Influence of surface oceanographic variability on abundance of the western winter-spring cohort of neon flying squid *Ommastrephes bartramii* in the NW Pacific Ocean

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ABSTRACT: Abundance of the *Ommastrephes bartramii* winter-spring cohort fluctuated greatly from 1995 to 2004. To understand how abundance was influenced by sea surface conditions, we examined the variations in the proportion of thermal habitats with favourable sea surface temperature (SST). The SST data of both the spawning and feeding grounds were used to calculate the monthly proportion of favourable-SST areas (PFSSTA). Catch per fishing day per fishing boat (catch per unit effort, CPUE) of the Chinese mainland squid-jigging fleet was used as squid abundance index. The relationships between CPUE and monthly PFSSTA at spawning and feeding grounds were analyzed, and the relationship between CPUE and selected PFSSTA was quantified with a multiple linear regression model. Results showed that February PFSSTA at the spawning ground and August to November PFSSTA at the feeding ground could account for about 60 % of the variability in *O. bartramii* abundance between 1995 and 2004, that February was the most important period influencing squid recruitment during the spawning season, and that feeding ground PFSSTA during the fishing season would influence CPUE by causing squid to aggregate. Our forecast model was found to perform well when we compared the model-predicted CPUEs and the average CPUEs observed during August to November in 2005 and 2006 from the Chinese squid-jigging fishery.

KEY WORDS: Sea surface temperature · Abundance index · *Ommastrephes bartramii* · Northwest Pacific Ocean

INTRODUCTION

The role of environmental variables in regulating the dynamics of fishery stocks has been an important research topic, in particular for short-lived squid species (Roberts 1998, Agnew et al. 2002). The life span of most squid species is less than 1 yr (Boyle 1987). For such short-lived species, recruitment success dominates annual variations of stock abundance, and is influenced greatly by the physical and biological environments of spawning and nursery grounds (Sakurai et al. 2000). The abundance and distribution of squid populations tend to be influenced greatly by environmental variables and respond quickly to changes in the environment (Wadley & Lu 1983, Yatsu et al. 2000, Anderson & Rodhouse 2001, Rodhouse 2001, Waluda et al. 1999, 2001, 2006, Bazzino et al. 2005). Waluda et al. (2001) suggested that about 55 % of the variability in recruitment of the Falkland Island *Illex argentinus* fishery could be explained by variation in the total area of putative favourable-sea surface temperature (SST) areas at spawning grounds during spawning season. Variability in the abundance of *Todarodes pacificus* in the Sea of Japan was found to be related to changes in

their favourable-SST areas for larval develop-
ment (Sakurai et al. 2000). As a result, envi-
ronmental indices are increasingly being used
to predict recruitment strength in squid
(Agnew et al. 2002). Tamaki (1987) reported
that fishing conditions for diamond squid
Thysanoteuthis rhombus in the Sea of Japan
could be forecasted based on flow pattern and
strength of the Tsushima Current, and water
temperature on fishing grounds, but he did not
clearly quantify any of these relationships.
Miyahara et al. (2005) analyzed the fluctuation
of *T. rhombus* and developed models to fore-
cast catch per unit effort (CPUE) based on
environmental factors.

The neon flying squid *Ommastrephes bar-
tramii* is an oceanic cephalopod widely distrib-
uted in subtropical and temperate waters of
the world (Roper et al. 1984). It supports a major com-
mercial squid fishery in the northwest Pacific Ocean.
Japan began the commercial fishery in 1974 after
catches of the Japanese common squid *Todarodes
pacificus* dropped sharply during the early 1970s;
Korea and Taiwan, ROC, followed suit. In the late
1980s, with the development of a drift-netting fishery,
annual catch increased rapidly. Estimated annual
catch varied from 150 000 to 350 000 t in the 1980s and
1990s (Bower & Ichii 2005). Mainland China started a
small-scale commercial neon flying squid fishery in
1994; since then the fishery has expanded greatly. The
annual catch continued increasing every year from
1994 to 1999, but after 1999 the annual landing fluctu-
ated greatly from year to year (Fig. 1; Chen et al. 2008).

The North Pacific population of *Ommastrephes bar-
tramii* comprises 2 seasonal cohorts (autumn and winter-
spring) and 4 stocks: (1) central stock of the autumn co-
hort, (2) eastern stock of the autumn cohort, (3) western
stock of the winter-spring cohort, and (4) central-eastern
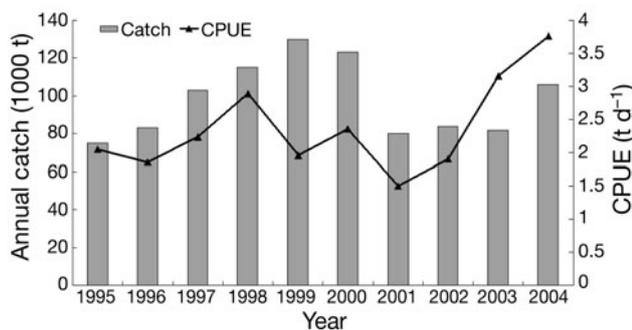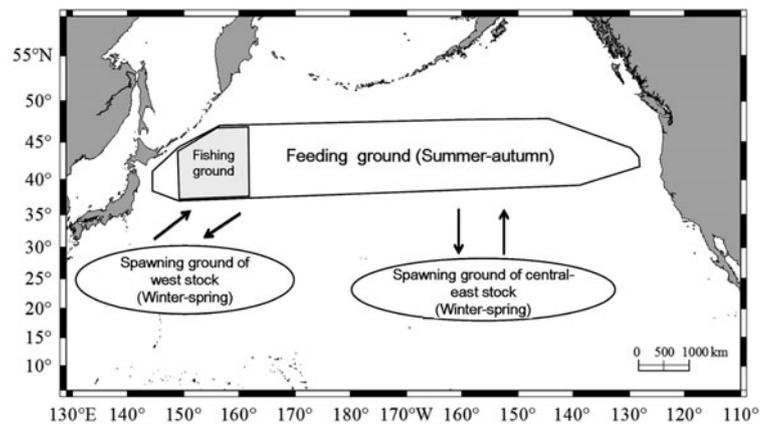stock of the winter-spring cohort (Bower & Ichii 2005).

Fig. 2. *Ommastrephes bartramii.* Migration pattern of the winter-spring
cohort in the North Pacific Ocean, showing the spawning ground and
feeding ground

The western stock of the winter-spring cohort is the main
target of the Chinese jigging fishery (Chen et al. 2007,
2008). This stock spawns mainly in the area between 130
to 170° E and 20 to 30° N during January to April (Fig. 2;
Bower 1996, Nagasawa et al. 1998, Yatsu et al. 1998).
The fishing ground of the Chinese jigging fishery is in
the area 150 to 165° E and 38 to 46° N; it operates during
August to November (Fig. 2; Chen et al. 2008). This is the
feeding ground of the western stock of the winter-spring
cohort (Chen et al. 2008).

Ommastrephes bartramii has a life span of less than
1 yr and its life cycle is closely related to the environ-
ment of the North Pacific Ocean (Yatsu et al. 1997,
1998). Its abundance and distribution are strongly
influenced by environmental variables such as water
temperature and salinity (Chen & Chiu 1999). La
Niña/El Niño events have resulted in abnormal envi-
ronmental conditions that in turn influenced squid
recruitment (Chen et al. 2007). The early life stage of
O. bartramii mainly occurs in surface waters. Paralar-
vae can be collected in surface tows both day and night
(Young & Hirota 1990, Saito 1994a,b), and they are
abundant in the upper 25 m (Saito & Kubodera 1993).
Therefore, surface conditions and environment are
critical in determining squid recruitment success. The
distribution of paralarvae suggests that they hatch in
areas with SST ranging from 21 to 25°C (Hayase 1995,
Saito 1994a, Bower 1996, Bower & Ichii 2005). On the
feeding ground, monthly optimum SSTs for *O. bar-
tramii* are 15 to 19°C, 14 to 18°C, 10 to 13°C, and 12 to
15°C for August, September, October and November,
respectively (Chen 1997, 1999, Chen & Tian 2005).

Previous studies of oceanographic variability influ-
encing life process of squid suggested that SST is a
major factor of oceanographic variability and has sig-
nificant impacts on squid recruitment (Hayase 1995,
Saito 1994a, Bower 1996, Chen 1997, 1999, Chen &

Fig. 1. *Ommastrephes bartramii.* Total annual catch of the
western winter-spring cohort by the Chinese squid-jigging
fleet in the North Pacific Ocean from 1995 to 2004, and aver-
age catch per unit effort (CPUE) in the area of 150 to 165° E,
38 to 46° N in the same period

Tian 2005, Semmens et al. 2007). However, more studies need to be done to evaluate how changes in SST influence the abundance of the western winter-spring cohort of *Ommastrephes bartramii*. In this study, we assume that changes of SST and other physical and climatic variables that may influence squid abundance are ultimately contained in the change of proportion of favourable-SST areas (PFSSTA). This study aims to evaluate how the abundance of western winter-spring stock of *O. bartramii* in the northwestern Pacific Ocean is related to surface oceanographic variability represented by PFSSTA on the spawning and feeding grounds, and to develop a fishery forecast model for predicting the fishery abundance of western winter-spring stock of *O. bartramii*. Such a study can yield information critically important to understanding and predicting recruitment dynamics of western winter-spring cohort of *O. bartramii*.

MATERIALS AND METHODS

Fishery data. Data on daily catch (t), effort (days fished), and fishing locations were obtained from the Chinese commercial jigging fleet operating in the area of 150 to 165° E and 38 to 46° N. For the Chinese squid-jigging fleet, this area yielded more than 80% of the total catch (Chen et al. 2008) during August to November from 1995 to 2006; most of the catch was from the western winter-spring stock of *Ommastrephes bartramii*, with a small amount from the autumn cohort (Chen et al. 2007, 2008). CPUE was quantified as t squid d^{-1}, and calculated yearly from 1995 to 2006. One unit of fishing area is defined as 1° latitude by 1° longitude. Chinese jigging vessels are almost identical in fishing power, and the fishery operates at night. Bycatch is almost nonexistent (Wang & Chen 2005). Therefore, CPUE is considered to be a reliable index of stock abundance for *O. bartramii* because the fishing vessels are homogeneous in their characteristics and operating behavior (Richards & Schnute 1986, Waluda et al. 1999, 2001, Chen et al. 2007, 2008).

Environmental data. Previous studies demonstrate that squid recruitment is mainly determined by the range of favourable-SST waters on their spawning ground (Sakurai et al. 2000, Waluda et al. 2001). Thus we selected PFSSTA of spawning ground as the environmental variable in evaluating the relationship between recruitment and environmental variability. CPUE was used as an indicator of abundance (Chen et al. 2007). SST is also an important environmental factor in affecting squid distribution (Chen 1997, 1999,

Chen & Tian 2005). In order to understand how SST at the feeding ground influenced CPUE, we also selected PFSSTA of feeding ground as one of the environmental variables to be considered.

Data on monthly SST at the spawning ground (130 to 170° E, 20 to 30° N) and feeding ground (150 to 165° E, 38 to 46° N) were obtained at the resolution of 1° latitude by 1° longitude from the Joint WMO/IOC Technical Commission for Oceanography and Marine Meteorology Products Bulletin Data Products (http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.data_products.html 2008). We used Marine Explorer 4.0 software (Environment Simulation Laboratory) to map the monthly SST on the spawning (January to April) and feeding (August to November) grounds. The monthly PFSSTA from 1995 to 2006 was calculated based on SST ranges considered optimal for hatch and paralarvae distributions (21 to 25°C) on the spawning ground (Hayase 1995, Saito 1994a, Bower 1996) and on SST ranges considered optimal for the distribution of *Ommastrephes bartramii* in feeding activity on the feeding ground (15 to 19°C, 14 to 18°C, 10 to 13°C, and 12 to 15°C for August, September, October and November, respectively) (Chen 1997, 1999, Chen & Tian 2005). An example of these plots is given in Fig. 3.

Forecast model and test. Inter- and intra-annual variability in PFSSTA of spawning and feeding grounds during 1995 to 2004 was examined using ANOVA. We took arcsine square-root transformation for proportional data to make data normally distributed with a constant variance. Correlation analysis was used for testing the relationship between CPUE and PFSSTA of spawning and feeding grounds during 1995 to 2004. According to the results of ANOVA and correlation analysis, we selected PFSSTA of either one of or both of the spawning and feeding grounds during 1995 to 2004 as the environmental variables in establishing a CPUE forecast model. The forecast model can be written as:

$$CPUE_i = \alpha_0 + \alpha_1 P_1 + \alpha_2 P_2 + \varepsilon_i \qquad (1)$$

where $CPUE_i$ is the catch per fishing day from August to November in year i (t d^{-1}) during 1995 to 2004, P_1
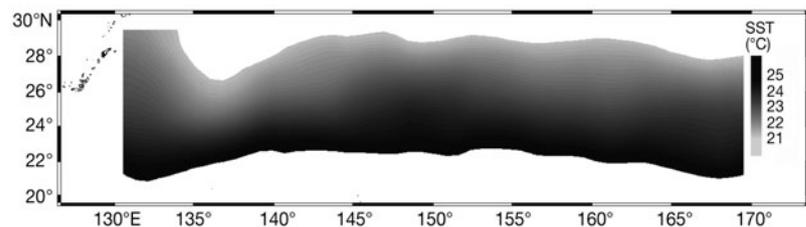

Fig. 3. *Ommastrephes bartramii.* Example image of proportion of favourable sea surface temperature areas (PFSSTA) in February 1995 at the spawning ground. Shaded area represents favourable-SST (21 to 25°C) waters

and P$_2$ are the variables describing PFSSTA of spawning and feeding grounds, α_0, α_1, and α_2 are model parameters to be estimated, and ε_i is an error term following normal distribution with mean of 0 and constant variance. We used a least-squares method to estimate model parameters. Residuals of above modeling were evaluated to ensure that the assumptions associated with the regression analysis were satisfied. The actual formulation of Eq. (1) was not determined until we completed the correlation analysis between CPUE and PFSSTA of spawning and feeding grounds.

Based on the established forecast model, we estimated the predicted CPUE by applying the PFSSTA of spawning and feeding grounds in 2005 and 2006, and compared it with the corresponding CPUE observed from Chinese squid-jigging fishery.

RESULTS

Spawning ground

The total area of the spawning ground (130 to 170° E, 20 to 30° N) was estimated to be 2 860 506 km^2. From 1995 to 2004 the total area of PFSSTA on the spawning ground during spawning season (January to April) varied from 1 557 048 (April 1999) to 2 837 771 (January 1997) km^2, corresponding to 54.4% and 99.2% of the total spawning area, respectively. The inter-annual variability in PFSSTA of spawning ground was not significant ($F_{9,30}$ = 2.25, p > 0.05, ANOVA), whereas the intra-annual variability was significant ($F_{3,36}$ = 8.93, p < 0.0001, ANOVA). This result indicates that the yearly change of PFSSTA was not statistically significant during the period of 1995 to 2004, but the monthly change was significant, suggesting seasonal variability was greater than annual variability in the PFSSTA of spawning ground. The average PFSSTA steadily decreased from 86.8% ± 6.47% (mean ± SD) in January to 69.8% ± 9.90% in April. Further analyses suggested that positive correlations between PFSSTA of spawning grounds and CPUE appeared in February (r = 0.48, p < 0.01) and April (r = 0.38, p < 0.05). The correlations were not significant for January (r = 0.12, p > 0.05), March (r = 0.01, p > 0.05) and the average of 4 mo (r = 0.27, p > 0.05). During the spawning season (January to April) the average PFSSTA was highest in January from 1995 to 2004; it decreased between January and April (Fig. 4).

Feeding ground

The total area of feeding ground (150 to 165° E, 38 to 46° N) was estimated at 890 406 km^2. The estimated
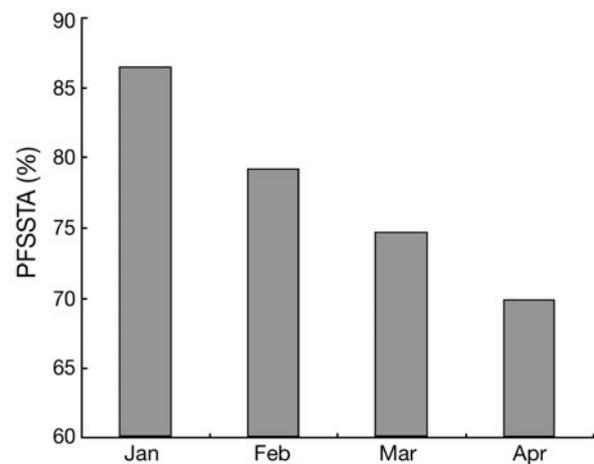

Fig. 4. *Ommastrephes bartramii.* Average PFSSTA during January to April from 1995 to 2004 at the spawning ground

PFSSTA of feeding ground during the fishing season (August to November) from 1995 to 2004 ranged from 136 923 (October 2000) to 504 110 (June 1996) km^2, corresponding to 15.3% and 56.6% of the total feeding areas, respectively. The inter-annual variability in PFSSTA of feeding ground was not significant ($F_{9,30}$ = 0.89, p = 0.54, ANOVA), whereas the intra-annual variability was significant ($F_{3,36}$ = 12.30, p < 0.001, ANOVA). Like the spawning ground, the inter-annual change of PFSSTA of feeding ground was not statistically significant from 1995 to 2004, but the monthly change was significant, suggesting seasonal variability was much higher than the annual variability. The average PFSSTA decreased from 39.9% ± 7.80% in August to 25.1% ± 2.36% in November. The correlation analysis showed that for from 1995 to 2004 the relationship between CPUE and PFSSTA of feeding ground was not significant for any month (r = –0.06, p > 0.05 in August; r = –0.15, p > 0.05 in September; r = 0.08, p > 0.05 in October; r = –0.37, and p > 0.05 in November). This suggests that PFSSTA during the fishing season (August to November) at the feeding ground was not significantly related to CPUE.

Regression analyses of CPUE versus SST

Based on the results of ANOVA and correlation analyses, we selected PFSSTA of the spawning ground in February (the month with the highest correlation in the spawning season) and the fourth root of products of monthly PFSSTA during August to November (correlation between CPUE and PFSSTA of the feeding ground was not significant for any month during fishing season) on the feeding ground as the independent variables in Eq. (1) to evaluate how PFSSTA at the spawning and feeding grounds affected CPUE of squid. Thus,

P_1 and P_2 in Eq. (1) were defined as the PFSSTA of February on the spawning ground, and the fourth root of products of monthly PFSSTA from August to November on the feeding ground, respectively. The fourth root of products of monthly PFSSTA from August to November on the feeding ground was selected as one of the independent variables because we found that PFSSTA of the feeding ground was not significantly related to CPUE for any single month of the fishing season and hypothesized that the combination of PFSSTAs of all months during fishing season would influence CPUE.

The resultant empirical model was significant ($p < 0.05$), suggesting that CPUE was positively and significantly correlated with PFSSTA of the spawning ground in February. The parameter α_1 associated with PFSSTA in February in the model had a larger value and was more significant than parameter α_2 associated with PF-SSTA on the feeding ground (Table 1). This indicates that PFSSTA of the spawning ground in February has a greater impact on squid recruitment than that of the feeding ground. The regression analysis suggested that there was a significant and positive relationship between CPUE and PFSSTA of the spawning ground in February. Thus in February, when PFSSTA was large, squid were abundant in the fishery, except in 1995 (Fig. 5; $p < 0.05$). Examples of SST images showing the distribution of favourable-SST areas on the spawning ground are given in Fig. 6, in which a high PFSSTA corresponded to a high abundance of squid in February 2004 (Fig. 6a). An intermediate PFSSTA corresponded to an average abundance in February 1997 (Fig. 6b) and a low PFSSTA corresponded to a low abundance in February 2001 (Fig. 6c).

A significant and negative correlation between CPUE and the fourth root of products of PFSSTA of the feeding ground from August to November suggested that the overall PFSSTA during the fishing season (August to November) on the feeding ground was important in determining CPUE.
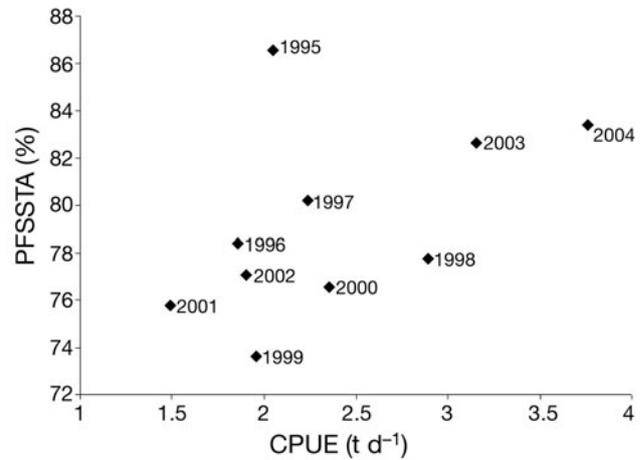

Fig. 5. *Ommastrephes bartramii.* Plot of February PFSSTA at the spawning ground against CPUE from 1995 to 2004

Test of forecast model

In order to evaluate the performance of our forecast model, we used actual fishery CPUE data in 2005 and 2006 from Chinese squid-jigging fleets to compare with the CPUE predicted from the forecast model. We used bootstrap to calculate the total variance (σ^2) and predicted confidence intervals based on samples collected from 1995 to 2004. Results indicate that the actual CPUEs in 2005 and 2006 were all within the confidence intervals of predicted CPUEs (Table 2).

DISCUSSION

The significant regression model identified between the CPUE and environmental variables indicates that PFSSTA is important for explaining the variability in CPUE at both spawning and feeding grounds. This result is consistent with our hypothesis that CPUE is likely to be influenced by recruitment, represented by PFSSTA, at the spawning ground and squid distribution, represented by PFSSTA, at the feeding ground; this is also consistent with other similar studies. Waluda et al. (2001) examined the inter-annual variability in mesoscale oceanographic conditions in terms of the area occupied by frontal waters and by waters of favourable SST at inferred hatching area of winter-spawned *Illex argentinus*, and found that high squid abundance was associated with a higher proportion of favourable-SST waters or a lower proportion of frontal waters. However, he did not examine the conditions in the fishing ground during fishing season, which might influence CPUE as well. Additionally, we found that variability in recruitment was determined by PFSSTA at the spawning ground in February, which month had
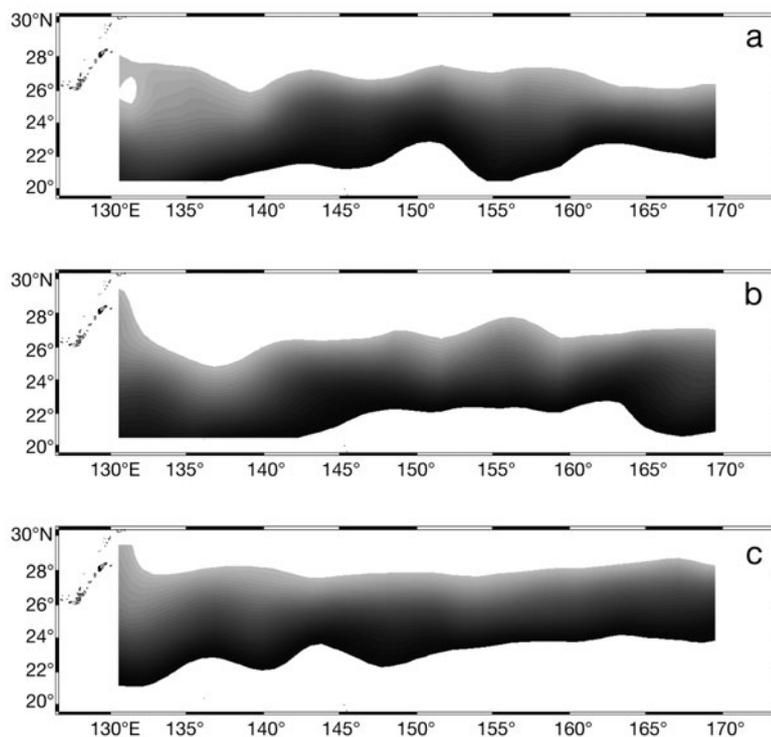
Table 1. *Ommastrephes bartramii.* Regression model between proportion of favourable-sea surface temperature areas (PFSSTA) and catch per unit effort (CPUE)

Model	95% CI	p
CPUE = $\alpha_0 + \alpha_1 P_1 - \alpha_2 P_2$		
$\alpha_0 = -9.5350$	-18.8267 to -0.2433	0.045
$\alpha_1 = 20.0663$	5.2710 to 34.8616	0.014
$\alpha_2 = -12.7812$	-24.8188 to -0.7436	0.040
P_1 = PFSSTA of February on spawning ground		
$P_2 = 4^{th}$ root of continued product of PFSSTA from Aug–Nov		
Multiple = 0.77, R^2 = 0.60, Residual SD = 4.3426, F = 5.1627, Significance F = 0.0419		

Fig. 6. *Ommastrephes bartramii.* Intra-annual variability in PFSSTA at the spawning ground: (a) high PFSSTA (Feb. 2004); (b) intermediate PFSSTA (Feb. 1997); and (c) low PFSSTA (Feb. 2001). Shaded areas represent favourable-SST (21–25°) waters

conditions on the spawning grounds, whereas an El Niño event would lead to environmental conditions favourable to squid recruitment (Chen et al. 2007). From 1995 to 2004, La Niña events occurred 3 times on the spawning ground, in February 1999, 2000 and 2001 (Chen et al. 2007). It is noted that PFSSTA on the spawning ground of these 3 yr were the lowest during the 1995 to 2005 study period (Fig. 5). An El Niño event on the spawning ground in February corresponded to a high PFSSTA in 2003 (Fig. 5; Chen et al. 2007). Therefore, we believe La Niña/El Niño events or ENSO influence squid recruitment mainly by changing PFSSTA on the spawning ground in February. Additionally, PFSSTA on the spawning grounds representing favourable conditions for squid recruitment may also be related to the strength and distribution of North Equatorial Current (NEC) and Kuroshio Current (Chen et al. 2007). When the NEC was strong and bifurcation of the NEC was strongly deflected north between 130°E and 170°E, the 25°C isotherm on the spawning ground would be correspondingly deflected north and PFSSTA would be lower (Fig. 7a). On the other hand, almost the whole of the southern spawning ground features favourable SST (Fig. 7b). When the Kuroshio Current is strong, it forms a V-like path between 135 and 140°E, the 21°C isotherm on the northwest spawning ground tends to be deflected further south, and the northwest area of spawning ground is controlled by less favourable-SST waters (Fig. 7b). Conversely, the PFSSTA is higher on the northwest spawning ground (Fig. 7a). We have extreme environments for squid recruitment, the most favourable (Fig. 7a) and unfavourable conditions (Fig. 7b) on the spawning ground. The above discussion covers possible scenarios which can be used to explain the changes of PFSSTA. The interaction of these environmental factors and their influence on the PFSSTA require further study.

In the absence of data on the abundance of paralarvae in this study, we could not directly set up a predictive model between variability in marine environment condition and squid recruitment. Instead, CPUE was used to reflect interannual variability in abundance of *Ommastrephes bartramii* (Chen et al. 2007). However, because *O. bartramii* lives less than 1 yr, abundance was only determined by the recruitment of current year. Thus, we can use CPUE as a surrogate for squid recruitment in this study. The same approach has been used for other short-lived species. For example para-
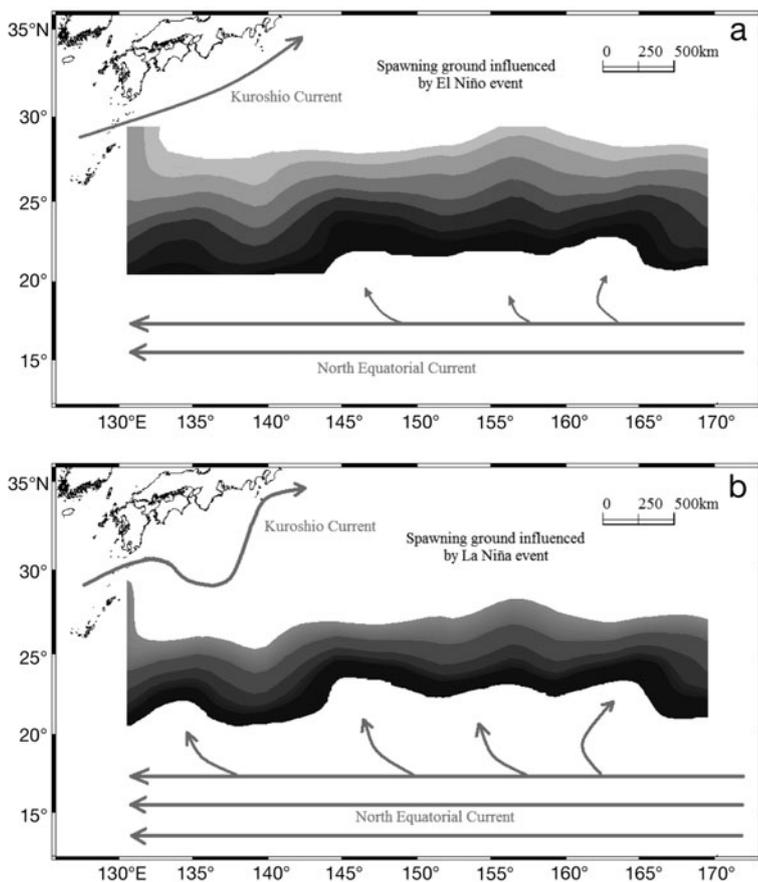
the second-highest average PFSSTA during the spawning season (Fig. 4). Therefore we suggest based on this study that February may be the peak time of hatching for *Ommastrephes bartramii*.

Seasonal change can lead to significant changes in SST in spawning and fishing areas, which also can cause squid to do a south-north seasonal migration. However, the inter-annual variability in PFSSTA on the spawning ground may be driven by climate changes and some large-scale oceanographic processes (O'Dor & Balch 1985). A La Niña event would result in a decrease in squid recruitment through variability in environmental

Table 2. *Ommastrephes bartramii.* Results of model test for predicting fishery catch per unit effort (CPUE) in 2005 and 2006

Variables	2005	2006
P_1 (%)	89.29	81.37
P_2 (%)	31.10	35.72
Actual CPUE (t d^{-1})	4.82	1.95
σ^2	0.2038	0.2038
Predicted CPUE (t d^{-1})	4.41	2.23
Confidence intervals (t d^{-1})	(4.00, 4.83)	(1.94, 2.35)

Fig. 7. *Ommastrephes bartramii.* Extreme environmental conditions for recruitment at the spawning ground: (a) most favourable conditions (widest possible area of favourable-SST); and (b) least favourable conditions (least possible area of favourable-SST)

the study of early *O. bartramii*'s early life stage, and the development of models for quantifying impacts of environmental and oceanographic variability on the early life stage of squid.

Ommastrephes bartramii are mainly distributed in the area with favourable-SST waters on the feeding ground (Chen et al. 2007); we consider that the oceanographic structure of the feeding ground plays a key role in the process. The feeding ground of *O. bartramii* is a transition area formed by the warm Kuroshio Current and cold Oyashio Current (Roden 1991). The dynamics of physical structures in this region, including meandering eddies and frontal zones, yield a highly productive habitat that serves as a feeding ground for various commercially important species, including *O. bartramii* (Zainuddin et al. 2006). On the feeding ground, *O. bartramii* prefer to aggregate in favourable-SST frontal areas (Wang & Chen 2005) because frontal zones may supply more food. For that reason the mechanism for *O. bartramii* gathering in favourable-SST frontal areas and the roles of different environmental variables in this favourable-SST ranges need to be identified in future studies.

Additionally, in this study, since the migration route of *Ommastrephes bartramii* was not well known, we did not examine the environmental variability in migration process of *O. bartramii*, which might influence abundance. However, based on our study we considered that when the Kuroshio Current meanders considerably, mortality of *O. bartramii* increases during migration. In 1995 the proportion of optimum-SST waters of February (Fig. 4) on the spawning ground was highest in the 10 yr study period, but CPUE in the
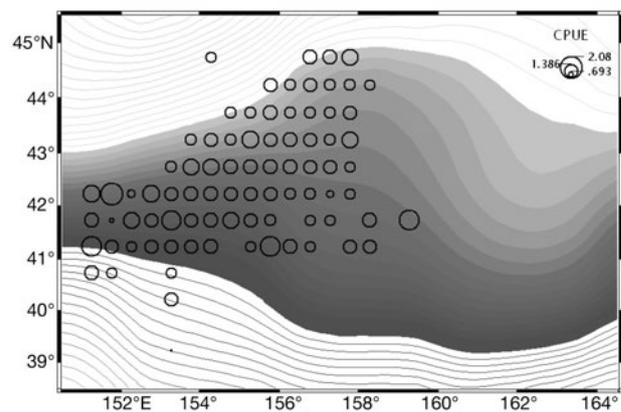
larval density index (PDI) as an index of recruitment was strongly correlated with CPUE in *Todarodes pacificus* cohorts, and PDI was also used to reflect the stock abundance of *T. pacificus* (Sakurai et al. 2000). Recruitment strength was also used to forecast the population abundance of *Illex argentinus* (Laptikhovsky et al. 2001).

According to this study, CPUE may also be affected by PFSSTA on the feeding ground in addition to recruitment. The distribution of CPUEs was mainly in favourable-SST areas on the feeding ground from August to November according to this study (Fig. 8). With the decreased PFSSTAs of August to November the distribution of *Ommastrephes bartramii* tended to be more aggregated, resulting in many more fishing boats locating in favourable-SST areas on the feeding ground. This increased the CPUE of Chinese squid-jigging fishery. In the future we need to directly forecast recruitment based on environmental variability using survey data from paralarvae and young squid on the spawning ground. Future work should also focus on

Fig. 8. *Ommastrephes bartramii.* Distribution of favourable-SST waters and CPUE on the feeding ground August 2001

same year was low. We evaluated the monthly distribution of Kuroshio Current during 1995 to 2004 and found that in 1995 the Kuroshio followed a V-like path during the migration period. Previous studies also showed that a V-like path of Kuroshio resulted in a low CPUE of the same year (Shao et al. 2005).

To develop more powerful predictive models for recruitment in future we should consider more comprehensive processes of squid life history, which may be significantly influenced by environmental variables. Such a study can help us to better develop predictive models for squid recruitment.

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