus gigas* in the Southeast Pacific Ocean. The impacts of two Niño indices and regional water surface temperature on the two squids during 2006–2015 were evaluated, which possibly can explain the observed synchronicity. Catch per unit effort (CPUE) and the latitudinal gravity centers (LATG) of fishing effort were used to indicate squid abundance and distribution, respectively. The results indicated that both the CPUE and LATG showed highly interannual variations and synchronous fluctuation with significant negative associations between the two squid species from September to November. Strong positive cross-correlations with 2-month lag was found between sea surface temperature (SST) anomaly in the Niño 3.4 and Niño 1+2 regions, which have significant linkage with the SST on the fishing ground of *O. bartramii* and *D. gigas*, respectively. Moreover, the proportion of favorable-SST area (PFSST) and the latitudinal location of the optimal SST for *O. bartramii* and *D. gigas* were positively correlated with the CPUE and LATG, respectively. Increased *O. bartramii* PFSST clearly corresponded to decreased *D. gigas* PFSST in phase as well as the latitudinal location of the optimal SST from September to November over 2006–2015. Our findings suggest that synchronous changes in abundance and distribution of the two squids were due to simultaneous variations in the PFSST and the latitudinal location of the optimal SST front which were affected by the SSTA changes in the Niño 3.4 and Niño 1+2 regions.

Key words *Ommastrephes bartramii*; *Dosidicus gigas*; distribution and abundance; synchronous variability; environmental effects

1 Introduction

Ommastrephid squids are characterized by short life-cycle, rapid growth, early maturation, high migratory capacity, and complicated recruitment patterns (Boyle, 1990; Dunning and Wormuth, 1998; Rodhouse, 2008). Most squids inhabit in the waters of the shelf, slope, and open oceans, with the depths from the surface to 2000 m (Anderson and Rodhouse, 2001). Squids play a critical role in the marine food webs, serving as prey for large-size marine animals and predator for small-size fish and zooplankton (Cherel and Weimerskirch, 1995; Parry, 2006). Many squids are

economically important and considered as the crucial commercial fishery target among global distant-water fisheries (Arkhipkin *et al.*, 2015). Annual catches of Ommastrephid squids in the recent decade are over two million tons, accounting for about 50% of the cephalopod catches in the world (Chen *et al.*, 2008). Among the Ommastrephid squids, the oceanic squid such as Japanese flying squid *Todarodes pacificus* in the Sea of Japan, the East China Sea and the westerns Pacific Ocean (Kang *et al.*, 2002; Lee *et al.*, 2019), the *Nototodarus sloanii* in New Zealand waters (Jackson *et al.*, 2000), the neon flying squid *Ommastrephes bartramii* in the North Pacific Ocean (Bower and Ichii, 2005) and the jumbo flying squid *Dosidicus gigas* in the Eastern Pacific Ocean (Nigmatullin *et al.*, 2001) are the most important species in terms of catches

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and economic values. The two latter squid species are the main fishing targets by Chinese squid-jigging fisheries. Mainland China started to exploit *O. bartramii* in 1993 and *D. gigas* in 2001. Both catches accounted for a large amount of the total catches in China (Chen *et al.*, 2008).

Ommastrephes bartramii is an abundant squid species widely distributed in the North Pacific Ocean (Bower and Ichii, 2005). The *O. bartramii* population includes two seasonal spawning cohorts: the winter-spring cohort and the autumn cohort. Each cohort has different geographical stocks (Chen and Chiu, 2003). The former cohort comprises the western and central-eastern stocks, and the latter cohort comprises the central and eastern stocks (Ma *et al.*, 2011). Both cohorts perform south-to-north migration from the spawning ground in the subtropical front to the feeding ground in the subarctic domain. At present, *O. bartramii* is mainly captured by China (including Chinese Taipei) and Japan (Ichii *et al.*, 2006). Mainland China targeted the western winter-spring cohort on the fishing ground between 35°–50°N and 150°–175°E (Chen *et al.*, 2009; Yu *et al.*, 2015). The annual catch in China accounts for more than 80% of the total catches of *O. bartramii* in the North Pacific Ocean (Chen *et al.*, 2008).

For *D. gigas*, it is a large-size squid species widely distributed in the Eastern Pacific Ocean (Argüelles *et al.*, 2001). This squid is largely utilized by hundreds of international squid-jigging fishing vessels from Asia-Pacific (*e.g.*, China and Japan) and South America-Pacific countries (*e.g.*, Peru and Chile) (Taipe *et al.*, 2001; Chen *et al.*, 2008). Most fishing operations occur at night, using powerful lamps attracting the squids. At present, four major fishing grounds are largely exploited in the Gulf of California, the offshore waters of the Costa Rica Dome, the high seas at the equator between 5°N–5°S and 130°–90°W, and the coastal and oceanic regions off Peru and Chile (Hernández-Herrera *et al.*, 1998; Waluda *et al.*, 2004; Zeidberg and Robison, 2007; Morales-Bojórquez and Pacheco-Bedoya, 2016). In the Southern Hemisphere, the most abundant fishing grounds are located in the oceanic regions off Peru, which are mainly exploited by Chinese fishing vessels (Hu *et al.*, 2019). The total catches of *D. gigas* from China are the highest and accounted for about 50% of the total catches in the world (Chen *et al.*, 2008).

The yearly catch of *O. bartramii* and *D. gigas* from China is high; however, it tends to demonstrably fluctuate across years (Paulino *et al.*, 2016; Igarashi *et al.*, 2017). According to previous studies, one important reason causing the fluctuation is the climate-driven regional environmental changes on the fishing ground, which can strongly affect squid distribution and abundance (Igarashi *et al.*, 2018; Frawley *et al.*, 2019). Pelagic fishery enterprises from China have assigned hundreds of squid-jigging vessels into the Pacific Ocean to exploit *O. bartramii* and *D. gigas*. Without understanding the impacts of local environmental variability on squid abundance and distribution, or the cause of synchronous fluctuations in *O. bartramii* and *D. gigas*, the enterprises are difficult to decide where to fish and what the number of the fishing vessels should be assigned in the Northwest Pacific Ocean and in the

Southeast Pacific Ocean. Thus, for more effective fisheries management, it is essential to examine the associations between the two squid species, especially the synchronous fluctuations in abundance and distribution in relation to the climatic and environmental factors.

In this study, catch per unit effort (CPUE) and the latitudinal gravity centers (LATG) of fishing effort were used to indicate squid abundance and distribution, respectively. The synchronous fluctuations in abundance and distribution of *O. bartramii* in the Northwest Pacific Ocean and *D. gigas* in the Southeast Pacific Ocean were investigated. The impacts of two Niño indices (*i.e.*, Niño 3.4 and 1+2 region) and regional water surface temperature on the two squid species were further assessed. The purposes of this study were to 1) examine the synchronous fluctuations in CPUE and LATG between *O. bartramii* and *D. gigas*; 2) evaluate the impacts of environmental factors on variability of squid abundance and distribution; and 3) explore the possible cause that responsible for the observed synchronicity and provide some important implications for Chinese squid-jigging fisheries.

2 Materials and Methods

2.1 Fisheries Data Collection

Commercial logbook data for Chinese *O. bartramii* and *D. gigas* squid-jigging fisheries grouped by 0.5°×0.5° grid cell and by month were obtained from the National Data Center for Distant-water fisheries of China, Shanghai Ocean University. The fishing months from September to November for both squids were the most important fishing seasons due to the extremely high squid abundance and catches. Thus, data from September to November during 2006–2015 were used in the analysis. The data contained fishing effort (days fished), the location of fishing ground (latitude and longitude in degrees) and catch (unit: tonnes). Fishing locations for the *O. bartramii* and *D. gigas* fisheries were primarily bounded by 36°–48°N and 150°–170°E in the Northwest Pacific Ocean and by 8°–20°S and 95°–75°W in the Southeast Pacific Ocean, respectively (Fig.1).

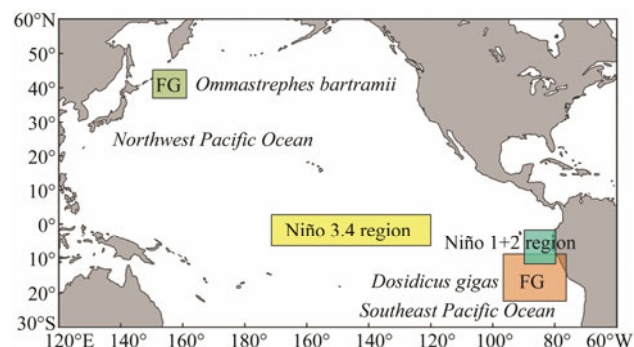


Fig.1 The geographical distribution of fishing ground (FG) for *Ommastrephes bartramii* in the high seas of Northwest Pacific Ocean and *Dosidicus gigas* outside of the exclusive economic zone off Peru in the Southeast Pacific Ocean. The Niño 3.4 and Niño 1+2 regions are also shown on the map.

In this study, we examined the variability in the abundance and distribution of *O. bartramii* and *D. gigas* from September to November during 2006–2015. For short-lived squid species, abundance and distribution can be effectively indicated by CPUE and the latitudinal gravity centers (LATG) of fishing effort (Cao *et al.*, 2009; Yu *et al.*, 2016). The CPUE (catch per unit effort) within a $0.5^\circ \times 0.5^\circ$ fishing grid for the two squid species were calculated by the following equation (Cao *et al.*, 2009):

$$\text{CPUE} = \frac{\sum \text{Catch}}{\sum \text{Fishing effort}}, \quad (1)$$

where $\sum \text{Catch}$ is the sum of catch for all the fishing vessels within a fishing grid; and $\sum \text{Fishing effort}$ is the sum of fishing days for all the fishing vessels within a fishing unit. For Chinese squid-jigging fishing vessels in the western and southeastern Pacific Ocean, they were equipped with almost same fishing powers with similar engines, lamps. And fishing activities were all performed at night without bycatch (Chen *et al.*, 2008). Thus, CPUE was used as a proxy to indicate squid abundance for the two squids.

The monthly LATG for the two squid fishery was calculated using the following equation (Li *et al.*, 2014; Yu *et al.*, 2016):

$$\text{LATG}_m = \frac{\sum (\text{Latitude}_{(i,m)} \times \text{Fishing effort}_{(i,m)})}{\sum \text{Fishing effort}_{(i,m)}}, \quad (2)$$

where $\text{Latitude}_{(i,m)}$ is the latitude within the i th fishing unit in month m ; $\text{Fishing effort}_{(i,m)}$ is the total fishing efforts within the i th fishing unit in month m . In addition, correlations between annual CPUE and LATG for each squid fishery were examined statistically using Pearson's r correlation analysis.

2.2 Oceanographic Variables and Climatic Index

Sea surface temperature (SST) was considered as a critical environmental driver for the distribution and abundance of squid species (Yu *et al.*, 2015). In this study, the monthly SST was from the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation (OI) SST Version2 with spatial resolution of $0.25^\circ \times 0.25^\circ$. The SST data were grouped on a $0.5^\circ \times 0.5^\circ$ latitude/longitude grid to match with the spatial resolution of fishery data.

The monthly SST anomaly (SSTA) in the Niño 3.4 region (between 5°N – 5°S and 120° – 170°W , close to *O. bartramii* fishing ground) and Niño 1+2 region (between 0° – 10°S and 90° – 80°W , close to *D. gigas* fishing ground) were used as indicators to represent the climate variability in the Northwest and the Southeast Pacific Ocean, respectively. Many studies have proved that Niño 3.4 and 1+2 SST yielded significant impacts on environmental changes on the fishing ground of *O. bartramii* and *D. gigas*, respectively (Chen *et al.*, 2007; Alabia *et al.*, 2016; Yu *et al.*, 2016). Therefore, the climate index data from Niño 3.4 and 1+2 regions were selected and obtained from the IRI/

LDEO Climate Data Library during the period from January 2005 to December 2015 (<http://iridl.ldeo.columbia.edu/SOURCES/.Indices/>).

2.3 Impacts of Environmental Changes on Squids

To explore the connection between the climate variability in the Northwest and the Southeast Pacific Ocean, the relationship between the SSTA in the Niño 3.4 and Niño 1+2 regions were initially evaluated by using cross-correlation functions (CCF). Moreover, in order to understand the impacts of large-scale climate variability on the local water thermal conditions, correlations between monthly Niño 3.4 SSTA/Niño 1+2 SSTA and monthly SST anomaly on each fishing ground were also calculated based on spatial correlation analysis.

Histogram analysis was applied to define the suitable and optimal environmental range for *O. bartramii* and *D. gigas* by relating fishing effort to the SST (Zainuddin *et al.*, 2006). Through the analysis above, the proportion of favorable-SST area (PFSST) and the latitudinal location of the optimal SST were further determined and compared between *O. bartramii* and *D. gigas* by month. The monthly PFSST from September to November was calculated based on the percentage of suitable SST ranges favorable for the distribution of *O. bartramii* and *D. gigas* accounting for the whole fishing ground. Moreover, the relationships between PFSST and the optimal SST latitude and the CPUE and LATG were examined to explore how squid abundance and distribution varied with different environmental conditions. Finally, the years of 2007 (a La Niña year), 2012 (a normal climate year) and 2015 (an El Niño year) were selected to compare the SST change on the fishing ground and its influence on the movement of LATG of *O. bartramii* and *D. gigas* under different climate conditions.

3 Results

3.1 Temporal Variations in CPUE and LATG

The monthly CPUE from July to November for *O. bartramii* and from January to December for *D. gigas* were shown in Fig.2. Both squid fishery displayed a high degree of monthly variability. The *O. bartramii* CPUE tended to increase from July to August and then decreased in the following months. For the *D. gigas* CPUE, it decreased from January to April and then increased in the subsequent fishing months. By comparing the two squid fisheries, opposite fluctuation trends in the monthly average CPUE were observed from September to November. Decreased *O. bartramii* CPUE corresponded to increased *D. gigas* CPUE in each month.

The CPUE and LATG from September to November over 2006–2015 were chosen to compare the two squid fisheries (Fig.3). Interannual variability and synchronous fluctuation were observed in the *O. bartramii* and *D. gigas* CPUEs with significant negative correlations between them ($r = -0.889$, $P < 0.001$). With an opposing annually variability trend, statistically significant negative correla-

tions were also found between the LATG of *O. bartramii* and *D. gigas* ($r = -0.820$, $P < 0.001$), suggesting that the

LATG of *O. bartramii* performed northward movement, while the *D. gigas* also generally shifted northward.

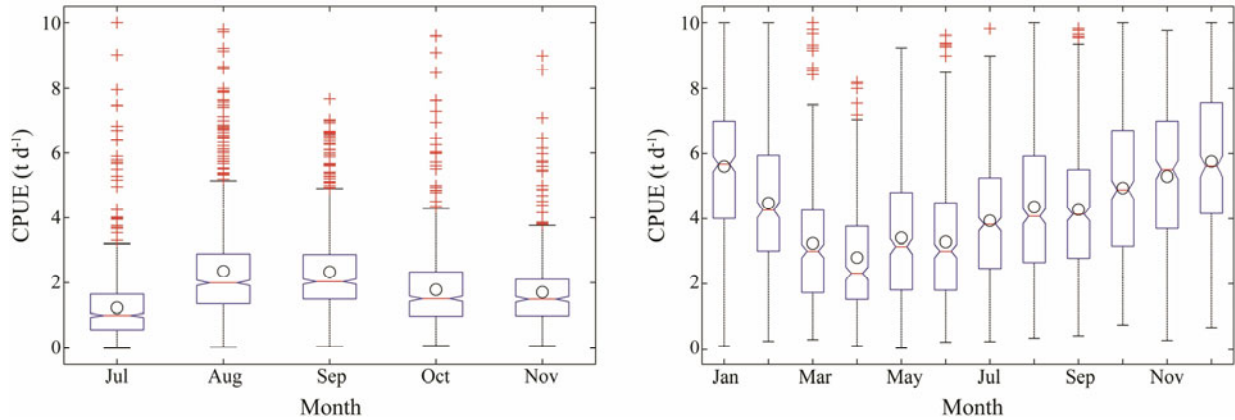


Fig.2 Monthly catch per unit effort (CPUE) of *Ommastrephes bartramii* from July to November and *Dosidicus gigas* from January to December during 2006–2015. The open circles indicate the monthly average CPUE.

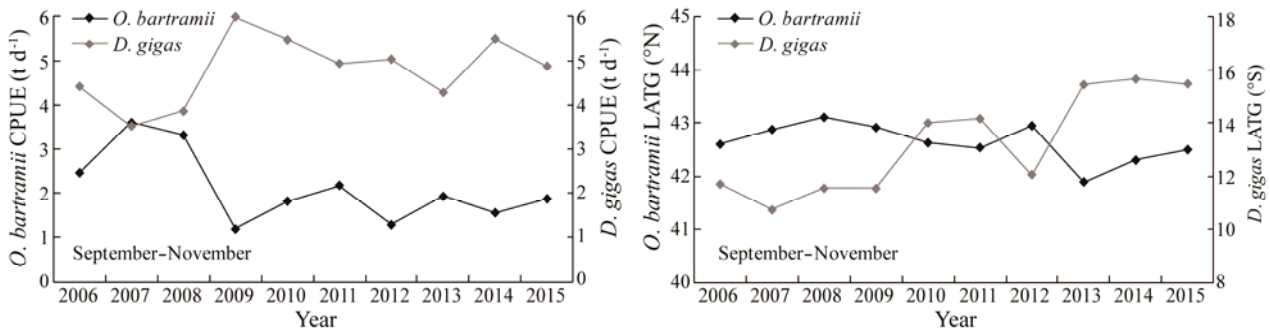


Fig.3 Squid abundance (catch per unit effort, CPUE) and distribution (latitudinal gravity centers, LATG) of *Ommastrephes bartramii* and *Dosidicus gigas* from September to November over 2006–2015.

3.2 Variability in the Environmental Conditions

Time series of SSTA in the Niño 3.4 and Niño 1+2 were examined from 2005 to 2015 (Fig.4). Results suggested that a basically consistent trend was observed between them. Furthermore, a significantly positive cross-correlation

was found between the Niño 3.4 SSTA and Niño 1+2 SSTA at time lag of (–3)–7 months. With time-lag of 2 months, the highest correlation coefficient was 0.7135, implying that the variability trends of the SSTA within the two Niño regions were largely similar and synchronously occurred.

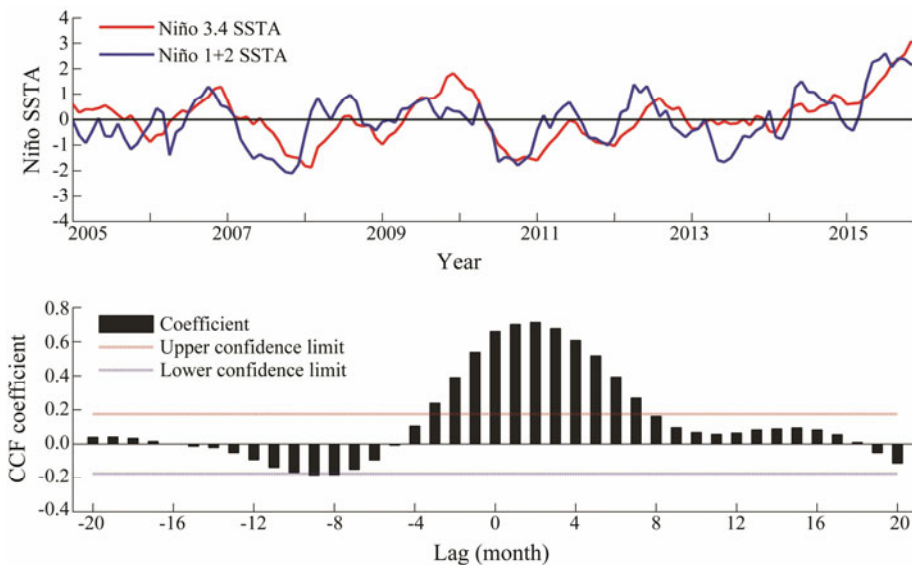


Fig.4 The time series of Niño 3.4 index and Niño 1+2 index from 2005 to 2015 (upper panel) and the cross-correlation coefficient between them (lower panel).

Because the *O. bartramii* fishing ground and *D. gigas* fishing ground were close to the Niño 3.4 region and Niño 1+2 region, respectively (Fig.1), we then examined the influences of Niño 3.4 SSTA/Niño 1+2 SSTA on the SSTA in each adjacent fishing ground. Correlations between the Niño 3.4 SSTA and the SSTA on the *O. bartramii* fishing ground showed a significant negative relationship (Fig.5). However, in terms of the SSTA on the *D. gigas* fishing ground, the Niño 1+2 SSTA was positively correlated with it (Fig.5).

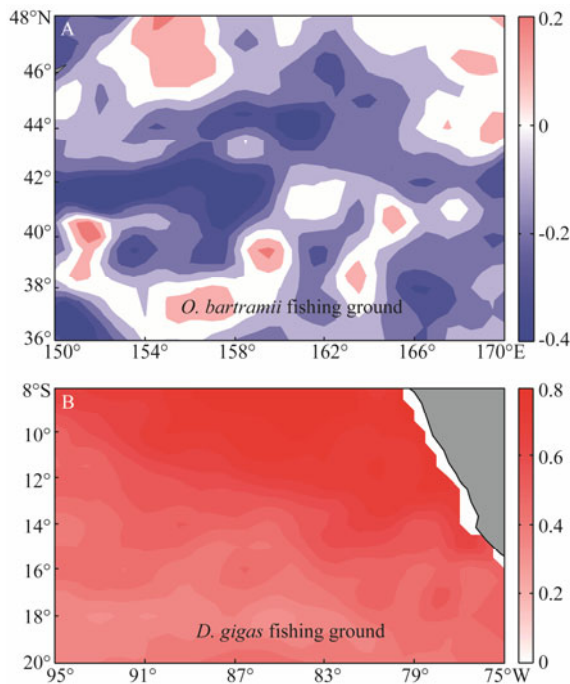


Fig.5 Spatial distribution of correlation coefficient (A) between the Niño 3.4 index and the sea surface temperature anomaly (SST) anomaly on the fishing ground of *Ommastrephes bartramii* (upper panel); and (B) between the Niño 1+2 index and the sea surface temperature (SST) anomaly on the fishing ground of *Dosidicus gigas* (lower panel).

3.3 Influences of Environmental Conditions on Squid CPUE and LATG

Using the histogram analysis, the fishing efforts for *O. bartramii* fishery during September to November occurred in areas where SST ranged from 4°C to 25°C. However, most high fishing efforts were obtained in the waters where SST varied primarily between 11°C and 20°C. The highest fishing effort in fishing ground tended to be centered at 15°C SST (Fig.6). Distribution of fishing effort of *D. gigas* fishery in relation to SST indicated that the *D. gigas* fishing ground occurred between 10°C and 25°C SST. The high fishing effort was mainly taken in fishing grounds where the SST ranged from 16°C to 20°C. The highest fishing efforts most frequently occurred at 18°C SST (Fig.6). Based on these results, the suitable SST ranges for *O. bartramii* and *D. gigas* during September to November were defined at 11–20°C and 16–20°C, respectively. The optimal SST for *O. bartramii* and *D. gigas* corresponded to 15°C and 18°C, respectively. The suitable SST ranges for the two

squids were then used to determine the PFSST.

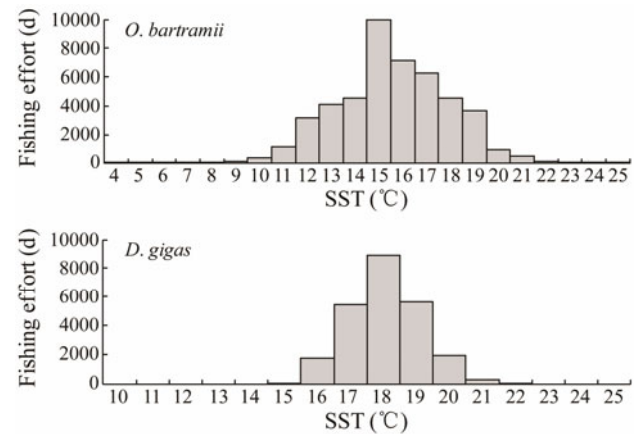


Fig.6 Fishing efforts in relation to sea surface temperature (SST) for *Ommastrephes bartramii* (upper panel) and *Dosidicus gigas* (lower panel) from September to November over 2006–2015.

The monthly *O. bartramii* CPUEs were significantly increased with the PFSST (areas with SST between 11–20°C) on the fishing ground in the Northwest Pacific Ocean (Fig.7A) ($P < 0.05$). For the correlation between *D. gigas* CPUEs and PFSST (areas with SST between 16–20°C) in the Southeast Pacific Ocean, no significant relationship was found; however, most high CPUEs occurred with enlarged PFSST (Fig.7B). Significant positive relationships were also found between the monthly latitudinal location of 15°C isotherm and *O. bartramii* LATG (Fig.7C) ($P < 0.001$), as well as between the monthly latitudinal location of 18°C isotherm and *D. gigas* LATG (Fig.7D) ($P < 0.05$).

We compared the interannual variability in PFSST on the *O. bartramii* fishing ground and *D. gigas* fishing ground month by month from September to November (Fig.8). During September, *O. bartramii* PFSST ranged from 45.1% in 2012 to 64% in 2015. For *D. gigas*, the PFSST varied between 60.6% and 89.6%. Statistically significant negative correlations ($r = -0.714$, $P < 0.05$) were found between *O. bartramii* PFSST and *D. gigas* PFSST in September. In October, the range of *O. bartramii* PFSST was from 42.2% in 2009 to 59.1% in 2006. The highest *D. gigas* PFSST reached up to 89.6% in 2013, while the lowest value was observed in 2015. A significantly negative relationship ($r = -0.787$, $P < 0.01$) was also found between them in October. However, for the PFSST in November, the relationship between the squid stocks was not significant ($r = -0.326$, $P = 0.179$). It was observed that opposite fluctuation in the PFSST was found from 2006 to 2008 and from 2010 to 2014, while the variability trend was similar with other years.

The location of the most preferred SST isotherms for *O. bartramii* and *D. gigas* were drawn in Figs.9 and 10. It was found that the 15°C isoline from September to November in 2007 and 2012 was distributed in the northern regions on the fishing ground of *O. bartramii* relative to the year in 2015. For *D. gigas*, it was clear that the 18°C isoline for each month was distributed in the northern,

middle and southern regions on the fishing ground. Specifically, the 18°C isotherm moved out of the fishing ground

in November 2015, as the SST on the fishing ground was higher than 18°C.

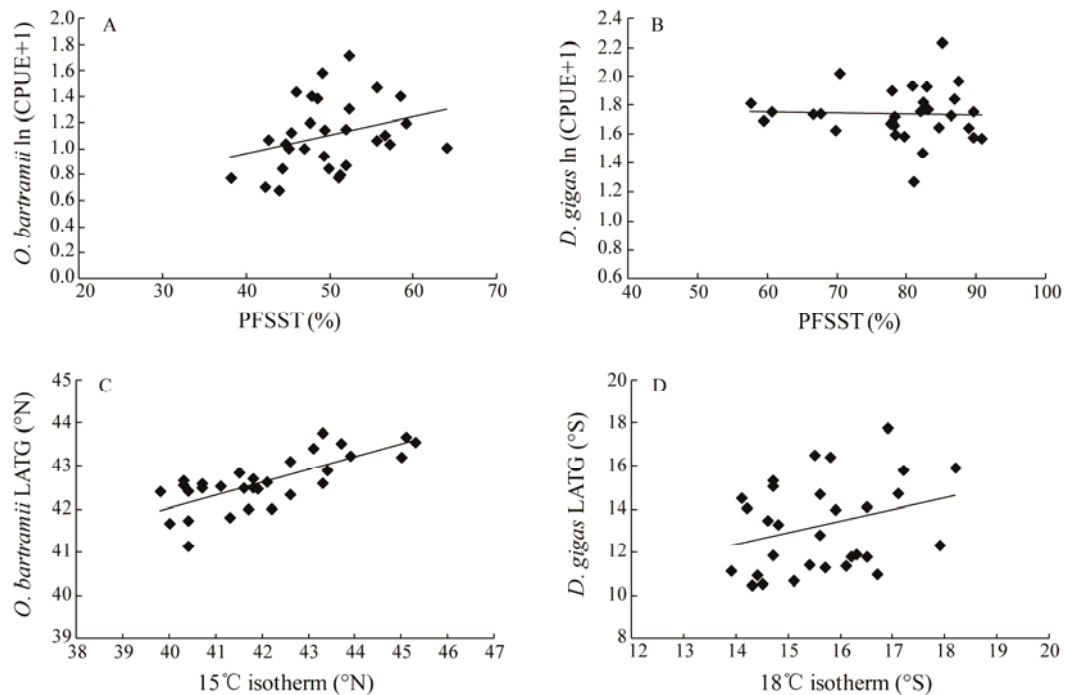


Fig. 7 The relationship between the natural log-transformed catch per unit effort (CPUE) and proportion of favorable-SST area (PFSST) for (A) *Ommastrephes bartramii* and (B) *Dosidicus gigas*, and between the latitudinal gravity centers (LATG) and the average latitude of the optimal SST isotherm for (C) *Ommastrephes bartramii* and (D) *Dosidicus gigas* during September–November 2006–2015.

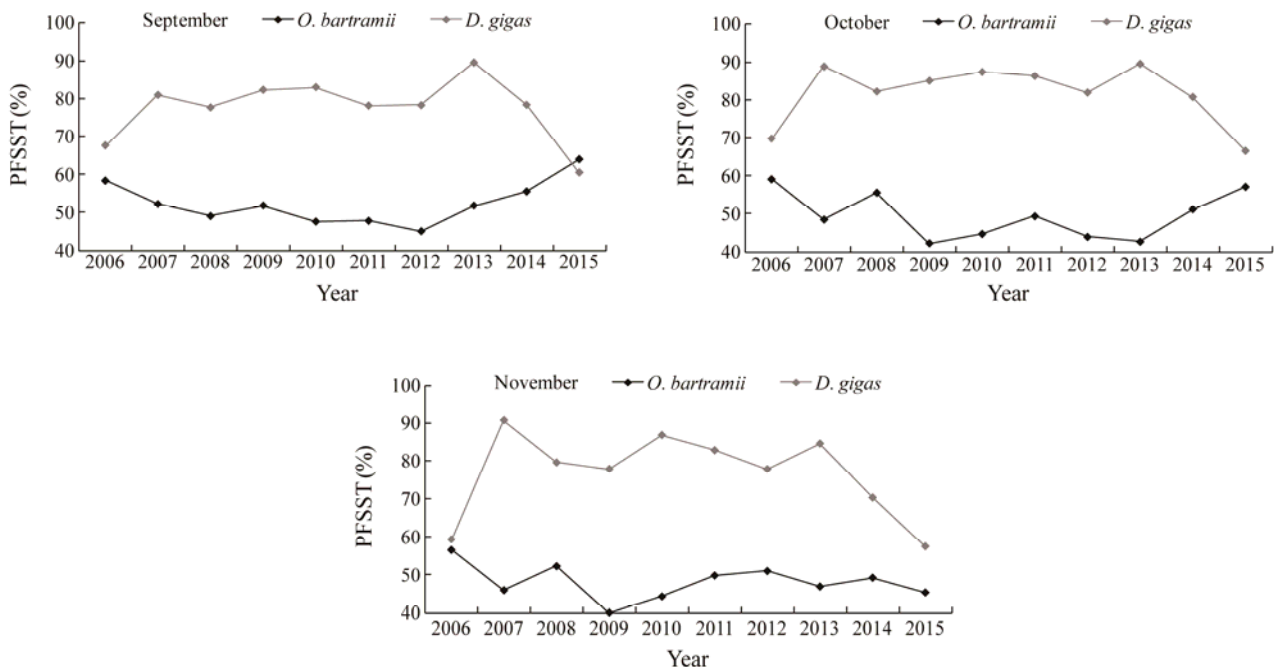


Fig. 8 Monthly proportion of favorable-SST area (PFSST) for *Ommastrephes bartramii* and *Dosidicus gigas* from September to November, respectively.

4 Discussion

4.1 Monthly and Yearly Variations of *O. bartramii* and *D. gigas* Abundance and Distribution

Due to only 1-year life cycle, both *O. bartramii* and *D.*

gigas are very sensitive to the climatic and environmental conditions on the spawning and fishing grounds at various spatio-temporal scales (Wang *et al.*, 2017). Therefore, the catch, CPUE and LATG of the two squid species showed significant monthly and yearly variations (Ibáñez *et al.*, 2016; Yu *et al.*, 2019). For *O. bartramii*, its abun-

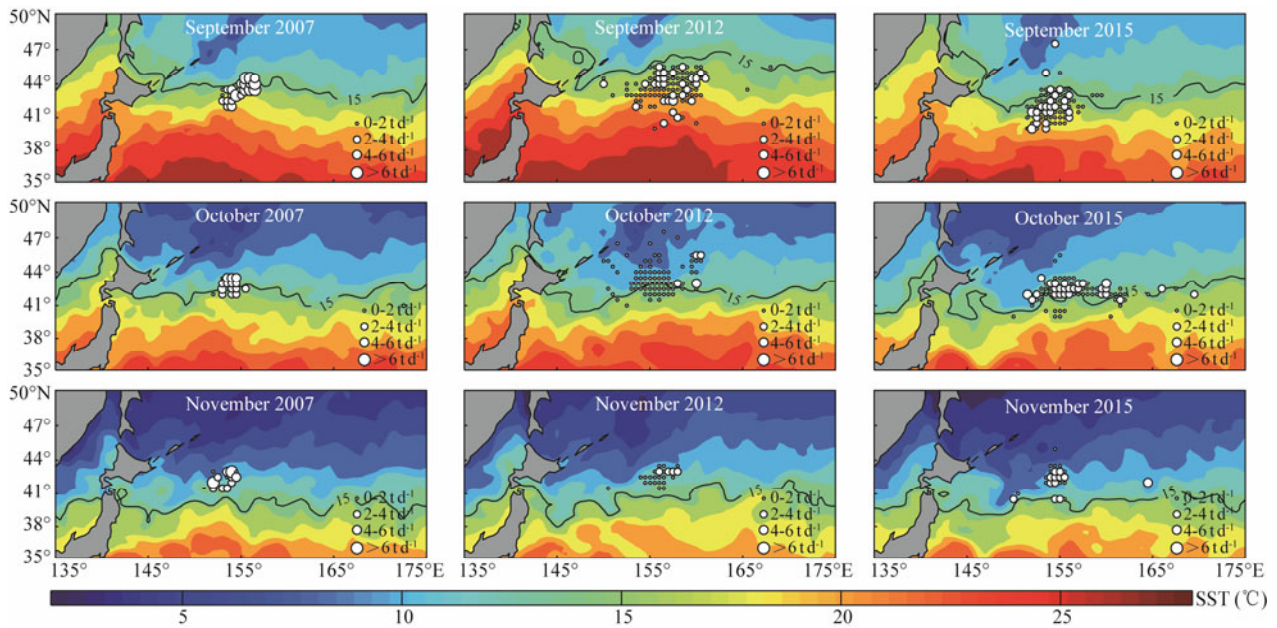


Fig.9 Contour maps of sea surface temperature (SST) with optimal SST isotherm (15°C) for *Ommastrephes bartramii* from September to November over 2007, 2012 and 2015.

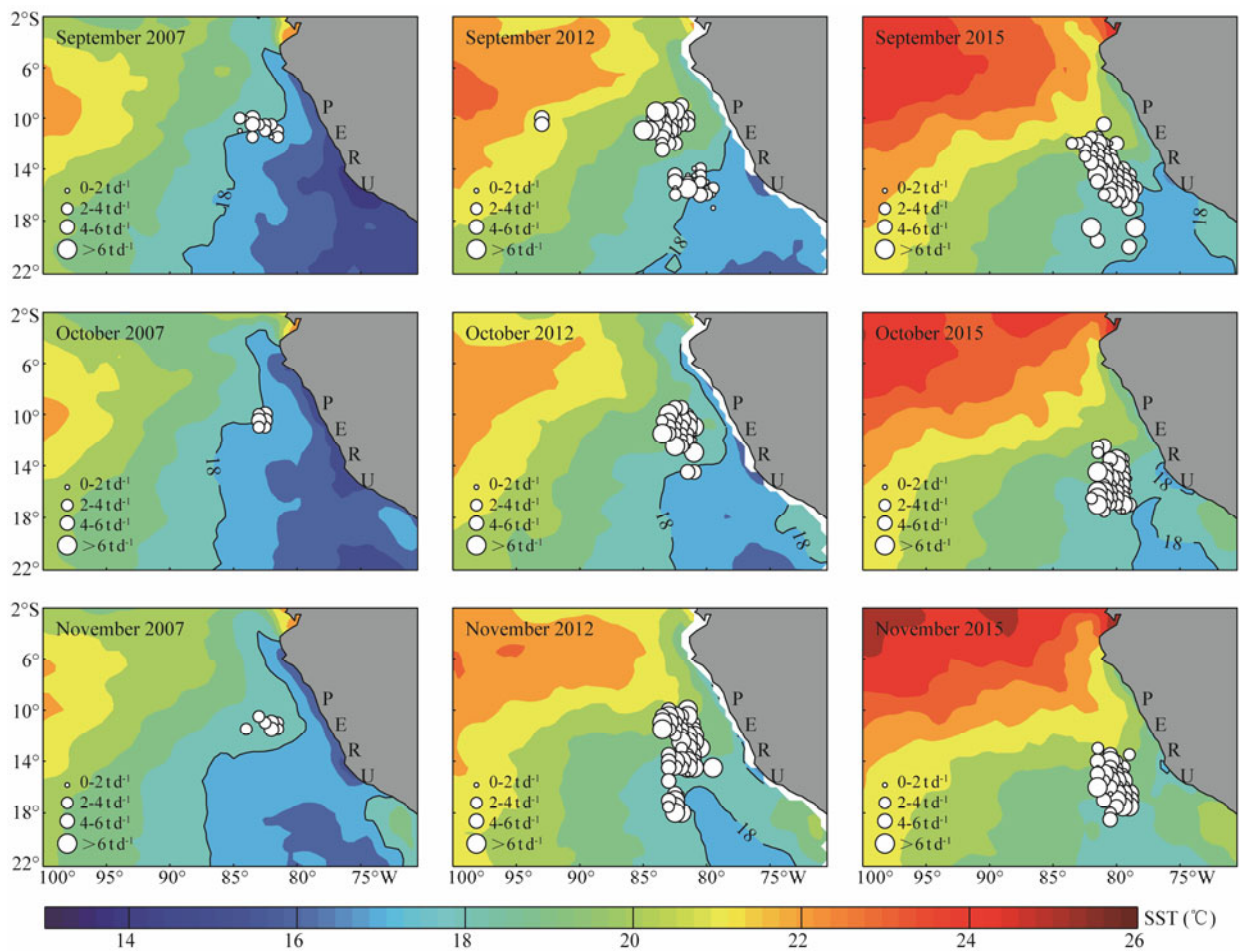


Fig.10 Contour maps of sea surface temperature (SST) with the optimal SST isotherm (18°C) for *Dosidicus gigas* from September to November over 2007, 2012 and 2015.

dance was low in July and relatively high from August to November. Such variability trends in CPUE of *O. bartramii* were consistent with its migration behavior (Yu *et al.*, 2016). The western winter-spring *O. bartramii* stock most-

ly migrated into the fishing ground in August and back into the spawning ground in November (Bower and Ichii, 2005). Based on the characteristics of the life history, Chinese fishermen started to fish *O. bartramii* in July every

year (Yu *et al.*, 2015). For *D. gigas* fishery off Peru, the high CPUE occurred from July to December, it also corresponded to the migration route of *D. gigas* from the near-shore waters off Peru to the open sea outside the EEZ waters off Peru (Xu *et al.*, 2018). Our results were consistent with previous conclusions on seasonal changes of abundance of *O. bartramii* and *D. gigas*.

Regarding the annual CPUE and LATG between *O. bartramii* and *D. gigas*, our results showed the significantly negative relationship between them, while both CPUE and LATG changed synchronously for the two squids. To our knowledge, this is the first study to find such results. Interestingly, it was found that high CPUE of *O. bartramii* generally corresponded to low CPUE of *D. gigas*, and the movements of LATG of these two squid species were basically similar from September to November during 2006–2015. For *O. bartramii* stock, the CPUE was low in 2009 and 2015 and high in 2007 and 2008. Based on previous findings, *O. bartramii* was strongly affected by the El Niño and La Niña events (Chen *et al.*, 2007). Generally, the El Niño events are not favorable for the formation of fishing ground with productive squid abundance (Yu *et al.*, 2019). Therefore, the occurrence of the El Niño events in 2009 and 2015 led to the low CPUE of *O. bartramii*. On the contrary, in 2007 and 2008, the La Niña event and the normal climate condition resulted in high abundance of *O. bartramii*. However, it was found that the CPUEs of *D. gigas* in 2009 and 2015 were high in this study. According to the findings from the previous studies, the El Niño events commonly yielded enlarged poor habitats for *D. gigas* and consequently led to relatively low abundance of it (Ichii *et al.*, 2002; Waluda *et al.*, 2006; Xu *et al.*, 2012). The opposite results were likely due to the different data used in the analysis. This analysis only included the months with high CPUEs of *D. gigas* from September to November. The influences of the El Niño and La Niña events on *O. bartramii* and *D. gigas* are quite complicated, depending on the intensity and type of the anomalous climate conditions.

4.2 The Effect of SST on *O. bartramii* and *D. gigas* Abundance and Distribution

It was well known that various environmental factors such as SST, sea surface height (SSH), chlorophyll-*a* (Chl-*a*) concentration played crucial roles in regulating the abundance and distribution of squid species (Waluda and Rodhouse, 2006; Robinson *et al.*, 2013; Yu *et al.*, 2015). However, among these factors, SST was considered as the most important one during the whole life of ommastrephid squids (Yatsu *et al.*, 2000; Ichii *et al.*, 2009). SST directly affects squid spawning location, breeding time and behavior, migration, feeding, growth, survival and physiological metabolism, *etc* (Pecl and Jackson, 2008; Rosa *et al.*, 2011; Frawley *et al.*, 2019). Squid species can quickly respond to SST changes. They will move to suitable habitat if the SST in the original region is not favorable for inhabiting (Xu *et al.*, 2016; Yu and Chen, 2018). SST is frequently used in many studies to model the habitat formation and identify spatio-temporal changes of fishing ground for squid

species (Chen *et al.*, 2010; Yu *et al.*, 2019).

In the Northwest Pacific Ocean, the SST is the most suitable index to explore fishing grounds of *O. bartramii*. For example, the fishing ground of *O. bartramii* can be identified by dense distribution of isotherm surface water layer, convergence of warm and cold waters and thermal layer based on the SST (Shen *et al.*, 2004). The suitable SST range for *O. bartramii* varied with seasons and fishing locations. The seasonal and spatial distributions of *O. bartramii* were largely explained by 7–17°C SST in winter and 11–18°C in summer (Alabia *et al.*, 2015). The 17°C and 20°C SST isotherms are regarded as the fishing ground index with high *O. bartramii* abundance in the west of 155°E, and between 155° and 160°E (Chen, 1997). These results are consistent with our findings. Moreover, the SST contributes the highest to the habitat model gain comparing to other factors, indicating that the habitat formation of *O. bartramii* is highly vulnerable to drastic changes in SST (Alabia *et al.*, 2015).

With regard to *D. gigas*, there are four major fishing grounds in the Eastern Pacific Ocean, the suitable ranges of SST for *D. gigas* vary with seasons and different geographical distributions (Medellín-Ortiz *et al.*, 2016; Yu *et al.*, 2018). Previous studies showed that jumbo squids off Peru usually live in waters with SST ranging from 17 to 22°C (Waluda *et al.*, 2006), which is in accordance with the results in this study. Habitat modeling method revealed that the weighing of SST relative to SSH and Chl-*a* also contributed the highest to the suitable habitat model (Hu *et al.*, 2010). Furthermore, strong relationship was found between SST and CPUE for the two squids. Interannual variability in squid abundance and distribution are closely linked to variations in SST on the spawning and fishing ground (Cao *et al.*, 2009; Ichii *et al.*, 2011). Given that SST can define the limits of the habitat of squids, this study employed SST as the only environmental variable to analyze the SST-related synchronous fluctuations in abundance and distribution of *O. bartramii* and *D. gigas*.

4.3 Possible Causes of Synchronous Fluctuations of *O. bartramii* and *D. gigas* and Its Implications

A growing number of studies proved that large-scale climate changes have yielded strong impacts on local environmental conditions on the fishing ground of pelagic fish (Tian *et al.*, 2003; Zainuddin *et al.*, 2006). In this study, it was found that the change trends of SSTA in the Niño 3.4 and Niño 1+2 regions showed the similar variability pattern during 2006–2015. The negative relationship was found between Niño 3.4 SSTA and the SSTA on the fishing ground of *O. bartramii*, while the positive one was found between the Niño 1+2 SSTA and the SSTA on the fishing ground of *D. gigas*, suggesting that the SST on the fishing ground of these two squids was dramatically influenced by the large-scale synchronous SSTA variability in the Niño 3.4 and 1+2 regions. Considering all the information, the possible causes of synchronous fluctuations in abundance and distribution of *O. bartramii* and *D. gigas* can be indicated. The fishing ground of the two

squids *O. bartramii* and *D. gigas* are in the Northern Hemisphere and Southern Hemisphere respectively. Synchrony in SST changes occurred in the Niño 3.4 and Niño 1+2 regions, leading to the synchronous opposite fluctuations in the SST on the fishing ground of *O. bartramii* in the Northwest Pacific Ocean and on the fishing ground of *D. gigas* in the Southeast Pacific Ocean off Peru. Opposite changes in SST led to increased *O. bartramii* PFSST corresponding to decreased *D. gigas* PFSST from September to November over 2006–2015, resulting in synchronous opposing changes in CPUE. At the same time, the movement of the latitudinal location of the optimal SST for *O. bartramii* was in phase with the shift of optimal SST for *D. gigas*, yielding similar movement pattern of the LATG. Our findings suggest that the potential mechanism behind synchronous opposing changes in abundance and similar movement in the latitudinal distribution of the two squid species was due to simultaneous variations in the PFSST and the latitudinal location of the optimal SST front, which were strongly influenced by the large-scale variability of the SSTA in the Niño 3.4 and Niño 1+2 regions. Understanding synchronous fluctuations in CPUE and LATG of *O. bartramii* and *D. gigas* has important implications for Chinese squid fisheries management. Based on the present study, how the CPUE and LATG of the two squids synchronously fluctuated with the environmental conditions can be deduced. The fishermen then can make correct fishing decisions. For example, with the decreasing trends in CPUE of *O. bartramii* and the concurrent increasing trends for *D. gigas* CPUE, the fishermen can decrease the number of fishing vessels in the western Pacific and increase the number of fishing vessels in the southeastern Pacific off Peru.

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