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Response of winter cohort abundance of Japanese common squid *Todarodes pacificus* to the ENSO events

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Abstract

The Japanese common squid *Todarodes pacificus* is an economically important species with one year lifespan, which is significantly influenced by climatic and environmental variability. According to the fishery data of the winter cohort of *T. pacificus* from 2003 to 2012, as well as environmental data and the Oceanic Niño index (ONI, which was defined by the sea surface temperature (SST) anomaly in the Niño 3.4 region), variations in the SST, chlorophyll *a* (Chl *a*) concentration, suitable spawning area (SSA) and sea surface height anomaly (SSHA) on the spawning ground of *T. pacificus* were examined under the El Niño and La Niña conditions. Their influences on squid abundance (defined by catch per unit effort, CPUE) were further assessed. The results showed that seasonal changes were found in SST, Chl *a* and SSA on the spawning ground of *T. pacificus*. Correlation analysis suggested that annual CPUE was significantly positively correlated with Chl *a* and SSA (p<0.05), but had insignificant relationship with SST (p>0.05). Moreover, the El Niño and La Niña events tended to dominate the changes of SSA and Chl *a* concentration in the key area between 25°–29°N and 122.5°–130.5°E, driving the variability of squid abundance. However, this influence varied with the intensity of each anomalous climatic event: the weak El Niño event occurred, the spawning ground was occupied by waters with enlarged SSA but with extremely low Chl *a* concentration, leading to low squid recruitment, the CPUE then decreased; the moderate intensity of El Niño event resulted in shrunk SSA but with high Chl *a* concentration on the spawning ground, the squid recruitment and CPUE increased; the moderate intensity of La Niña events yielded elevated SSA and high Chl *a* concentration on the spawning ground, the squid recruitment and CPUE dramatically increased. Our findings suggested that the ENSO events played crucial effects on the incubating and feeding conditions of the winter cohort of *T. pacificus* during the spawning season and ultimately affected its abundance.

Key words: *Todarodes pacificus*, squid abundance, spawning ground, El Niño, La Niña

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1 Introduction

It is well known that large-scale climate variability in the Pacific Ocean, particularly the El Niño-Southern Oscillation (ENSO), with its cycle including the warm (El Niño) and cold (La Niña) phases, significantly affects pelagic fish stocks (Lehodey et al., 2006). ENSO-driven environmental variability in the habitat coincides well with changes in distribution and abundance of many commercially important fish species, such as skipjack tuna *Katsuwonus pelamis* (Lehodey et al., 1997) and Pacific saury *Cololabis saira* (Tian et al., 2003). As to short-lived ommastrephid squid species, this species-environment relationship tends to be more sensitive (Anderson and Rodhouse, 2001). For example, recruitment conditions of the western winter-spring cohort of neon flying squid *Ommastrephes bartramii* as well as its fishing ground distributions were mediated by the El Niño and La Niña events. The sea surface temperature (SST) on the spawning ground during the El Niño years tended to be favorable for squid recruitment, and fishing ground would shift southward. However, the SST on the spawning ground appeared to be adverse to recruitment during the La Niña years, and the fishing ground shifted northward (Chen et al., 2007). In the Southeast Pacific Ocean, habitat quality and presence of jumbo flying squid *Dosidicus gigas* experienced dramatic fluctuations due to the anomalous environments. Suitable habitat areas of *D. gigas* were likely to expand under the La Niña conditions and shrink under the El Niño conditions (Yu et al., 2016).

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The Japanese common squid *Todarodes pacificus* is an ecologically important squid species extensively distributed throughout the temperate and warm waters between 20°N and 60°N in the Northwest Pacific Ocean (Murata, 1990). Due to its highly economic value, *T. pacificus* supports internationally commercial cephalopod fisheries in Japan, Korea and China, attracting large numbers of fishing vessels operating in the East China Sea (ECS), Sea of Japan and coastal waters along Japanese Islands in the Pacific side (Choi et al., 2008; Sakurai et al., 2013; Tang et al., 2015). According to spawning seasons, *T. pacificus* stock can be divided into summer, autumn and winter cohorts (Sakurai et al., 2000). The summer cohort of *T. pacificus* has a relatively small stock size. However, the winter cohort is the largest and most important one to make up the biomass of *T. pacificus* stock (Kawabata et al., 2006). In general, the distributions of spawning areas vary with seasons. The autumn cohort of *T. pacificus* mainly spawns in the Sea of Japan off southern Honshu Island and the Tsushima Strait between Korea and Japan. Eggs of this cohort are largely spawned between September and December (Goto, 2002; Yamamoto et al., 2002). For the winter cohort, spawning grounds occur in the East China Sea from the Kyushu Island south of Japan to Chinese Taiwan, with spawning peaking from January to April. Both cohorts migrate seasonally around the Japanese Islands from the southern spawning ground to the northern feeding ground (Hatanaka et al., 1985).

Previous studies have proved that climatic and oceanographic variations play far-reaching influences on *T. pacificus* stock (Rosa et al., 2011). The climate regime shift on decadal scales in the Northwest Pacific Ocean is considered as one of major drivers to determine the stock level of *T. pacificus*. Some studies have recognized that an inter-decadal recurring pattern of warm and cold regimes in the western Pacific perfectly corresponded to alternating high and low catches of *T. pacificus* in Korea and Japan (Sakurai et al., 2000). The importance of environmental conditions on the spawning ground, such as the size and spatial distribution pattern of suitable spawning area (SSA), is highly emphasized, which can be used to explain stock fluctuation of this squid (Sakurai et al., 2000; Rosa et al., 2011). However, currently, few studies have related this catch or stock size changes to interannual climate variability such as the ENSO phenomenon. How the *T. pacificus* stock responds to the El Niño and La Niña events has not yet been examined and discussed.

In this study, based on the fisheries data and three critical environmental factors including SST, SSA and chlorophyll *a* (Chl *a*) concentration, the relationship between the abundance of winter cohort of *T. pacificus* and the ENSO-related environmental variability has been examined. We hypothesize that variability in the abundance of the winter cohort of *T. pacificus* is primarily attributed to the change of its recruitment level during the early life stage. By analyzing the incubation and feeding conditions on the spawning ground under the El Niño and La Niña events with different intensity, we evaluate the potential effects of emerging event-to-event diversity of the ENSO conditions on the abundance of *T. pacificus* during 2003–2012. The purpose of this study is to elucidate response of abundance variation of *T. pacificus* to impacts of ENSO-mediated environmental variability on the spawning ground.

2 Materials and methods

2.1 *Fishery and environmental data*

The fishery data during 2003–2012 were obtained from the annually Japanese fisheries report for the winter cohort of *T. pacificus* (http://abchan.fra.go.jp/digests27/details/2718.pdf). Data information included annual catches in Japan and Korea and the estimated catch per unit effort (CPUE) data. Fishing power in the study period was basically constant. Therefore, CPUE was regarded as a reliable index to indicate the squid abundance (Chen et al., 2008).

The environmental variables contained SST, Chl *a* concentration and sea surface height anomaly (SSHA) on the spawning ground (between 25°–35°N and 120°–135°E) of the winter cohort of *T. pacificus*. Data were obtained from remote sensing satellite databases. All the environmental data covered the main spawning months from January to April over 2003–2012. The monthly SST and SSHA data were acquired from the Live Access Server of National Oceanic and Atmospheric Administration (NOAA) OceanWatch dataset (http://oceanwatch.pifsc.noaa.gov/las/servlets/dataset). The spatial resolution of SST and SSHA was 0.1°×0.1° and 0.25°×0.25°, respectively. The monthly MODIS Chl *a* concentration data with spatial resolution of 0.05°×0.05° were sourced from the Asia-Pacific Data-Research Center (APDRC), University of Hawaii (http://apdrc.soest.hawaii.edu/data/data.php). All the environmental data were averaged on a 0.25°×0.25° latitude/longitude grid prior to analyses.

2.2 *Climate index*

The oceanic Niño index (ONI) becomes one standard measure for identifying the El Niño and La Niña events in the tropical Pacific (Li and Zhai, 2000; Tzeng et al., 2012). In this study, the ONI was estimated by 5-month running mean of SST anomalies (SSTA) in the Niño 3.4 region (5°N–5°S, 120°–170°W). The ONI data from January to December during 2003–2012 were obtained from the following website: http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears2011.shtml. Based on a threshold of +/–0.5°C, the warm and cold periods of above and below normal SSTs were defined as the El Niño and La Niña events, respectively, when the threshold was met for a minimum of five consecutive overlapping months.

The intensity of El Niño or La Niña events were further categorized as weak, moderate, strong or very strong. The threshold was broken down into weak (with a 0.5 to 0.9 ONI, and with a –0.9 to –0.5 ONI), moderate (1.0 to 1.4, and –1.4 to –1.0), strong (1.5 to 1.9, and –1.9 to –1.5) and very strong ($\geqslant$2.0, and $\leqslant$–2.0) events (http://ggweather.com/enso/oni.htm). For each intensity type, ONI must have equaled or exceeded the threshold for at least three consecutive overlapping three-month periods.

2.3 *Evaluating variations in incubation and feeding conditions of T. pacificus*

Todarodes pacificus dies immediately after breeding, its stock level, to a great extent, is determined by the recruitment (Sakurai et al., 2013). The incubation and feeding condition on the spawning ground during the early life stage are the main drivers to cause recruitment variability and consequently affect the abundance of *T. pacificus* (Sakurai et al., 1996; Yamamoto et al., 2007). Therefore, by examining the recruitment conditions under different ENSO periods, we could recognize the biophysical process how squid abundance responded to climate variability. In addition, in order to keep temporal and spatial consistency in this study, the spawning ground between 25°–35°N and 120°–135°E was chosen as the study area. Annual spawning month from January to April was regarded as our study period. The years with occurrence of anomalous climate events during spawning month were chosen to understand how the environmental conditions varied with the climate variability.

Todarodes pacificus generally lays spherical, neutrally buoyant egg masses near the sea surface waters between 25°–35°N and 120°–135°E, with the highest survival rate at the SST of 19.5–23°C (Sakurai, 2007). Cao et al. (2009) had successfully defined the SSA based on the suitable SST for spawning and related it to the CPUE. Thus, we used the SST and SSA (areas with SST between 19.5°C and 23°C accounting for the total spawning ground) on the spawning ground to indicate the incubation condition. Moreover, *T. pacificus* paralarvae and juvenile exhibit rapid growth and high survival rate with adequate prey items such as productive crustaceans biomass (Uchikawa and Kidokoro, 2014), which mostly occur in waters with high primary productivity. The Chl *a* concentration, indicating the feeding environment for squids, was therefore used to evaluate the ocean productivity. The SSHA on the spawning ground was also examined in relation to the Chl *a* concentration. By combining the analyses of the incubation and feeding conditions, we could examine the recruitment variability and evaluate the potential impacts of the ENSO events with different intensity on squid abundance. Linear regression analysis was ultimately conducted to establish a CPUE forecast model for the winter cohort of *T. pacificus*, with environmental factors on the spawning ground as independent variables.

3 Results

3.1 *ENSO episodes and squid abundance*

Based on the definition of ENSO events, large fluctuations were observed in oceanic environments during 2003–2012 (Fig. 1). The Pacific Ocean experienced four El Niño events and three La Niña events during our study period. The former events occurred during January 2003–February 2003, July 2004–April 2005, September 2006–January 2007 and July 2009–April 2010, respectively. The latter events occurred in August 2007–June 2008, July 2010–April 2011 and August 2011–March 2012, respectively. Moreover, for each anomalous event, the intensity varied from year to year (Fig. 1). For example, the intensity of 2004/2005 and 2006/2007 El Niño events was categorized as weak intensity; the 2002/2003 and 2009/2010 El Niño events were categorized as moderate intensity; the 2011/2012 La Niña events were categorized as weak intensity; the 2007/2008 and 2010/2011 La Niña events were categorized as moderate intensity. No strong or very strong events were found during 2003–2012. Furthermore, spawning months from January to April in 2005, 2008, 2010 and 2011 corresponded to anomalous environmental events. The years of 2005 and 2010 were El Niño years, weak El Niño occurred in 2005, however, moderate El Niño occurred in 2010. Both 2008 and 2011 were moderate La Niña years. Thus, those four specific years were chosen in this study to examine how the recruitment conditions varied with the emerging event-to-event diversity of the ENSO conditions.

Annual CPUE of winter cohort of *T. pacificus* exhibited interannual variability over 2003–2012 with an average of 2.6×10^3 ind./(vessel·d) (Fig. 2). The CPUEs during 2007–2012 were higher than those during 2003–2006. The lowest CPUE occurred in 2006 with a value of 1.8×10^3 ind./(vessel·d); the highest CPUE reached up to 3.3×10^3 ind./(vessel·d) in 2007 and 2009. Additionally, the CPUE was 2.3×10^3 ind./(vessel·d), 2.5×10^3 ind./(vessel·d), 2.8×10^3 ind./(vessel·d) and 3.1×10^3 ind./(vessel·d), respectively, in 2005, 2010, 2008 and 2011. It was clearly found that the CPUEs were low in El Niño years (2005 and 2010) and high in La Niña years (2008 and 2011).

3.2 *Seasonal environmental variations on the spawning ground*

Environmental conditions on the spawning ground of *T. pacificus* showed apparently seasonal variations (Fig. 3). Comparing to other months, SST from January to April was relatively low ranging from 16.1°C to 17.9°C. The lowest SST occurred in February. After May, it gradually increased and reached a peak value of 28.6°C in August. The SST then decreased in the following months. Overall, the SST was high in summer and autumn, and low in spring and winter. Monthly Chl *a* concentration initially increased from January to May, followed by a decreasing trend between June and December. The Chl *a* concentration from March to June was much higher than that in other months, with a highest value of 1.83 mg/m³ in April and May. The lowest Chl *a* concentration was 1.29 mg/m³ in January. For SSA, it gradually decreased from January to June, high value concentrated in the spawning months. However, its value dramatically reduced and was approximately close to 0% during the summer season from July to September, and then increased after October. The highest SSA was 38.1% in January.

3.3 *Relationship between CPUE and environmental variables*

Correlation analysis was performed between CPUE and SST,

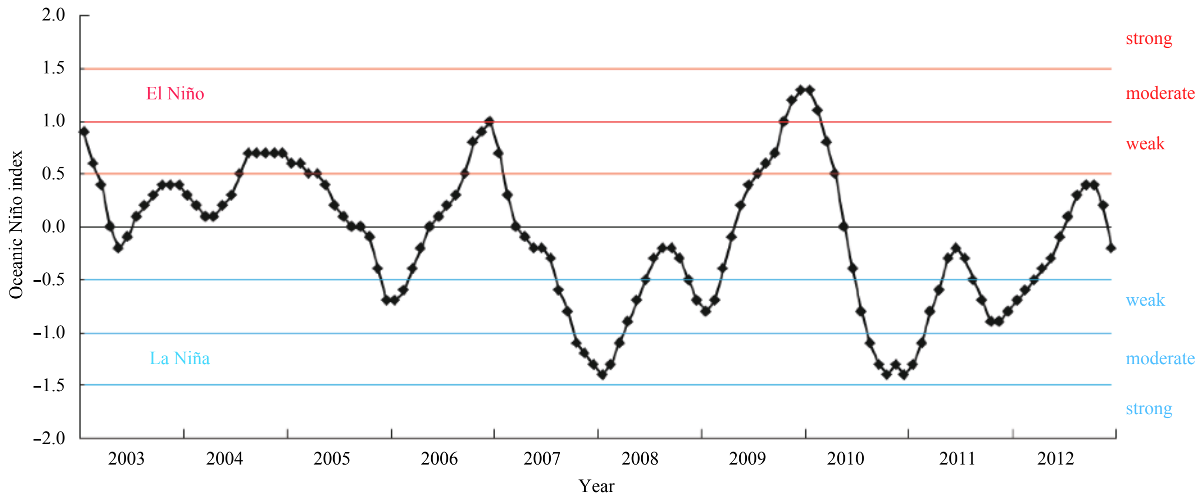

Fig. 1. The definition and intensity of El Niño and La Niña events during 2003–2012 based on the ONI.

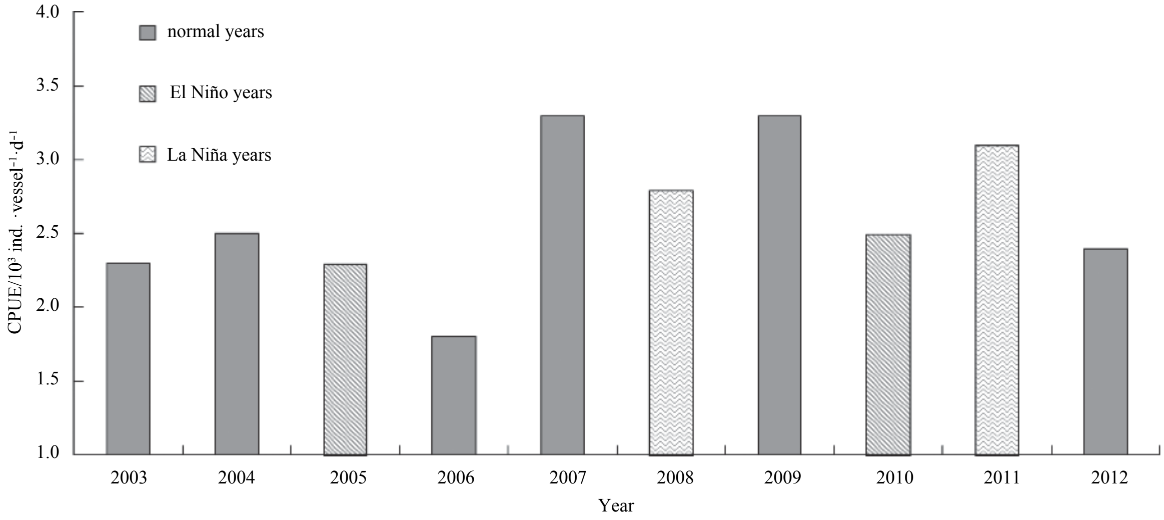

Fig. 2. Annual CPUE of the winter-cohort of Japanese common squid *Todarodes pacificus* during 2003–2012.

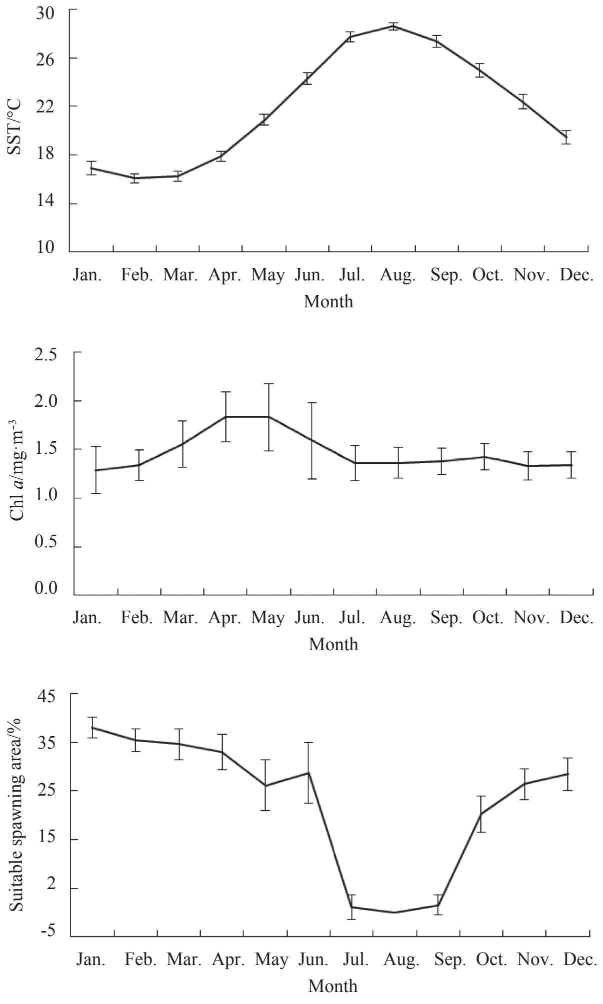

Fig. 3. Monthly averaged SST, Chl *a* concentration and SSA on the spawning ground of the winter-cohort of Japanese common squid *Todarodes pacificus* during 2003–2012.

Chl *a* and SSA from January to April over 2003–2012 (Table 1). The results suggested that SST on the spawning ground was not significantly correlated with the CPUE for each month ($p>0.05$). Chl *a* concentration in January and April was significantly and positively correlated with the CPUE ($p<0.05$). Moreover, a significantly positive relationship was also found between CPUE and SSA in April ($p<0.05$). In addition, except the SST, annual average Chl *a* concentration from January to April as well as SSA was significantly positively correlated with the CPUE ($p<0.05$).

3.4 *Variations in the environmental changes under different ENSO events*

Figure 4 showed that SSA for winter cohort of *T. pacificus* mainly occupied the waters from the northeast region of Chinese Taiwan to the southeast coast of Japan. Large SSA areas occurred along the eastern side of the Kuroshio Current in the western Pacific Ocean. Monthly SSA fluctuated in the four years, especially the SSA in 2010 obviously decreased. Furthermore, the sizes of SSA during 2005, 2010, 2008 and 2011 were quantified (Fig. 5). The SSA from January to April in 2005, 2008 and 2011 was larger than that in 2010. For details, the SSA in 2005 ranged from 34.2% to 37.1% with the highest value occurring in January and the lowest value occurring in March. The four-month average SSA in 2005 was 35.6%. In 2010, the SSA varied from 27.3% in April to 38.2% in January with an average value of 31.7%. In 2008, the SSA was between 31.7%–36.6%, the highest SSA occurred in January with the lowest value occurring in March, the average SSA was 34.4%. The SSA in 2011 ranged from 33.5% in February to 36.6% in April, the average SSA was 35.9%.

Obviously, the Chl *a* concentration in the coastal waters of China and Japan was higher than that in the offshore waters. Variations of the Chl *a* concentration in the near-shore regions tended to strongly fluctuate. Moreover, spatial and temporal changes of Chl *a* concentration were also found during the four years (Fig. 6). Figure 7 showed the monthly average Chl *a* concentration. The Chl *a* concentration was high in 2008, 2010 and 2011, and low in 2005. The Chl *a* concentration in 2005 ranged from 1.13 mg/m^3 in February to 1.45 mg/m^3 in April with an average of 1.32 mg/m^3. In 2010, the Chl *a* concentration varied from 1.32 mg/m^3 in February to 2.05 mg/m^3 in April with an average of 1.57 mg/m^3. The range of Chl *a* concentration in 2008 was between 1.39–1.79 mg/m^3, the highest value occurred in February with the lowest value occurring in April, four-month average

Table 1. Correlation between the environmental variables including SST, SSA and Chl *a* concentration and the CPUE of Japanese common squid *Todarodes pacificus* during 2003–2012

Month	Environmental variables		
	SST	Chl *a*	SSA
Jan.	–0.018	0.612 (p<0.05)	0.182
Feb.	0.417	0.211	0.502
Mar.	0.361	0.148	0.309
Apr.	0.177	0.710 (p<0.05)	0.631 (p<0.05)
4-month average	0.280	0.694 (p<0.05)	0.637 (p<0.05)

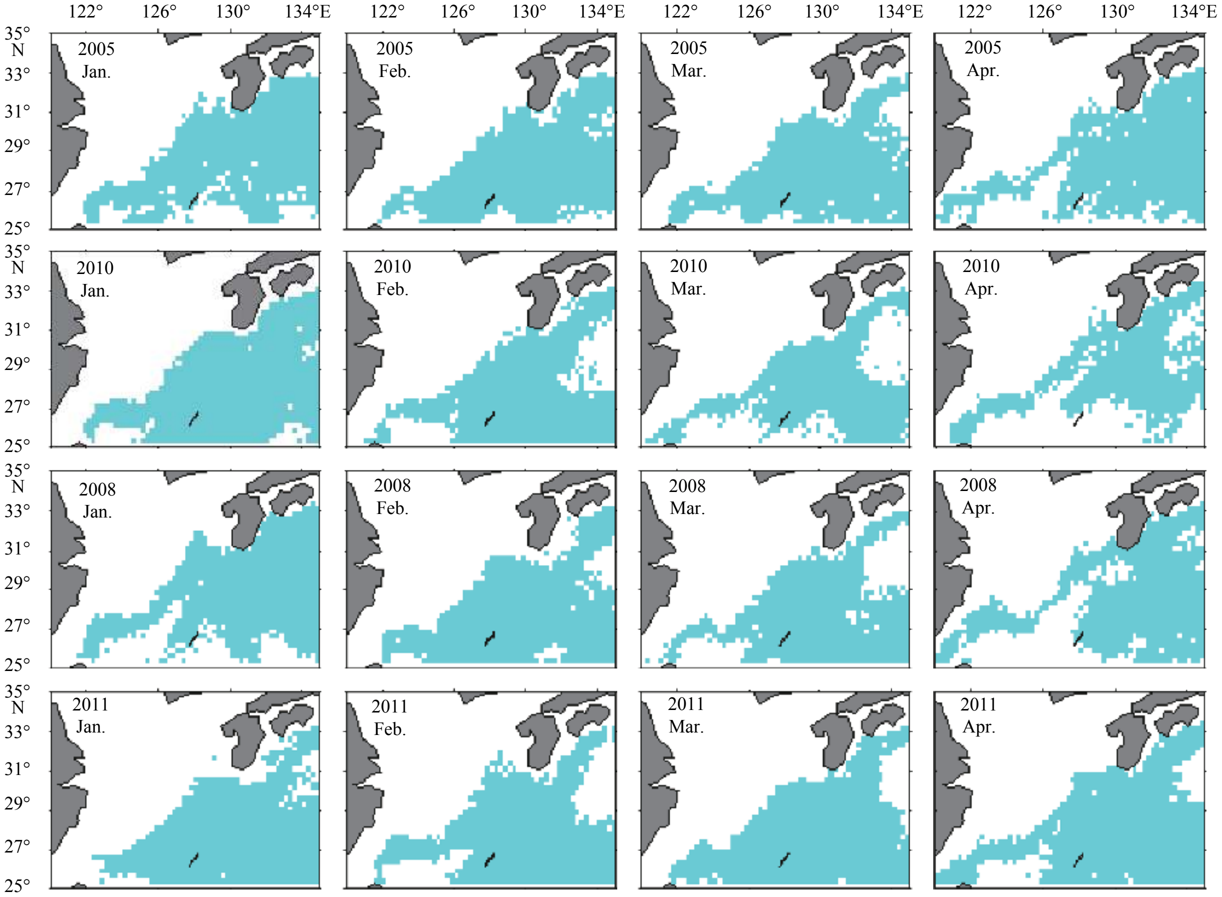

Fig. 4. Spatial distribution of SSA on the spawning ground of the winter-cohort of Japanese common squid *Todarodes pacificus* from January to April in the El Niño years of 2005/2010 and in the La Niña years of 2008/2011, respectively.

value was 1.57 mg/m^3. For the Chl *a* concentration in 2011, it ranged from 1.31 mg/m^3 in February to 2.03 mg/m^3 in April with an average of 1.56 mg/m^3.

In fact, the Chl *a* concentration spatially consistent with the SSA area in Fig. 4 was very low (<1.0 mg/m^3) comparing to other regions on the spawning ground. Variability of the Chl *a* concentration in these areas was difficult to differ in the four years. On the other hand, small difference was found in the four years by using the four-month average Chl *a* concentration on the spawning ground. Therefore, it was biased using the average Chl *a* concentration on the whole spawning ground to examine the feeding environment for *T. pacificus*. To address this question, we examined the spatial distribution of the correlation coefficients between Chl *a* concentration on the spawning ground and the CPUE of *T. pacificus* during January–April in the period of 2003–2012. A region with extremely high positive correlation coefficients occurred in the waters between 25°–29°N and 122.5°–130.5°E (Fig. 8). The location of this area was in consistence with the spatial distribution of the SSA. Thus, we considered the feeding environment in this area was a key factor that strongly influenced the CPUE of *T. pacificus*.

The Chl *a* concentration in the key area between 25°–29°N and 122.5°–130.5°E was examined in these four years (Fig. 9). High and low Chl *a* concentration occupied the northwestern and southeastern waters of this area, respectively. Comparing with the year of 2010, monthly Chl *a* concentration during January to April in 2005 was low. The Chl *a* concentration in 2008 and 2011 tended to be enhanced for each month. By quantitative analysis, the results indicated that the Chl *a* concentration in 2005 ranged from 0.28 mg/m^3 in February to 0.42 mg/m^3 in April with an average of 0.35 mg/m^3. The Chl *a* concentration in 2010 ranged from 0.33 mg/m^3 in January to 0.71 mg/m^3 in April with an average of 0.47 mg/m^3. In 2008, the Chl *a* concentration varied from 0.27 mg/m^3 in January to 0.65 mg/m^3 in March with an

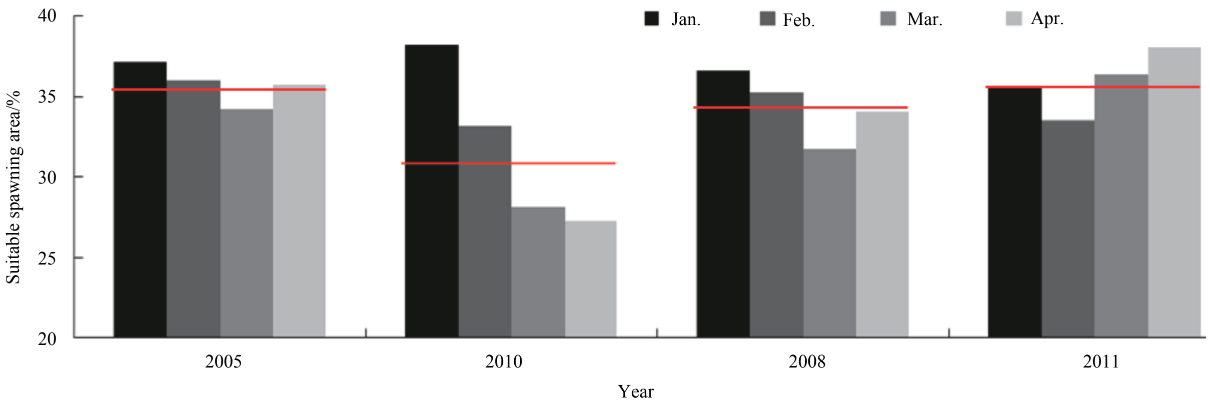

Fig. 5. Monthly SSA on the spawning ground of the winter-cohort of Japanese common squid *Todarodes pacificus* from January to April in the El Niño years of 2005/2010 and in the La Niña years of 2008/2011, respectively. The red line indicated the average SSA from January to April in each year.

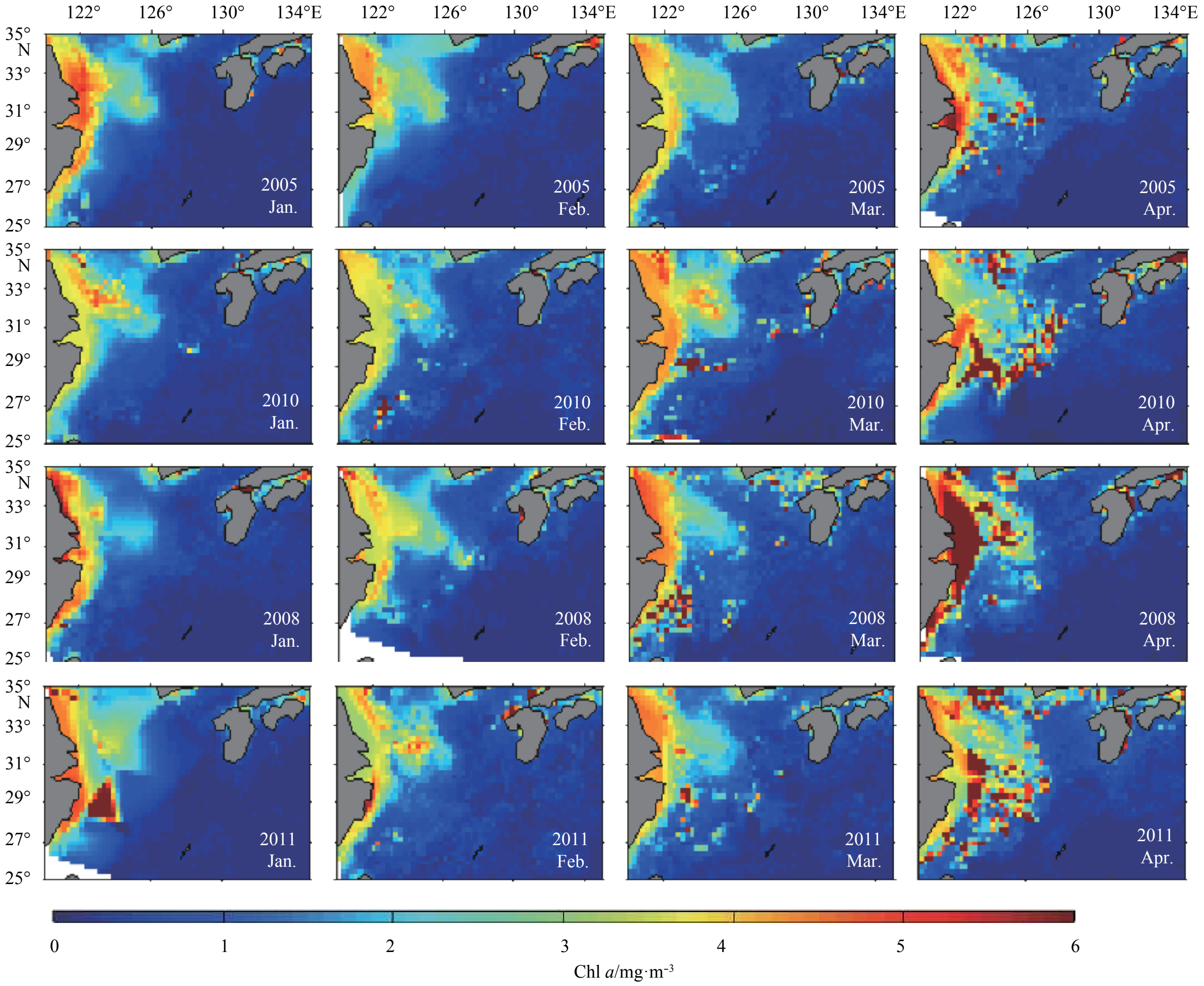

Fig. 6. Spatial distribution of Chl *a* concentration on the spawning ground of the winter-cohort of Japanese common squid *Todarodes pacificus* from January to April in the El Niño years of 2005/2010 and in the La Niña years of 2008/2011, respectively.

average of 0.45 mg/m^3. The Chl *a* concentration in 2011 fluctuated from 0.48 mg/m^3 in February to 0.86 mg/m^3 in April with an average of 0.60 mg/m^3.

Variability of SSHA during January to April in 2005, 2010, 2008 and 2011 was showed in Fig. 11. Except in March, highly positive SSHA tended to occupy the regions between 25°–29°N and 122.5°–130.5°E and eastern waters of 131°E in January, February and April in 2005, indicating that the SSA areas were covered by highly elevated SSHA on the spawning ground in this year. On the contrary, large portion of waters with negative SSHA oc-

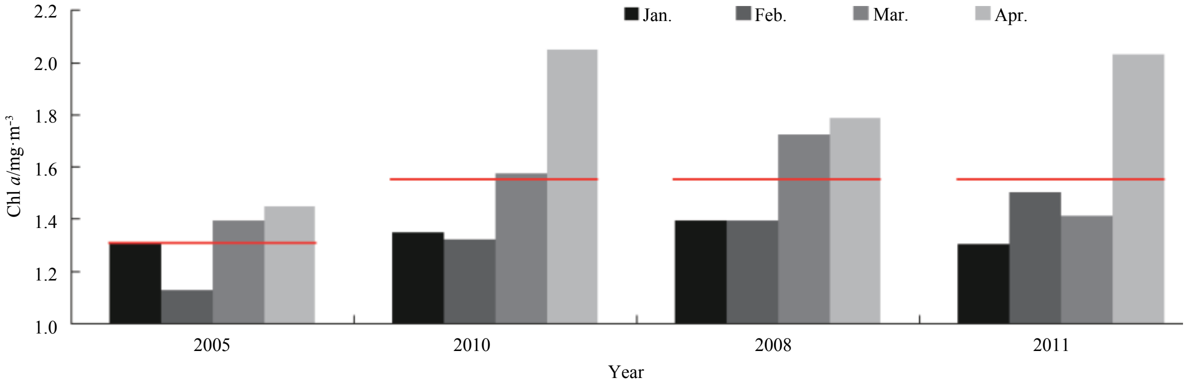

Fig. 7. Monthly Chl *a* concentration on the spawning ground of the winter-cohort of Japanese common squid *Todarodes pacificus* from January to April in the El Niño years of 2005/2010 and in the La Niña years of 2008/2011, respectively. The red line indicated the average Chl *a* from January to April in each year.

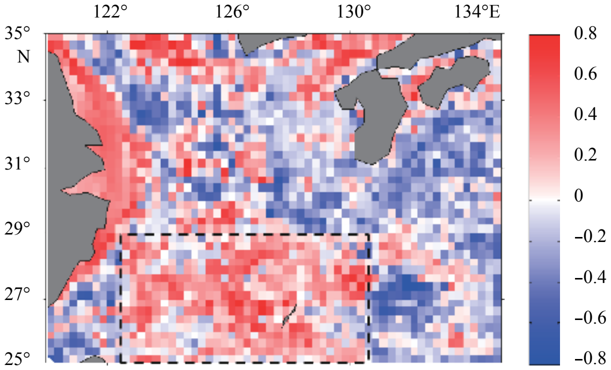

Fig. 8. The spatial distribution of the correlation coefficients between Chl *a* concentration on the spawning ground and the CPUE of the winter-cohort of Japanese common squid *Todarodes pacificus* during 2003–2012.

curred in 2010, 2008 and 2011 and basically extended to the entire spawning ground, especially the regions at the south of 29°N.

Based on the analyses above, we selected the SSA and Chl *a* concentration between 25°–29°N and 122.5°–130.5°E as the environmental variables in establishing a CPUE forecast model. The regression model was significant (p<0.05), suggesting that CPUE was positively and significantly correlated with the SSA and Chl *a* concentration in the key areas (Table 2).

4 Discussion

Understanding the interaction between climate variability and squid stock is a crucial step to explore the process how squid species respond to their surrounding environments and establish effective prediction and pursue sustainable management of fishery resources (Coelho, 1985; Postuma and Gasalla, 2010). With respect to one-year lifespan squid species, key linkage between its stock dynamics and recruitment condition has been highlighted to detect the variability in abundance (Roberts, 2005; Yu et al., 2013). Present studies suggested that recruitment variability during the early life stage for squids was highly vulnerable to the biological and physical environment (e.g., incubation and feeding conditions) on the spawning ground, and subsequently influenced the squid abundance during the adult stage (Nevárez-Martínez et al., 2006; Chen et al., 2007). Therefore, it necessitated the scientific issue that exploring the underlying causes of the links between the ENSO events, the dominant climate variability in the Pacific Ocean, and stock dynamics of *T. pacificus*. Such relationship often had good predictive capability for its abundance in a short term. However, it was poorly understood so far for *T. pacificus*. Hence, this study connected the ENSO-mediated variability in incubation and feeding conditions to CPUE in order to clarify the influences of climate variability on abundance of *T. pacificus*.

Due to profound influence of SST and Chl *a* density on temperature-depended survival rates, habitat suitability and prey density for squid paralarvae and juveniles, many efforts examined these two environmental factors on squid spawning ground to evaluate the potential impacts on fluctuations of squid abundance and catch (Waluda and Rodhouse, 2006). For example, Cao et al. (2009) related the abundance of *O. bartramii* during 1995–2004 with the SSA on the spawning ground and preferred habitat areas (PHA) on the feeding ground. They concluded that February SSA and August to November PHA could explain 60% CPUE variability of *O. bartramii*. By comparative studies, Yu et al. (2015) examined environmental conditions on the spawning ground in 1999 and 2009 for *O. bartramii*. They inferred that SSA had limited impacts on the recruitment between the two years. However, high SST waters falling within enhanced Chl *a* concentration on the spawning ground in 1999 might cause increased recruitment and squid abundance. Whereas low SST occurred on the spawning ground matching with reduced Chl *a* concentration resulted in decreased recruitment and squid abundance.

Our findings suggested that SST, Chl *a* concentration and SSA had substantial changes on a seasonal time scale. Relative low SST, high Chl *a* concentration and enlarged SSA during January to April could favor the adaptation of *T. pacificus* to their environment. Spawning in these months appeared to be in accord with the reproductive strategy (Rocha et al., 2001). Moreover, the results from the correlation analysis (Table 1) in this study indicated that variability in squid abundance was closely associated with the SSA and Chl *a* concentration on the whole spawning months from January to April. Particularly, January and April for Chl *a* and April for SSA tended to be the most important period influencing squid abundance of *T. pacificus*.

There were some studies that evaluate the relationship between the SSA and stock level of *T. pacificus*, but conclusions varied with different research. Sakurai et al. (2002) suggested that stock fluctuation of winter cohort of *T. pacificus* was related to

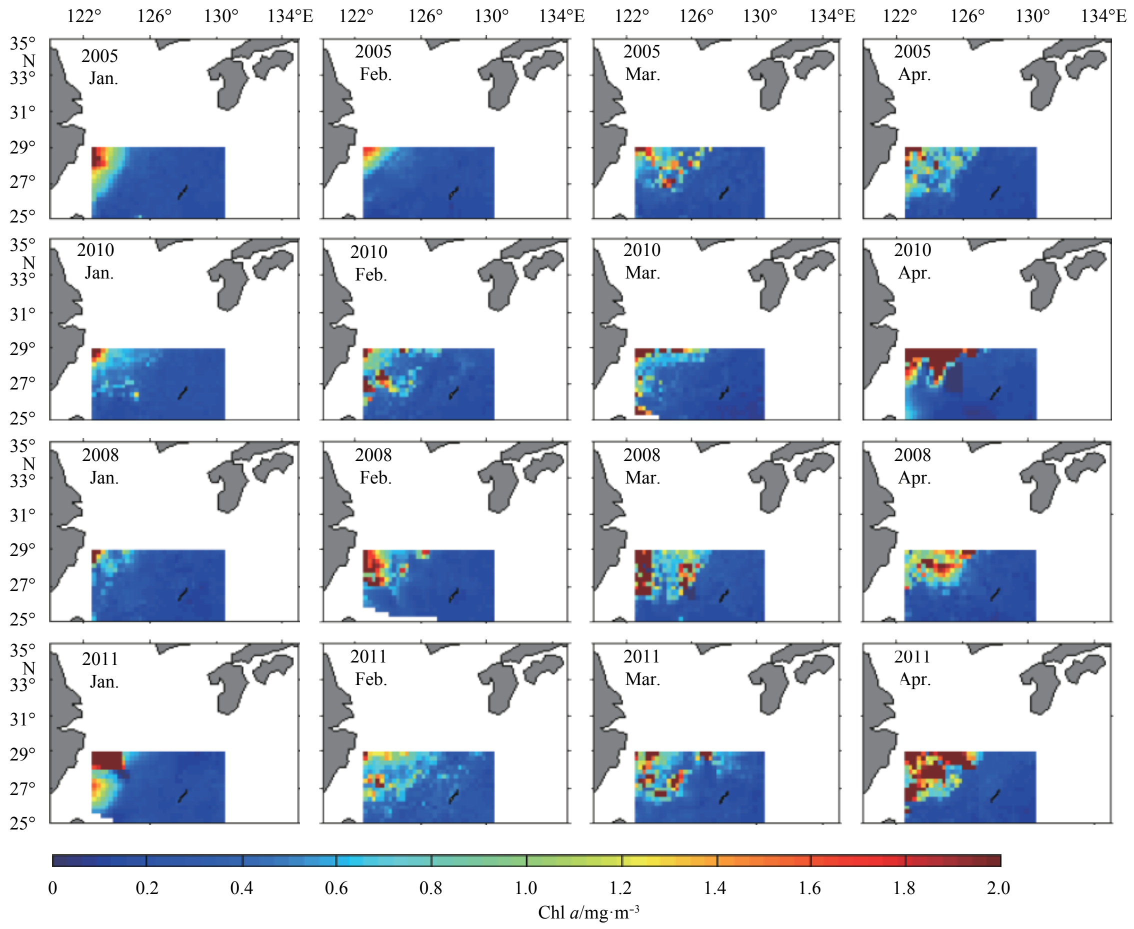

Fig. 9. Spatial distribution of Chl *a* concentration between 25°–29°N and 122.5°–130.5°E from January to April in the El Niño years of 2005/2010 and in the La Niña years of 2008/2011, respectively.

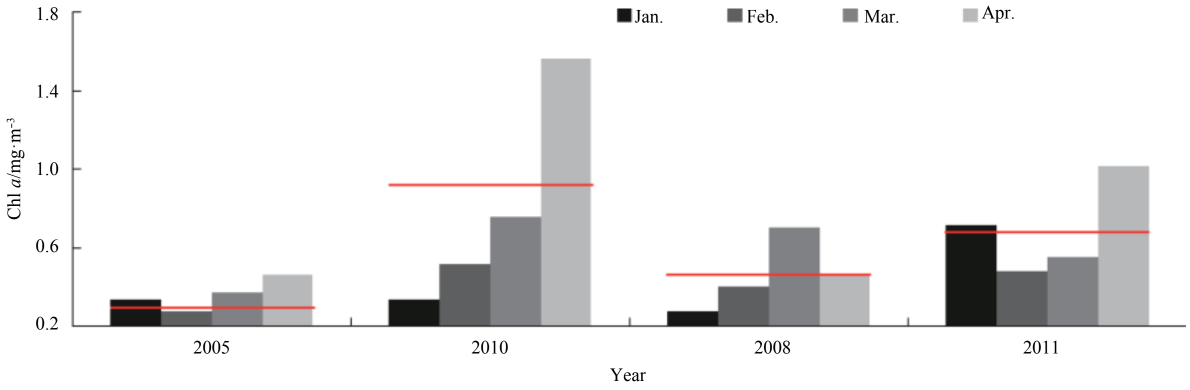

Fig. 10. Monthly Chl *a* concentration between 25°–29°N and 122.5°–130.5°E from January to April in the El Niño years of 2005/2010 and in the La Niña years of 2008/2011, respectively. The red line indicated the average Chl *a* concentration between 25°–29°N and 122.5°–130.5°E from January to April in each year.

winter-spawning area. A cool regime would shrink winter-spawning area in the East China Sea and decrease adult stock. While a warm regime would shift the distribution of winter-spawning ground in the Sea of Japan overlapping with autumn-spawning area in the East China Sea, such spatial distribution of spawning ground increased the stock size. However, for the autumn cohort, no significant changes of SSA on the spawning ground were reported between different climate regimes. Besides, Rosa et al. (2011) proposed that stock level of *T. pacificus* was determined by distribution patterns of spawning areas, not by the size of SSA. The discontinuity of spawning-ground distribution was likely to reduce the catch in the following fishing season. Comparing to their studies, our study used data sources with different study period, and the definition of SSA was only based on one factor (i.e., SST), which might cause the differences in these findings.

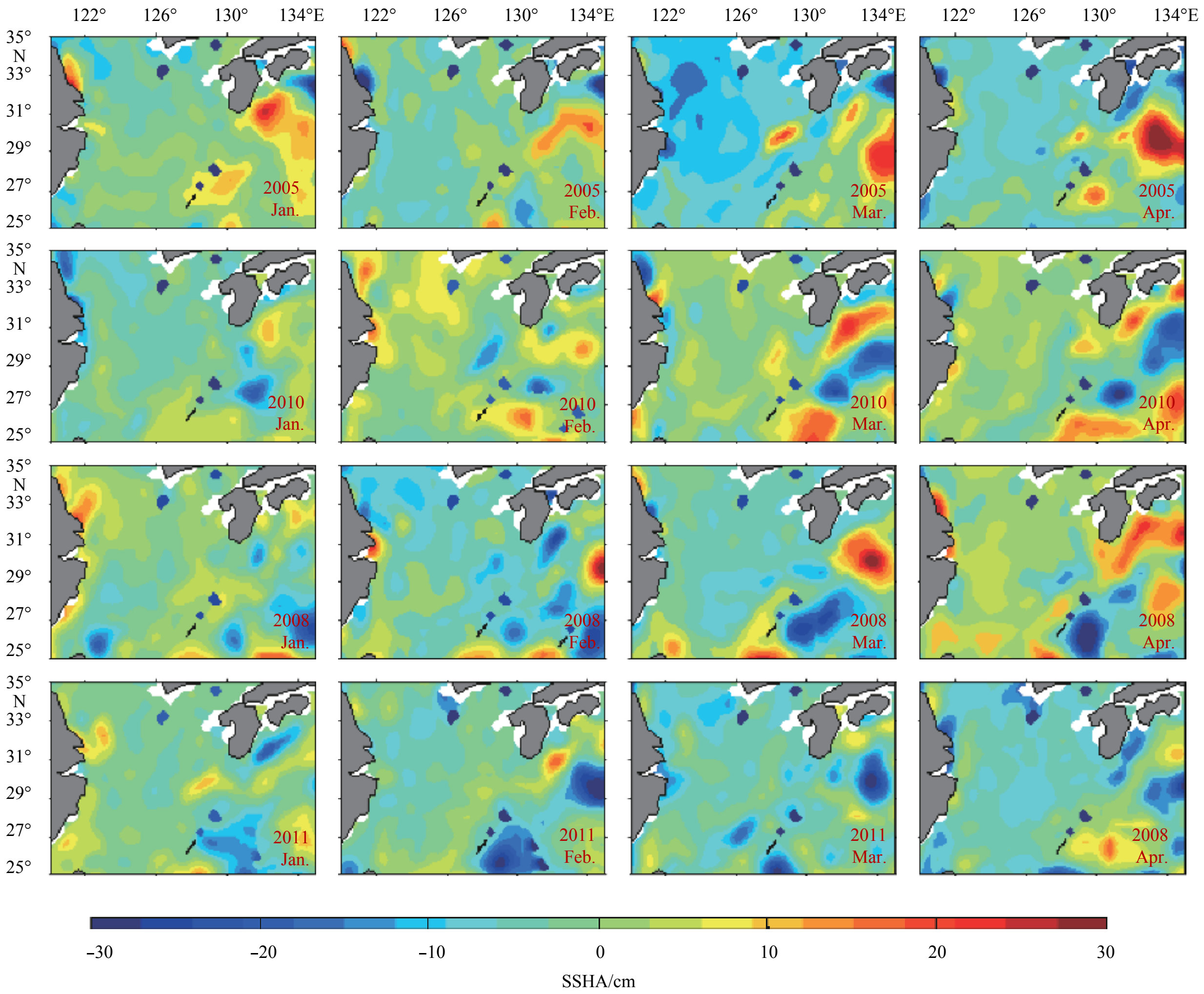

Fig. 11. Spatial distribution of SSHA on the spawning ground of the winter-cohort of Japanese common squid *Todarodes pacificus* from January to April in the El Niño years of 2005/2010 and in the La Niña years of 2008/2011, respectively.

Table 2. Regression model between the environmental variables (suitable spawning area, SSA and Chl *a* concentration) and the CPUE of Japanese common squid *Todarodes pacificus*

Model	95% CI	p
$CPUE_n=a_0+a_1P_{1,n}+a_2P_{2,n}$		
$a_0=-5.158$	−10.048 to −0.267	0.041
$a_1=0.196$	0.065 to 0.328	0.010
$a_2=1.669$	0.106 to 3.231	0.039
$P_{1,n}$: average SSA from January to April in year n		
$P_{2,n}$: average Chl *a* concentration between 25°–29°N and 122.5°–130.5°E from January to April in year n		
Correlation coefficient $r=0.830$; $R^2=0.689$; $F=7.762$; $p=0.017$		

The SSTA in the Niño 3.4 region was successfully used to define the ENSO events and related to the marine pelagic fish species (Arcos et al., 2001; Sun et al., 2006; Han et al., 2009). For example, the gravity centers of fishing ground of fish species such as *D. gigas* (Xu et al., 2011) and *K. pelamis* (Wang and Chen, 2013) were strongly regulated by the El Niño and La Niña events which were defined by the Niño 3.4 SSTA. Thus, we utilized the SSTA in the Niño 3.4 region to define the ENSO events in this study. Our studies suggested that variability in squid abundance of *T. pacificus* was primarily driven by the SSA and Chl *a* concentration in the key area between 25°–29°N and 122.5°–130.5°E, which were mediated by the El Niño and La Niña events. However, the influence of each anomalous climate event on squid abundance varied with its intensity. The weak El Niño event might yield enlarged SSA and extremely low Chl *a* concentration on the spawning ground, leading to low squid recruitment, the CPUE of *T. pacificus* decreased. The moderate intensity of El Niño event might result in shrunk SSA but with high Chl *a* concentration on the spawning ground, the squid recruitment and CPUE increased. The moderate intensity of La Niña events might yield both elevated SSA and enhanced Chl *a* concentration on the spawning ground, the squid recruitment and CPUE dramatically increased. Our findings presented recruitment variability of the winter cohort of *T. pacificus* in response to the El

Niño and La Niña events with different intensity.

Alabia et al. (2016) demonstrated the potential habitat of the autumn cohort of *O. bartramii* in response to ENSO flavors, they found the East Pacific (EP)-El Niño created better feeding environments and yielded larger suitable habitat while the Central Pacific (CP)-El Niño reduced the suitable habitat. Due to the El Niño and La Niña events showed difference in intensity, time duration and spatial distribution, response of squid stocks to ENSO events should be analyzed case by case. In fact, in our study, the anomalous climate event in 2005 was the EP-El Niño, whereas the anomalous climate event in 2010 was the CP-El Niño. Comparing to the EP-El Niño in 2005, the CP-El Niño in 2010 was stronger in intensity and longer in duration, leading to shrunk SSA and enhanced Chl *a* concentration in the study region, it facilitated the environmental effects and increased squid abundance of *T. pacificus*.

Though the SSA was low in 2010 and the Chl *a* concentration was high, the CPUE was still at a high level, implying that the feeding condition might be more important than the size of suitable spawning areas to the squid recruitment. This explained the reason why the CPUE in 2010 was higher than that in 2005. More so, the feeding environment bounded by 25°–29°N and 122.5°–130.5°E had important implications for the winter cohort of *T. pacificus* and was possibly affected by the SSHA on the spawning ground. We inferred the possible biophysical process through which the dynamic of SSHA influenced the Chl *a* concentration and further the squid abundance under different ENSO events (Figs 9, 10 and 11): in contrast to the weak EP-El Niño year in 2005, a large portion of negative SSHAs, which was indicative of strengthened upwelling (Yu et al., 2016), widely occurred on the spawning ground of *T. pacificus* in the moderate EP-El Niño year of 2010 and the moderate La Niña years of 2008 and 2011. The nutrient-rich bottom waters were transported to the surface spawning ground, this process led to extension of high Chl *a* in the key areas between 25°–29°N and 122.5°–130.5°E, thereby enhancing the primary productivity and prey availability and consequently increasing the abundance of *T. pacificus*.

As shown in Table 2, the regression model successfully captured the positive relationship between the CPUE of *T. pacificus* and the SSA and Chl *a* concentration in the key areas were between 25°–29°N and 122.5°–130.5°E. However, inevitably, there were some limitations in this study. For instance, as current (Kim et al., 2015) and salinity (Furukawa and Sakurai, 2008) shown importance in regulating the *T. pacificus* stocks, our studies only included SST and Chl *a* concentration. Besides, we only used the SST to define the SSA, which might introduce biases in the analysis. Comparing to the years with anomalous environments, the CPUE in the normal years also fluctuated, such as the lowest CPUE in 2006 and highest CPUE in 2007. In order to perform a comprehensive evaluation of impacts of different climatic events on *T. pacificus* stocks, future studies should involve with more environmental variables and extend the study period including the consideration of the normal climate condition.

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