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Impacts of oceanographic factors on interannual variability of the winter-spring cohort of neon flying squid abundance in the Northwest Pacific Ocean

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Abstract

The neon flying squid *Ommastrephes bartramii* is an economically important species in the Northwest Pacific Ocean. The life cycle of *O. bartramii* is highly susceptible to climatic and oceanic factors. In this study, we have examined the impacts of climate variability and local biophysical environments on the interannual variability of the abundance of the western winter-spring cohort of *O. bartramii* over the period of 1995–2011. The results showed that the squid had experienced alternant positive and negative Pacific Decadal Oscillation (PDO) over the past 17 years during which five El Niño and eight La Niña events occurred. The catch per unit effort (CPUE) was positively correlated with the PDO index (PDOI) at a one-year time lag. An abnormally warm temperature during the La Niña years over the positive PDO phase provided favorable oceanographic conditions for the habitats of *O. bartramii*, whereas a lower temperature on the fishing ground during the El Niño years over the negative PDO phase generally corresponded to a low CPUE. The same correlation was also found between CPUE and Chl *a* concentration anomaly. A possible explanation was proposed that the CPUE was likely related to the climate-induced variability of the large-scale circulation in the Northwest Pacific Ocean: high squid abundance often occurred in a year with a significant northward meander of the Kuroshio Current. The Kuroshio Current advected the warmer and food-rich waters into the fishing ground, and multiple meso-scale eddies arising from current instability enhanced the food retention on the fishing ground, all of which were favorable for the life stage development of the western squid stocks. Our results help better understand the potential process that the climatic and oceanographic factors affect the abundance of the winter-spring cohort of *O. bartramii* in the Northwest Pacific Ocean.

Key words: *Ommastrephes bartramii*, squid abundance, interannual variability, PDO-CPUE relationship, Kuroshio meandering, meso-scale eddies

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1 Introduction

Neon flying squid, *Ommastrephes bartramii*, an economically important oceanic squid, is widely distributed in the subtropical and temperate waters of the worldwide (Murata, 1990; Chen et al., 2009). In the North Pacific Ocean, it is abundant between 20°N and 50°N (Roper et al., 1984). Due to a drastic decline in the catch of Japanese common squid (*Todarodes pacificus*) in the early 1970s, *O. bartramii* became a commercially important fishing target by the Japanese squid-jigging vessels in 1974 (Bower and Ichii, 2005) and later by South Korea and Taiwan's fishing industries (Chen et al., 2008a). China's mainland undertook an exploratory investigation of this squid in 1993, and then has subsequently expanded it to be a large-scale commercial squid-jigging fishery since 1994 (Wang and Chen, 1998). Currently, *O. bartramii* in the Northwest Pacific has become the most important fishing target in China, which accounts for more than 80% of the total squid catch by Chinese fishing vessels per year (Chen and Tian, 2006). However, annual catches of *O. bartramii* tend to strongly vary. As a short-lived ecological opportunist, the abundance and distribution of *O. bartramii* fluctuate widely from year

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to year, with a significantly influence from the spatio-temporal variability of regional biophysical environmental conditions (Murphy and Rodhouse, 1999; Nigmatullin et al., 2001).

The North Pacific population of *O. bartramii* has a one-year lifespan comprising two putative seasonal cohorts (Yatsu et al., 1997, 1998): a winter-spring cohort (Murata and Hayase, 1993) and an autumn cohort (Chen and Chiu, 2003). For the winter-spring cohort, spawning behavior mainly occurs during January through May with a peak in March, and the spawning grounds are identified to be located in the areas between 20°–30°N and 130°–170°E, and between 20°–30°N and 130°–170°W, respectively (Bower, 1996; Yatsu et al., 1998; Nagasawa et al., 1998) (Fig. 1). The optimal range of sea surface temperature (SST) for *O. bartramii* hatch and paralarvae is 21–25°C (Mori et al., 1999a, b). The winter-spring cohort has a seasonal round-trip migration between feeding ground and spawning ground (Murata and Nakamura, 1998) (Fig. 1). During May to July, the squid is distributed between the subtropical region and the subarctic boundary in the North Pacific, and then shifts northward into the subarctic domain from August to November (Murata and Nakamura, 1998; Ichii et al., 2006).

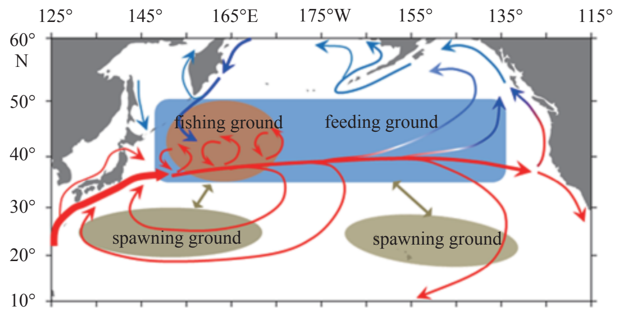

Fig. 1. Illustration of the schematic of the regional circulation and the migration pattern of winter-spring cohort of neon flying squid *Ommastrephes bartramii* in the North Pacific Ocean. Heavy red line represents the Kuroshio Current, heavy blue line the Oyashio Current, and anticylonic arrow line the subtropical gyre circulation.

Some studies have examined the impacts of El Niño-Southern Oscillation (ENSO) combined with local oceanographic conditions, such as SST, sea surface height (SSH), sea surface salinity (SSS) and chlorophyll *a* (Chl *a*) concentration, on the *O. bartramii* population dynamics (Shen et al., 2004; Chen and Liu, 2006; Tian et al., 2009). For example, Yatsu et al. (2000) analyzed the catch per unit effort (CPUE) data over the period of 1979–1998 and reported that the lower temperature water in El Niño years resulted in a sharp decline of the recruitment of the autumn cohort of *O. bartramii*. A controversial result was found for the western winter-spring cohort of *O. bartramii* by Chen et al. (2007), who suggested that El Niño events could lead to a favorable recruitment condition on the spawning ground of this cohort and make the fishing ground shift southward. However, in addition to the ENSO events, the Pacific Ocean has experienced an interannual-to-interdecadal recurring pattern of ocean-atmosphere climate variability centered over the mid-latitude Pacific basin (named as Pacific Decadal Oscillation, PDO) (Zhang et al., 1997; Newman et al., 2003), which plays significant influences on the fishery (Mantua and Hare, 2002). Few studies have related this phenomenon to the dynamics of *O. bartramii* stocks.

The PDO is characterized by the two phases of the SST anomaly: positive (warm) and negative (cool) phases. During the positive phase, the water becomes cooler in the northwestern and central Pacific Ocean and warmer in the East Pacific Ocean. The SST anomaly pattern is reversed during the negative phase: warmer in the Northwest Pacific Ocean and cooler in the East Pacific Ocean (Mantua and Hare, 2002). The ENSO events are highly related to PDO. El Niño (La Niña) events occur more frequently with stronger intensity during the positive (negative) phase of the PDO (Lü et al., 2005). For fisheries, Mantua et al. (1997) found that the dramatic shift in salmon catch regime in the Pacific Ocean was highly correlated with the PDO. Litz et al. (2011) concluded that seasonal expansion of Humboldt squid populations (*Dosidicus gigas*) in the northern California Current System might be related to the PDO. The recent study done by Lehodey et al. (2013) suggested that the PDO could play a significant role in regulating the dynamics of squid resources.

The life cycle of the winter-spring cohort of *O. bartramii*, from eggs, planktonic paralarvae, active swimming juvenile, subadult to mature adult, is highly influenced by the climatic and oceanographic variability (Yu et al., 2013). However, previous studies (Chen et al., 2007, 2012a, b) have simply described the superficial relationship between multi-scale environmental conditions (such as PDO, ENSO and the Kuroshio Current) and *O. bartramii* stock dynamics. Little effort, however, was made to examine the interannual variability in the abundance and distribution of the winter-spring cohort of *O. bartramii* under the physical environment conditions dynamically relating the ENSO with positive and negative phases of the PDO. In this paper, we evaluate the correlation of the CPUE of *O. bartramii* from the Chinese squid-jigging vessels over the period of 1995–2011 with the PDO/ENSO and the anomaly of sea surface oceanographic conditions including SST, Chl *a* concentration and mixed layer depth (MLD) on both spawning and fishing grounds. The influences of the Kuroshio variability during the positive and negative phases of PDO on the CPUE of *O. bartramii* were also examined. The purpose of this study are to characterize the variability of PDO and ENSO, to evaluate the correlation between squid abundance and climatic and local oceanographic factors (PDO, ENSO, SST, Chl *a* concentration, MLD, currents), and to explore the potential process that the climatic events combined with the oceanographic variability affecting the squid stocks.

2 Materials and methods

2.1 *Fishery data*

Fishery data used in this study were collected by Chinese commercial squid-jigging vessels in Northwestern Pacific fishing ground which located in 35°–50°N and 150°–175°E during July–November over the period of 1995–2011. These data were obtained from the Chinese Squid-jigging Technology Group of Shanghai Ocean University, including daily catch (tons), fishing effort (days fished), fishing dates (month and year) and locations (longitude and latitude). Most of the catches were the western winter-spring cohort of *O. bartramii* (Wang and Chen, 2005; Cao et al., 2009). All vessels operated simultaneously at night, with the same fishing power equipped by a main engine power of 120 kW×2, a squid-attracting lamp power of 112 kW, and 16 squid-jigging machines (Chen et al., 2007). In this study, the CPUE estimation from the homogeneous characteristics of the fishing vessels and their operating behaviors was assumed to be reliable index of squid stock abundance (Waluda et al., 1999, 2001; Chen et al., 2008b).

2.2 *Environmental data and climatic index*

Yu et al. (2015) have summarized that the SST, Chl *a* concentration, mixer layer depth (MLD) and currents are identified to greatly influence squid distribution and abundance. Thus, the environmental data used in our analysis included SST, Chl *a* concentration, the MLD and the 3-dimensional (3D) oceanic currents. These data were collected on the fishing ground (35°–50°N, 150°–175°E) and the spawning ground (20°–30°N, 130°–170°E) during July–November and January–May over the period of 1995–2011, respectively. Monthly SST data were obtained from the NOAA High-resolution Blended Analysis database with a resolution of 1° latitude by 1° longitude (http://apdrc.soest.hawaii.edu/data/data). Monthly Chl *a* concentration data were downloaded from the Live Access Server of the National Oceanic and Atmospheric Administration OceanWatch and then interpolated to 1°×1° resolution as SST data (http://oceanwatch.pifsc.noaa.gov/las/servlets/dataset). Monthly MLD was calculated directly from the Argo float-recorded temperature profiles in the Northwest Pacific Ocean, which were acquired from the NOAA Global Argo Data Repository (www.nodc.noaa.gov/argo/index.htm). We used 0.2°C to define the MLD. The oceanic current data were derived from the 36-year (1978–2013) simulation result of the Global-FVCOM (Gao et al., 2011; Chen et al., 2014). The Global-FVCOM was developed under the platform of the unstructured-grid Finite-Volume Community Ocean Model (FVCOM) and had a horizontal resolution up to ~2 km (Chen et al., 2012c, d).

The monthly PDO index (hereafter referred to as PDOI) data from 1995 to 2011 was downloaded from the website of the Joint Institute for the Study of the Atmosphere and Ocean (http://jisao.washington.edu/pdo/PDO.latest). The El Niño and La Niña events were defined based on the index of SST anomaly (hereafter referred to as SSTA) for the Niño 3.4 region. According to the operational standard from NOAA (http://www.noaanews.noaa.gov/stories2005/s2394.htm), El Niño is an abnormal environmental event in the equatorial Pacific Ocean characterized by a positive SSTA averaged over five consecutive months in the Niño 3.4 region which is greater than or equal in magnitude to 0.5°C, while La Niña, is an anomalous oceanographic phenomenon in the equatorial Pacific Ocean characterized by a negative SSTA averaged over five consecutive months in the Niño 3.4 region which is greater than or equal in magnitude to –0.5°C (Chen et al., 2007). The monthly Niño index (NI) data over the period of 1995–2011 was downloaded from the NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov/).

2.3 *Statistical and dynamical analyses*

Cross correlation analyses were employed to evaluate the relationship between CPUE and the annual indices of PDO and ENSO over the period of 1995–2011. The sample cross correlation function is an estimate of the correlation between two time series (for example PDOI and CPUE) at the significant temporal leads and lags, with the aims of determining whether there were time-lagged effects, with a significance level of $P<0.05$ for time-lags of years (George et al., 2005). The statistical analyses were performed by Matlab software. The same analyses were also performed between CPUE and other physical environmental variables including SST, Chl *a* and MLD anomalies. To examine the spatial and temporal variations of the correlation, we conducted these analyses on the fishing and spawning ground regions during July–November and January–May over the period of 1995–2011, respectively.

We have chosen 1998, 1999, 2002 and 2009 as examples to examine the characteristics of the squid abundance and distribution in relation to the oceanographic variables of SSTA, the Kuroshio and Oyashio Currents and meso-scale eddies within the Kuroshio extension region where the front zone bounded by the warm/salt Kuroshio and cold/fresher Oyashio waters were located. 1998 and 2002 were during the positive phase of PDO, while 1999 and 2009 were during the negative phase of PDO. Although both 1998 and 2002 were in the same positive phase, 1998 was a La Niña year and 2002 was an El Niña year. Similarly, 1999 and 2009 were La Niña and El Niño years during the negative phase of PDO, respectively. These four years were chosen because we attempted to explore how the variability of biophysical environments on the fishing ground of *O. bartramii* impacted the squid stock under different climate mode. We first characterized the SSTA under these four special years, and then investigated the physical environments with the corresponding anomalies of flow variability resulting in the systematic change of the thermal field. By tracking the north-south migration of the frontal zone defined by the boundary of Kuroshio and Oyashio waters, we qualified the influence level of these physical changes on squid abundance and distribution.

3 Results

3.1 *Interannual variability of catch/CPUE and correlations with PDO and ENSO*

The catch and CPUE of *O. bartramii* on the fishing ground of the Northwest Pacific Ocean varied over the period of 1995–2011 (Fig. 2). The catch fluctuated from high level to low level alternatively: a high catch of more than 100 000 tons over the periods of 1997–2000 and 2004–2008 and a low catch of 80 000 tons or less over the periods of 1995–1996 and 2001–2003, and of about 50 000 tons over the period of 2009–2011. The highest catch occurred in 1999, which was up to 132 000 tons, and the lowest catch appeared in 2009, which was less than 40 000 tons. The annual average CPUE fluctuate similarly, with a lowest value of 134.7 t/vessel in 2009 and a highest value of 502.5 t/vessel in 2004.

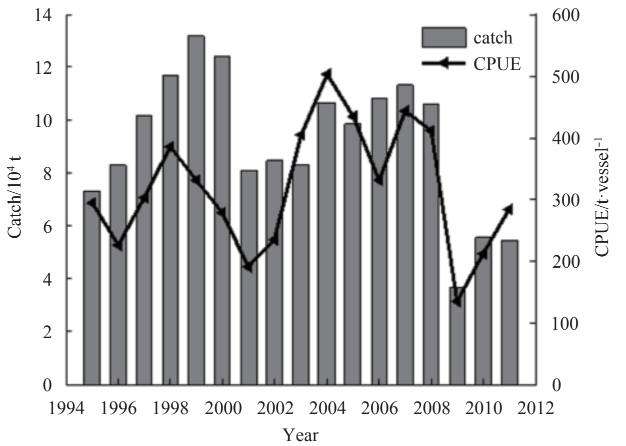

Fig. 2. Total annual catch and average CPUE of *Ommastrephes bartramii* for Chinese squid-jigging vessels. The fishery data were collected in the regions bounded by 35°–50°N and 150°–175°E in the Northwest Pacific over the period of 1995–2011.

The experienced two full PDO cycles in 1995–2011 include the positive PDO phases appearing over the periods of 1995–1998 and 2002–2006, and the negative PDO phases prevailing over the periods of 1999–2001 and 2007–2011 (Fig. 3). Correspondingly,

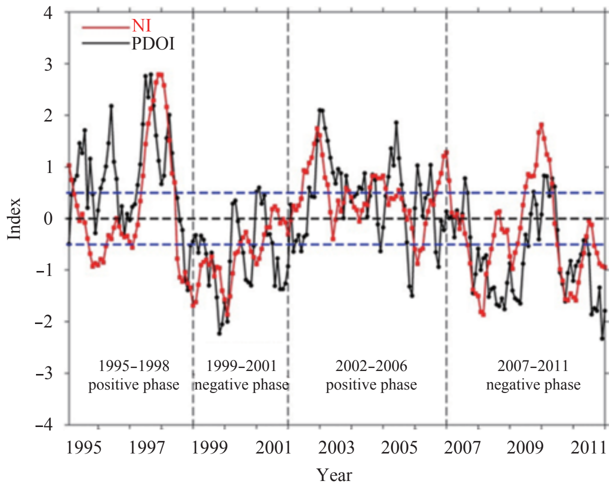

Fig. 3. Monthly values for the PDO index and time series of Niño 3.4 index from 1995 to 2011. PDOI indicates the Pacific Decadal Oscillation index and NI the Niño index.

during the positive PDO phase over the period of 1995–1998, the northwestern and central Pacific Ocean between 25°N and 43°N was occupied by a large portion of colder water that was characterized with a negative SST anomaly ranging from –0.4°C to –0.8°C (Fig. 4). The second positive PDO phase over the period of 2002–2006 was relatively weak compared with that over the period of 1995–1998, during which the colder water was only restricted within a narrow band off the eastern coast of Japan to the central Pacific Ocean in the region between 35°N and 45°N (Fig. 4). During both of the positive PDO phases, the East Pacific Ocean featured the unusual warmer water with a positive SST anomaly ranging from 0.4°C to 0.8°C. As the PDO phases shifted to the negative phase, however, this SST spatial distribution pattern was reversed. During the negative PDO phase over the period of 1999–2001, the West Pacific Ocean was occupied by the warmer water characterized with a positive SST anomaly ranging from 0.2°C to 0.8°C, while the East Pacific Ocean was filled with the colder water featured with a negative SST anomaly in a range of –0.6°C or low (Fig. 4). The negative PDO phase occurring over the period of 2007–2011 was much stronger compared with the previous one over the period of 1999–2001. Except near the northwestern shelf of the North America, the North Pacific Ocean in the region between 20°N and 45°N was filled with the warmer water with a positive SST anomaly of 0.2°C or up (Fig. 4).

According to the definition of El Niño and La Niña, during the two full PDO phases over the period of 1995–2011, it had experienced five El Niño events (May 1997–May 1998, June 2002–March 2003, July 2004–January 2005, August 2006–January 2007 and June 2009–April 2010) and eight La Niña events (September 1995–March 1996, June 1998–May 2000, October 2000–February 2001, December 2005–March 2006, August 2007–May 2008, December 2008–February 2009, June 2010–April 2011, and August 2011–December 2011) (Fig. 3). By cataloging these events over periods of positive and negative PDO phases, there were four El Niño and three La Niña events during the positive phase, and two El Niño and six La Niña events during the negative phase.

The interannual variability of CPUE was highly correlated with PDOI/NI (Fig. 5a). The cross correlation coefficient between CPUE and PDOI at a time lag of one year was 0.60, which was higher than the critical value of 0.49 at a 95% significance level (Fig. 5b). A one-year lag can be viewed clearly in Fig. 5a. For example, the CPUE of *O. bartramii* peaked in 1998, following a positive peak of PDOI in 1997. In turn, the CPUE of *O. bartramii* was significantly lower in 2009 after the lowest negative value of PDOI occurring in 2008. A similar cross correlation was found between CPUE and NI with a coefficient of 0.52 at a time lag of one to two years (Fig. 5c). Although this value was lower than that found between CPUE and PDOI, it was still higher than the critical value of 0.49 at a 95% significant level. Although PDOI and NI were highly correlated in phase with a coefficient value of 0.73 (Fig. 5d), peaks of PDOI and NI did not completely match each other (Fig. 5a). This result suggested that the CPUE of *O. bartramii* was closely correlated with PDOI, as well as NI. A one-year phase lag between CPUE of *O. bartramii* and PDOI was found in our study.

3.2 *Variability of environmental conditions on the spawning and fishing grounds*

Over the period of 1995–2011, the SSTA on the fishing ground (hereafter referred to as FGSSTA) during July through November varied from –1.0°C to 1.0°C (Fig. 6a). The correlation between the CPUE of *O. bartramii* and FGSSTA was insignificant (Fig. 7a). However, we could find the CPUE of *O. bartramii* had the same trend with FGSSTA in some years. For example, the CPUE gradually reduced as FGSSTA decreased from 1998 to 2001, and rose as FGSSTA increased from 2009 to 2011. FGSSTA was negatively correlated in phase with PDOI: a high/low FGSSTA usually cor-

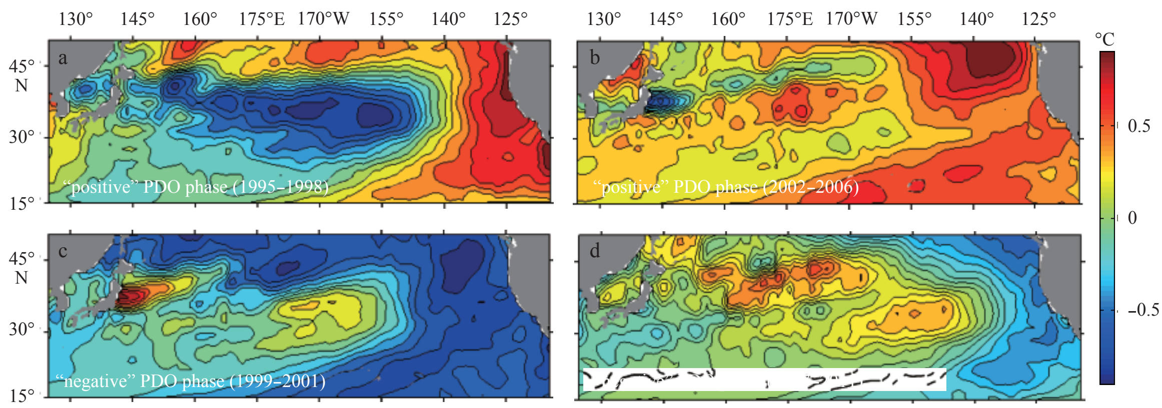

Fig. 4. Sea surface temperature anomalies in the North Pacific during the warm PDO phases over the periods of 1995–1998 (a) and 2002–2006 (b) and during the cold PDO phases over the periods of 1999–2001 (c) and 2007–2011 (d).

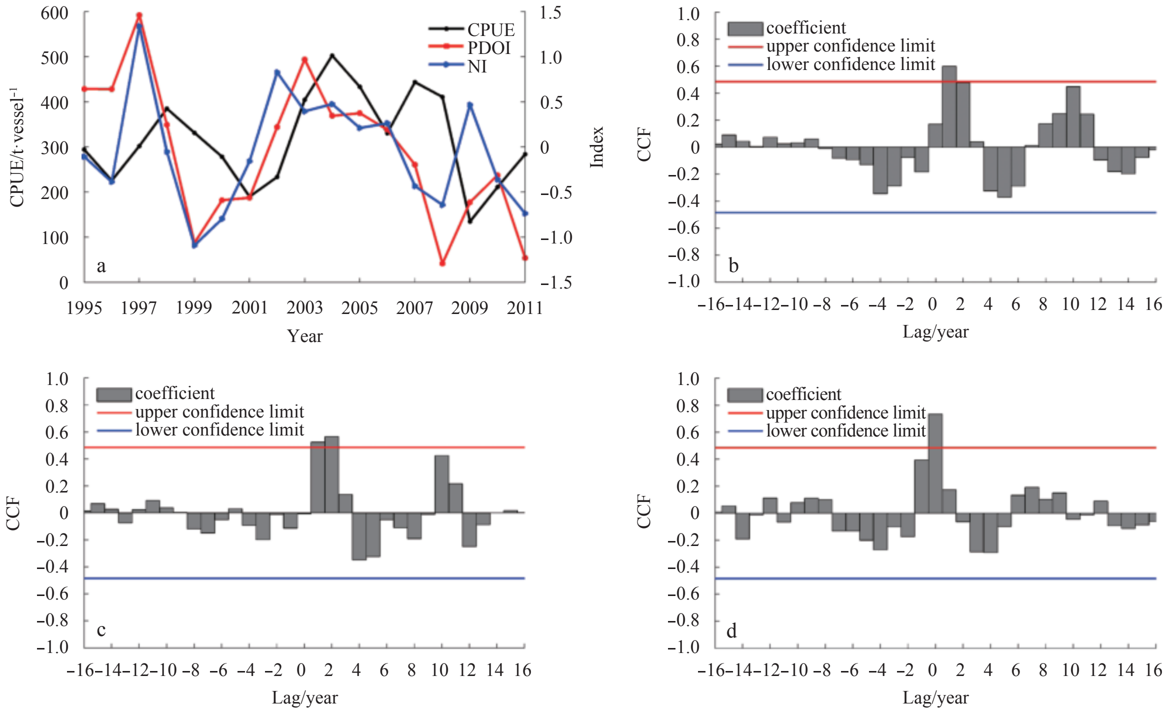

Fig. 5. Time series of annually averaged CPUE, PDOI and NI (a), and cross-correlation coefficient with the time lag between PDOI and CPUE (b), NI and CPUE (c), and PDOI and NI (d). The unit used for the time lag: year. Red and blue lines represent the upper and lower confidence limit at the 95% significant level, respectively.

responded to a low/high PDOI (Figs 6b and 7b). During the spawning season (January–May), the SSTA on the spawning ground (hereafter referred to as SGSSTA) varied in a range of –0.6°C to 0.9°C (Fig. 6c). The SGSSTA increased from 1995 to 1999 and then showed a decrease trend in the subsequent years. Although the relationship between SGSSTA and the PDOI was irregular (Fig. 6d) and their cross correlation at a time lag of 4 years was around a marginal level of the critical value at a 95% significant level (Fig. 7d), the SGSSTA showed a positive correlation with CPUE of *O. bartramii* at a time lag of 5–6 years (Fig. 7c).

During the fishing season, the annually averaged Chl *a* concentration anomaly on the fishing ground (hereafter referred to as FGCA) varied from the lowest value of –0.056 mg/m³ in 2009 to the highest value of 0.048 mg/m³ in 2007 (Fig. 6e). The annual CPUE of *O. bartramii* coincided with the variability of FGCA over the period of 1995–2011, with a cross correlation coefficient of 0.6 or higher at a time lag of 0–1 year (Fig. 7e). The high correlation was also valid for the annually averaged Chl *a* concentration on the spawning ground (hereafter referred to as SGCA) during January through May. Although the variability was much smaller in SGCA than in FGCA (Fig. 6g), the cross correlation between CPUE of *O. bartramii* and SGCA was over 0.6 at a time lag of one

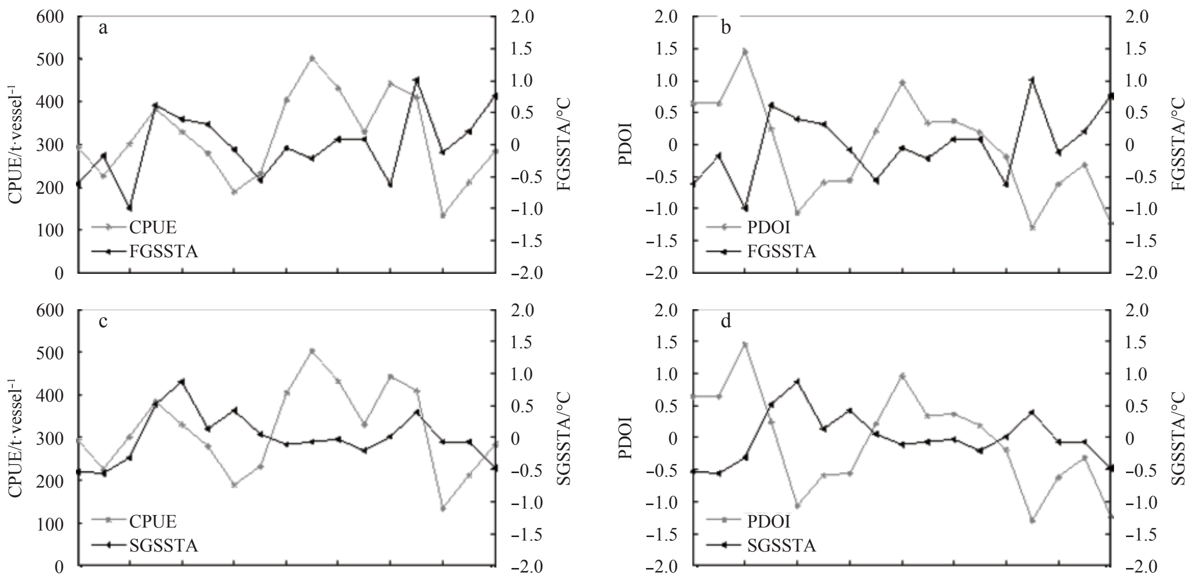

Fig. 6

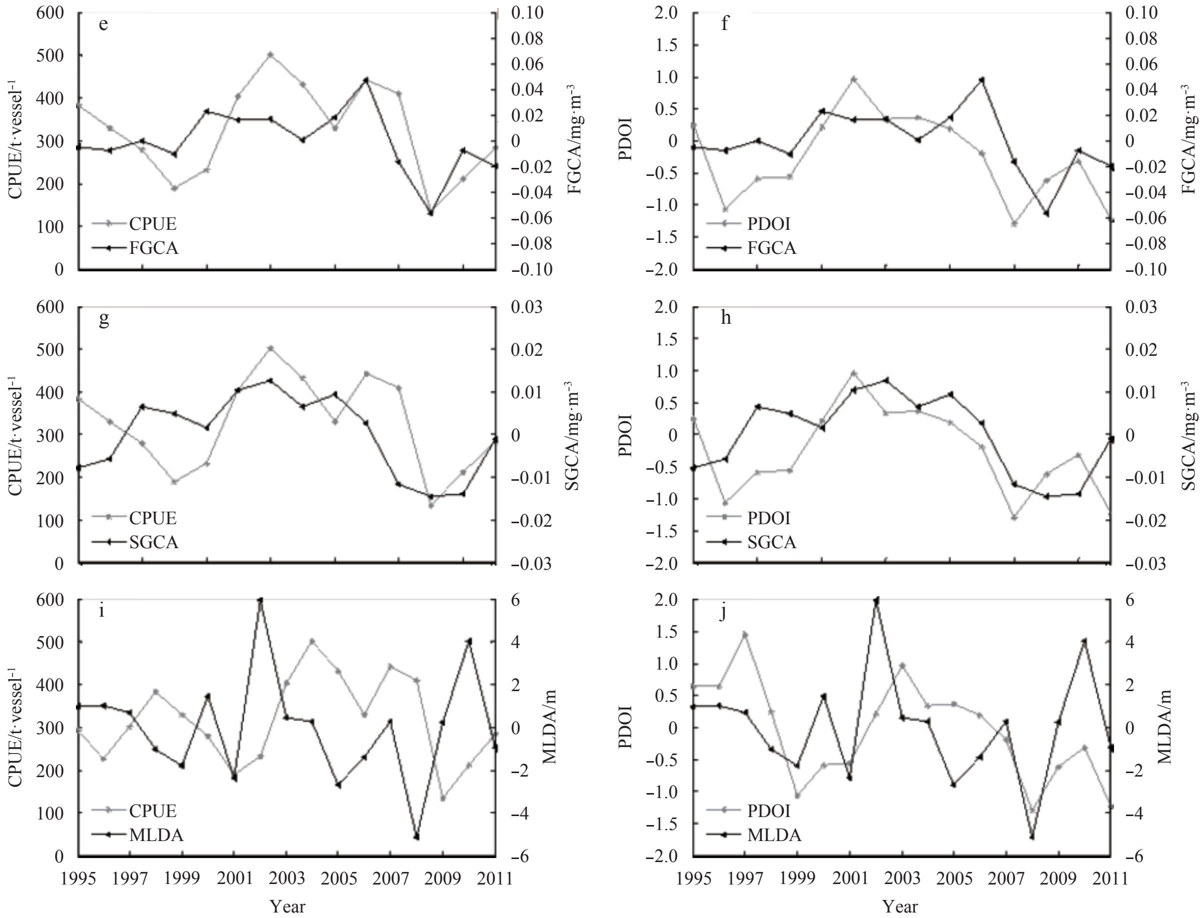

Fig. 6. Comparison of the CPUE and PDOI with the time series of annually averaged environmental variables over the period of July-November. a. CPUE and FGSSTA, b. PDOI and FGSSTA, c. CPUE and SGSSTA, d. PDOI and SGSSTA, e. CPUE and FGCA, f. PDOI and FGCA, g. CPUE and SGCA, h. PDOI and SGCA, i. CPUE and MLDA, and j. PDOI and MLDA.

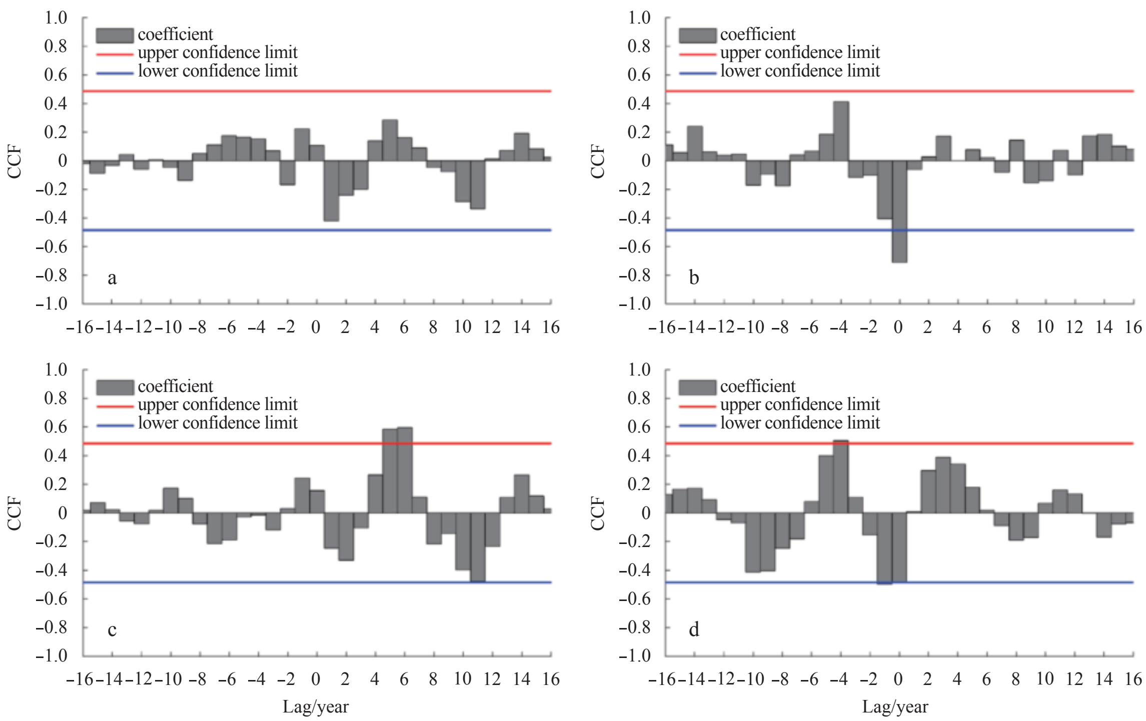

Fig. 7

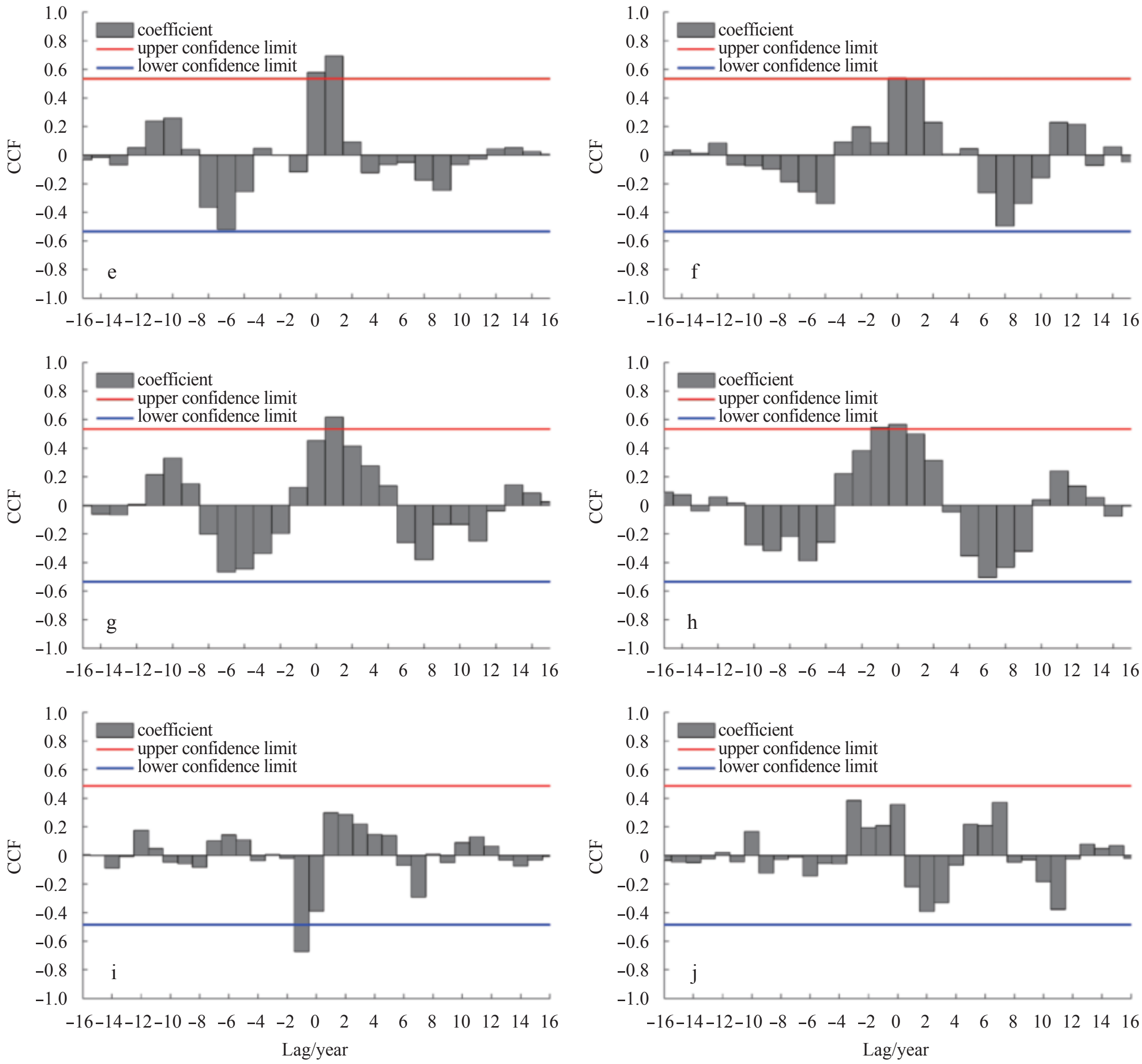

Fig. 7. Cross-correlations coefficient with the time lag between CPUE and FGSSTA (a), PDOI and FGSSTA(b), CPUE and SGSSTA (c), PDOI and SGSSTA (d), CPUE and FGCA (e), PDOI and FGCA (f), CPUE and SGCA (g), PDOI and SGCA (h), CPUE and MLDA (i), and PDOI and MLDA (j). Unit for the time lag: year. Red and blue lines represent the upper and lower confidence limit at the 95% significant level, respectively.

year (Fig. 7g). Both FGCA and SGCA varied synchronously with the PDOI (Figs 6f and h), and the highest cross correlation between PDOI and either FGCA or SGCA appeared at a zero-year time lag (Figs 7f and h).

Following Sverdrup's theory, the near-surface phytoplankton concentration in the interior of the ocean is controlled by the ratio of euphotic layer to the MLD (Sverdrup, 1953). Since the euphotic layer in the subtropical gyre region remained similar year to year, the MLD tended to be more critical for the variability of the phytoplankton concentration on both spawning and fishing grounds. Since the CPUE of *O. bartramii* and Chl *a* concentration were highly correlated in the interannual variability time scale, we directly compared the annually averaged MLD anomaly on the fishing ground (hereafter referred to as MLDA) during July through November with the CPUE of *O. bartramii*. Over the period of 1995–2011, the interannual variability of MLDA was in a range of –6.0 to 6.0 m (Fig. 6i). The CPUE of *O. bartramii* was negatively correlated with MLDA with a coefficient of –0.7 at a one-year preceding time lag (Fig. 7i). This corresponded to the positive correlation between the CPUE of *O. bartramii* with FGCA and SGCA, the shallow MLD provided a favorable condition to increase the phytoplankton concentration. Considering a mean MLD of ~60 m, however, the MLDA only accounted for ~10% of the MLD. The MLDA tended to coincide reasonably with the PDOI over the period of 1995–2011 (Fig. 6j), but their correlation was below the critical value at the 95% confidence level.

3.3 *Biophysical environments examination*

We have examined the variability of the physical environment during high catch years of 1998 and 1999 and low catch years of 2002 and 2009. 1998 was a La Niña year under the positive phase of PDO, the fishing ground from July to November was characterized by a positive SSTA, which was featured by warm-core eddies resulting from the instability of the Kuroshio Current (Fig. 8a). The fishing locations were overlapped well with warm water regions in which the SSTA was between 0.2°C and 0.8°C (Fig. 8a). As a result, the catch and CPUE were typically high in 1998. In general, during the positive phase of PDO the West Pacific Ocean should be characterized by negative SSTA. Because the La Niña occurred, however, it produced a highly positive

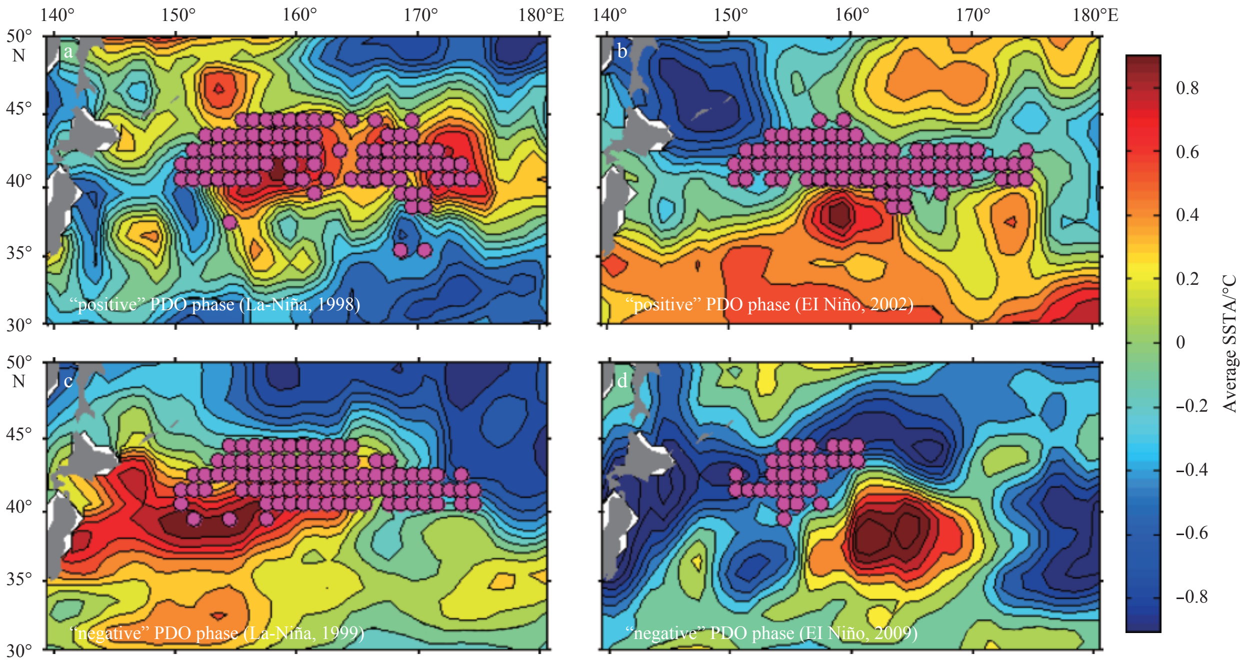

Fig. 8. Distributions of the average SSTA overlapped with the fishing locations during July through November in 1998 (a), 2002 (b), 1999 (c) and 2009 (d).

SSTA in the region bounded by 35°–45°N and 153°–176°E. The warming feature on the fishing ground provided a favorable physical condition for the catch of *O. bartramii*. 2002 was also under the positive phase of PDO but was an El Niño year. The area with a positive SSTA was located south of 40°N, and the fishing ground was characterized by a narrow long band of anomalously colder water that was connected to the southward cold/fresher Oyashio Current on the eastern coast of Japan (Fig. 8b). The fishing locations were overlapped with the colder water zone in which the SSTA was in a range of –0.4–0°C. As a result, the catch and CPUE significantly declined in 2002.

The year of 1999 was under the cold PDO phase but a La Niña year during which the fishing ground was characterized with positive SSTAs in a range of 0.2–0.8°C bounded by 30°–43°N and 140°–165°E, but with a sharp spatial gradient of SSTA in the frontal zone either north of 43°N or east of 168°E (Fig. 8c). The large portions of the fishing area were in warmer waters with SSTA in a range of 0.2°C to 0.7°C. While the small portion of the fishing area was in the frontal zone and colder water between 168°E and 175°E (Fig. 8c). As a result, the CPUE of *O. bartramii* in 1999 was slightly lower than that in 1998, but much higher than that in the 2002 El Niño year. The year of 2009 was also under the negative phase of PDO as in 1999, but it was an El Niño year. In this year, the fishing ground was characterized with large negative SSTAs varying from –0.8°C to –0.4°C in the region on the eastern coast of Japan and north of 42°N–45°N (Fig. 8d). In general, during the negative phase of PDO, the West Pacific Ocean should be featured by warm waters. Since the El Niño occurred in 2009, the warmer water mass was confined as an isolated meso-scale warm-core eddy in the areas between 35°–42°N and 157°–170°E (Fig. 8d). In this region, the value of SSTA exceeded 0.8°C. Because all fishing areas in 2009 were concentrated in the extremely low temperature water region, the catch and CPUE of *O. bartramii* suffered a dramatic decline.

Our findings suggested that although the interannual variability of PDOI and the CPUE of *O. bartramii* was highly correlated at a time lag of one year, the catch and CPUE of *O. bartramii* depended on whether or not the fishing area was in the warmer water region with a positive SSTA. In addition, the SSTA could dramatically differ in the local region from the large-scale feature during the positive and negative phases of PDO.

The flow field simulated by the Global-FVCOM considerably differed in the La Niña and El Niño years during the positive and negative phases of PDO (Fig. 9). For example, in the La Niña years of 1998 and 1999, in addition to the eastward offshore extension flow of the Kuroshio Current at around 35°N, a portion of the Kuroshio water meandered northward along the eastern coast of Japan up to ~43°N and then anti-cyclonically rotated back to the eastward flow around 40°N. When this happened, the Oyashio Current retreated northward with its southern boundary around 44°N or further north. In this situation, the fishing ground was largely occupied by the warm/salty Kuroshio water with a rich food supply characterized with the relatively high Chl *a* concentration. Between the two eastward Kuroshio extension flows between 35°N and 40°N, there existed multiple meso-scale eddies, which tended to intensify the retention mechanism for the food and also squid distributions.

In the El Niño years of 2002 and 2009, no northward intrusion of Kuroshio Current occurred along the eastern coast of Japan. The main stream of the Kuroshio Current left the coast around 35°N and moved eastward to form the Kuroshio extension current. As a result of the flow instability, the Kuroshio Current separated into two branches in the region east of 157°E, and thus multiple meso-scale eddies formed between these two branches of the Kuroshio extension flow. When this happened, the Oyashio Current shifted southward to advect the cold water into the region south of 43°N. In this case, the fishing ground was occupied by both warm/salty Kuroshio and cold/fresher Oyashio waters, and thus the catch and CPUE of *O. bartramii* were declined when the fishing area was located in the cold water zone characterized by either the Oyashio water or the Kuroshio and Oyashio mixed water.

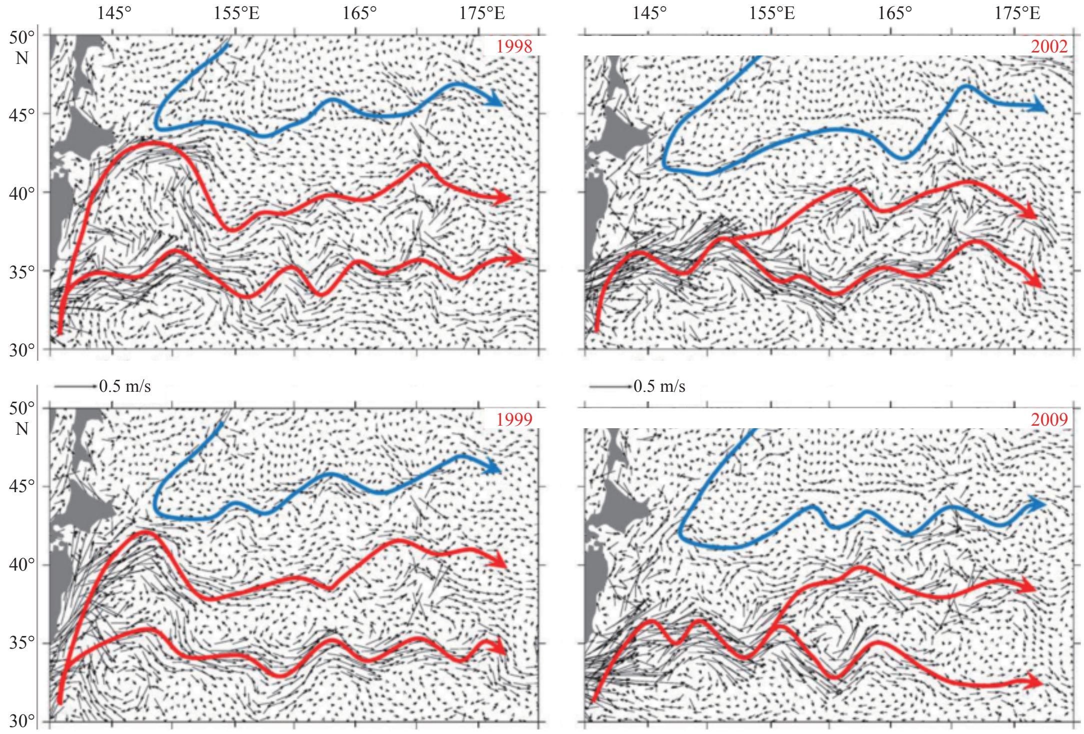

Fig. 9. Distribution of the regional circulation in the western Pacific Ocean during the fishing period in 1998 (upper-left panel), 1999 (lower-left panel), 2002 (upper-right panel) and 2009 (lower-right panel). Red lines with arrows indicate the main stream of the Kuroshio Current. Blue lines with arrows represent the main stream of the Oyashio Current.

Defining the Kuroshio Current Frontal Zone (KCFZ) as the 20°C isotherm and the Oyashio Current Frontal Zone (OCFZ) as the 10°C isotherm, we examined the variation of the KCFZ relative to OCFZ in the four years of 1998, 1999, 2002 and 2009 (Fig. 10). We noted that in the La Niña years of 1998 and 1999, both KCFZ and OCFZ moved northward approximately 1°–2°N compared with the locations of KCFZ and OCFZ in the El Niño years of 2002 and 2009. It was clear that for the habitat of *O. bartramii*, the northward intrusion of the warm Kuroshio Current water provided a favorable environmental condition, while the southward invasion of the cold Oyashio Current yielded an unfavorable environmental condition. Therefore, the stock assessment of the winter-spring cohort of *O. bartramii* should be done not only by statistics based on the fishery data but also by examining the change of the physical environment conditions on the fishing ground.

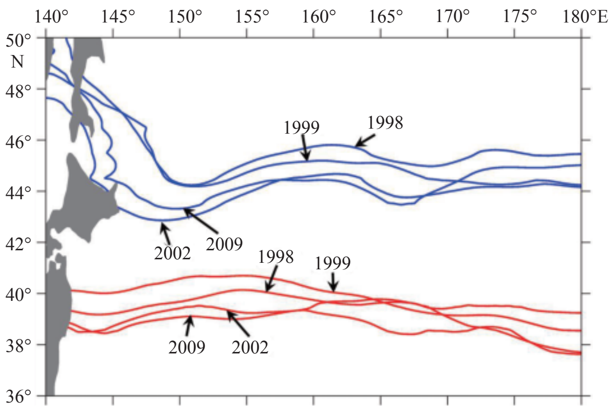

Fig. 10. Distributions of boundaries of the Kuroshio and Oyashio Current frontal zones defined as the 20°C (red) and 10°C (blue) isotherms in 1998, 1999, 2002 and 2009, respectively.

4 Discussion

The short lifespan of ommastrephid squid make their groups highly sensitive to large-scale climatic variability and local oceanographic conditions, which environmentally drove interannual variations in squid distribution and abundance (Anderson and Rodhouse, 2001). In this study, we attempted to explore the process that the climatic and oceanic factors affected the squid abundance by three steps: (1) analyze how the climate (PDO and ENSO) changed over times; (2) evaluate the biophysical conditions (SST, Chl *a* and MLD) on squid spawning and fishing grounds; (3) connect the climatic and oceanic variability with dynamics of squid stocks. Over the period of 1995–2011, the western stocks of the winter-spring cohort of *O. bartramii* experienced two full PDO cycles combined with a dozen El Niño/La Niña events. Variations in the SSTA in the North Pacific Ocean and the frequencies of occurrence of the ENSO events in different PDO phases were basically consistent with the previous studies (Mantua and Hare, 2002; Lü et al., 2005). The catch and CPUE of *O. bartramii* were positively correlated with PDOI and NI with a time lag of one year. This result suggested that climate variability tended to play significant influences on the catch and abundance of *O. bartramii*.

There have been a few efforts contributing to the evaluation of the influences of PDO combined with ENSO events on population dynamics of marine species. For example, Koslow et al. (2012) developed a 60-year time series of the abundance of the Californian spiny lobster (*Panulirus interruptus*) and found a positive relationship between early-stage phyllosoma abundance and PDO and El Niño events. Our results suggested that positive PDO tended to provide favorable oceanographic conditions for *O.bartramii* habitat in the Northwest Pacific Ocean and thus increased catches, while the negative PDO phase could provide unfavorable environmental conditions for the growth and survival of *O. bartramii*. Additionally, previous studies suggested that the environmental conditions affected by the El Niño/La Niña events in February on the spawning ground could influence the squid recruitment (Chen et al., 2007; Cao et al., 2009). Over the period of 1995–2011, La Niña events influenced the squid habitat seven times on the spawning ground in February of 1996, 1999, 2000, 2001, 2006, 2008 and 2009, the CPUE in the subsequent years dramatically declined. After El Niño events in February of 1998, 2003 and 2010, the CPUE increased in the subsequent years. Therefore, an El Niño event in the previous year could be favorable to squid recruitment and yield a high CPUE in the subsequent year. On the contrary, a La Niña event in the previous year could lead to declined squid recruitment and lead to a low CPUE in the subsequent year. Our results showed that the interannual variability in the squid abundance was controlled by synergetic influences associated with PDO and ENSO.

Many studies have been conducted to evaluate the influences of SST and Chl *a* concentration, but few in MLD, on the abundance and distribution of *O. bartramii*. Wang et al. (2010) studied the spatio-temporal relationship between the squid catch and SST and Chl *a* concentration and suggested that high SST variability coincided with productive squid catches, and the fishing ground seasonally migrated between 0.15 and 0.5 mg/m^3 on the sea color isoline. Based on the generalized additive model (GAM), Fan et al. (2009) concluded that a favorable SST for the winter-spring cohort of *O. bartramii* was between 10°C and 22°C with an optimal SST in a range of 15–17°C, and also the squid were mainly concentrated in the region with the Chl *a* concentration in a range of 0.1–0.6 mg/m^3. Chen et al. (2012b) established the integrated habitat suitable index (HSI) model and found that the vertical temperature profile in the upper 50 m was susceptible to MLD in this layer and could be used to predict potential fishing grounds for *O. bartramii*. Water temperature tended to be a critical factor affecting squid population. Our results showed that, both FGSSTA and SGSSTA were affected by the PDO, but the correlation between the SSTA and squid abundance was not significant if the estimation was based on the average value on the spawning and fishing ground. The analysis needs to consider the spatial variation of SSTA on the fishing ground. We examined the abnormal environmental conditions in high and low squid abundance years with La Niña and El Niño events corresponding to warm and cold PDO phases, which covered several potential scenarios that can be used to explain the variability of squid abundance to some extent. We found that an abnormally higher temperature on the fishing ground in La Niña years did show a favorable condition to a high CPUE, and lower temperature in El Niño years tended to result in a decrease in squid abundance.

As above-mentioned, the SSTA on the fishing ground of *O. bartramii* greatly varied with the climate modes. How the climate variability caused this spatial distribution of SSTA on the fishing ground? Actually, the fishing ground was in the Kuroshio extension region in the Pacific Ocean. Due to the two-mode meandering nature of the Kuroshio Current (Taft, 1972), it was also a region with an active interaction between the warm/salty Kuroshio Current and the cold/fresher Oyashio Current. The boundary of these two currents formed a thermal frontal zone with its location migrating meridionally over seasonal-interannual scale. It is clear that the variability of Kuroshio Current and the location of the thermal frontal zone could directly affect the catch of *O. bartramii*, but it is unclear what happened in this large-scale circulation system during the high and low catch years under the positive and negative phases of PDO. We thus linked this variability of SSTA with the regional circulation under different climate modes. We found that the climate-induced large-scale variability of the regional circulation in the Northwest Pacific Ocean played a significant role in regulating the oceanic condition on the fishing ground of *O. bartramii*. The northward intrusion of the Kuroshio Current tended to yield the warm temperature condition in the La Niña years of 1998 and 1999, whereas the invasion forces of the Oyashio Current led to the anomalously cool water in the El Niño years of 2002 and 2009. Since the interaction zone of the Kuroshio-Oyashio Currents varied significantly with the climate change-induced variability of the regional circulation, the catch and CPUE of *O. bartramii* were significantly influenced by the locations of fishing area. The high catch and CPUE could happen in the La Niña in both the positive and negative phases of PDO as a result of the large-scale variation of the regional circulation.

Few studies have evaluated the influence of Chl *a* anomaly on the abundance of *O. bartramii* on the spawning ground (Ichii et al., 2011). Actually, the primary productivity on the spawning ground played a significant role in the life cycle of the squid, fast growth rate and high abundance of *O. bartramii* generally occurred in the food-rich zone (Ichii et al., 2009). The *O. bartramii* paralarvae and juveniles generally remained in their spawning grounds during the early life stages (Nishikawa et al., 2014). They mainly fed on zooplankton, especially concentrated in the waters with high abundance of euphausiacea and amphipoda (Cheng and Huang, 2003; Xu et al., 2004). Our studies found that the FGCA and SGCA were closely related to the CPUE, yielding the strongest positive relationship with a lag of one year. The variability of FGCA and SGCA coincided with the PDOI. These findings indicated the variability of the annually averaged Chl *a* concentration on both spawning and fishing grounds changed in the same phase as PDOI and the interannual variability of the CPUE of *O. bartramii* was highly related to the change in the lower trophic level food web that varied with climate change. The positive PDO would yield high Chl *a* concentration on the spawning ground, leading good feeding environments for squid recruitment. Vice versa, the negative PDO would provide unfavorable feeding environments for squid paralarvae and juveniles. Additionally, the low variability found in SGCA was not surprising, since it as a portion of the spawning ground was in the subtropical gyre region where the biological desert zone was located (Chen, 2003). A one year lag correlation between Chl *a* and CPUE might explain why the highest correlation between the PDOI and CPUE showed one year lag. However, the MLD tended to be necessary but its contribution to the interannual variability of CPUE of *O. bartramii* was limited in this study.

It should be pointed out here that in this study, we found that spatio-temporal population dynamics of *O. bartramii* were significantly affected by large-scale climate variability and regional physical and biological environmental conditions on the spawning and fishing grounds. The mechanism described in this paper, however, still could not explain what the biophysical process was that caused the 1-year delay in the cross correlation between the PDOI and CPUE. The western winter-spring cohort of *O. bartramii* was mainly distributed in the Kuroshio-Oyashio interaction region in the western North Pacific, where the flow field was regulated by the Kuroshio meandering, meso-scale eddies and variation of the thermal front (Sassa et al., 2007). Fluctuations in the distribution of the Kuroshio Current and Oyashio Current, which resulted from the climate change, could drive the short-term (hourly to daily) and long-term (seasonal to annual or decadal) variability of physical and biological variables on the fishing ground. This complex dynamical system requires an eddy-resolving coupled physical and biological modeling study. Such an ocean model could help develop a capacity for predicting the dynamics of *O. bartramii* resources and improve the management of the fishery resource.

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