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Stock assessment for the western winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) using environmentally dependent surplus production models

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Summary: The western winter-spring cohort of neon flying squid, *Ommastrephes bartramii*, is targeted by Chinese squid-jigging fisheries in the northwest Pacific from August to November. Because this squid has a short lifespan and is an ecological opportunist, the dynamics of its stock is greatly influenced by the environmental conditions, which need to be considered in its assessment and management. In this study, an environmentally dependent surplus production (EDSP) model was developed to evaluate the stock dynamics of *O. bartramii*. Temporal variability of favourable spawning habitat with sea surface temperature (SST) of 21-25°C (P_s) was assumed to influence carrying capacity (K), while temporal variability in favourable feeding habitat areas with different SST ranges in different months (P_f) was assumed to influence intrinsic growth rate (r). The parameters K and r in the EDSP model were thus assumed to be linked to temporal variability in the proportion of P_s and P_f, respectively. According to Deviance Information Criterion values, the estimated EDSP model with P_s was considered to be better than the conventional surplus production model or other EDSP models. For this model, the maximum sustainable yield (MSY) varied from 210000 to 262500 t and biomass at MSY level varied from 360000 to 450000 t. The fishing mortality rates of *O. bartramii* from 2003 to 2013 were much lower than the fishing mortality at target level and MSY level (F_{tar} and F_{MSY}) and stock biomass was higher than B_{MSY}, suggesting that this squid was not in the status of overfishing and stock was not overfished. The management reference points in the EDSP model for *O. bartramii* were more conservative than those in the conventional model. This study suggests that the environmental conditions on the spawning grounds should be considered in squid stock assessment and management in the northwest Pacific Ocean.

Keywords: *Ommartrephes bartramii*; stock assessment; surplus production model; environmental factors; Northwest Pacific Ocean.

Evaluación de la cohorte occidental de invierno-primavera del calamar volador neon (*Ommastrephes bartramii*) utilizando modelos de producción excedente dependientes del medio ambiente

Resumen: La cohorte occidental de invierno-primavera de los calamares voladores neon, *Ommastrephes bartramii*, es objeto de las pesquerías chinas de calamares que operan con *jigging* en el Pacifico Noroeste, desde agosto a noviembre. Debido a que esta especie tiene un ciclo de vida corto y es ecológicamente oportunista, la dinámica de este stock de calamares está muy influenciada por las condiciones ambientales, las cuales necesitan ser consideradas en su evaluación y manejo. En este estudio fue desarrollado un modelo de producción excedente ambientalmente dependiente (PEAD), para evaluar la dinámica del stock de *O. bartramii*. Se asumió que la variabilidad temporal de un hábitat favorable para el desove sea a una temperatura superficial del mar de 21-25°C (P_s), para influir en la capacidad de carga (K); mientras que la variabilidad temporal en áreas con hábitat favorable para la alimentación, fue asumida con diferentes rangos de temperatura superficial del mar en diferentes meses (P_f), para influir la tasa intrínseca de crecimiento (r). Los parámetros K y r en el modelo PEAD fueron asumidos como vinculados a la variabilidad temporal en la proporción P_s y P_f, respectivamente. De acuerdo a los valores del Criterio de Información de la Desvianza, el modelo PEAD estimado con P_s fue considerado el mejor, comparado con los modelos de producción excedente convencionales, así como otros modelos PEAD. Para este modelo el rendimiento máximo sostenible (RMS) estuvo entre 210000 a 262500 t y la biomasa al nivel RMS, entre de 360000 a 450000 t. Las tasas de mortalidad por pesca de *O. bartramii* entre 2003 a 2013 fueron mucho menores que la mortalidad por pesca a nivel objetivo y nivel de RMS (F_{tar} and F_{RMS}) y la biomasa del stock fue superior a B_{RMS}, sugiriendo que este calamar no estuvo en el estado de sobrepesca y el stock no fue sobrepescado. Los puntos de referencia de manejo (PRMs) en el modelo PEAD para *O. bartramii* fueron más conservativos que aquéllos obtenidos en los modelos convencionales. Este estudio sugiere que las condiciones ambientales sobre las zonas de desove deberían ser consideradas en las evaluaciones y en el manejo de stock de calamares en el Océano Pacifico Noroeste.

Palabras clave: *Ommartrephes bartramii*; evaluación de stock; modelo de producción excedente; factores ambientales; Océano Pacifico Noroeste.

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INTRODUCTION

The neon flying squid, *Ommastrephes bartramii*, is an economically important oceanic species widely distributed in the northwest Pacific Ocean (Jereb and Roper 2010, Chen et al. 2008). This squid has been commercially exploited by Japanese squid-jigging fleets since 1974, and later by South Korea and Taiwan province of China. In 1993, the Chinese mainland squid-jigging fleets began exploratory fishing to investigate the abundance of *O. bartramii* in waters bounded by 38-42°N and 140-150°E. In 1999, several efforts further extended the fishing grounds eastward to 175°W (Wang and Chen 2005, Chen et al. 2008). In general, Chinese squid-jigging vessels mainly fish in the regions between 170°W and 175°W in June and July, and then shift to waters west of 165°E from August to November (Wang and Chen 2005). The total annual production of squid caught by Chinese mainland ranged from 36764 to 113200 t from 2003 to 2013.

The North Pacific population of *O. bartramii* has been classified into four stocks: the central stock of the autumn cohort, the eastern stock of the autumn cohort, the western stock of the winter-spring cohort and the central-eastern stock of the winter-spring cohort (Bower and Ichii 2005). Of the four stocks, the western winter-spring cohort of *O. bartramii* has become a traditional fishing target for the Chinese squid-jigging fleets in water between 150 and 165°E (Wang and Chen 2005). This cohort migrates from subtropical waters to the subarctic boundary during the first half of the summer and then moves northward into the subarctic domain from August to November. The squid mature gradually in autumn and are thought to begin their spawning migration in October and November (Murata and Nakamura 1998, Ichii et al. 2006).

Fishery biology, abundance and fishing ground distribution of *O. bartramii* have been well studied over the last few decades (Hayase 1995, Yatsu and Watanabe 1996, Yatsu and Mori 2000, Hikaru et al. 2004, Chen and Tian 2005, Wang and Chen 2005). Squid abundance and distribution are found to be significantly influenced by environmental conditions on the spawning and feeding grounds. For example, Chen et al. (2007) evaluated the sea surface temperature anomaly (SSTA) on the spawning and feeding grounds of *O. bartramii*, and concluded that high SSTA caused by La Niña events would lead to low recruitment, while the SSTA in an El Niño year tended to be normal and lead to high recruitment. Variability in the SST on the feeding ground could also result in different spatial distribution of the squid fishing ground. Cao et al. (2009) examined the variations in the proportion of thermal habitats with favourable sea surface temperature areas (PFSSTA) in 1995-2004, and suggested that PFSSTA in February on the spawning ground and from August to November on the feeding ground could explain about 60% of the variability in the abundance of *O. bartramii*. Additionally, Chen et al. (2011a) developed a habitat suitability index (HSI) model to identify the optimal habitat in relation to the oceanographic conditions, including sea surface temperature (SST), sea surface salinity (SSS), sea surface height anomaly (SSHA) and chlorophyll-*a* (Chl-*a*) concentration. They found that the highest monthly catch and fishing effort occurring in the different waters were closely related to those variables.

Previous studies evaluated the annual stock size of the autumn cohort and winter-spring cohort of *O. bartramii* on the basis of catch data analyses (Chen et al. 2008, Ichii et al. 2006). Due to the unique life history of this species, traditional age- or length-structured models are not appropriate for evaluating the influences of intensive commercial jigging fleets on its stock dynamics. Many methods have been proposed for assessing short-lived species such as the squid. Ichii and Mahapatra (2004) evaluated the annual biomass of the autumn cohort in 1982-1992 on driftnet fishing grounds using a stock production model incorporating covariates (ASPIC non-equilibrium dynamic model) (Prager 1994) and the DeLury depletion model (Hilborn and Walters 1992). For the winter-spring cohort, Chen et al. (2008) fitted a modified depletion model to the Chinese squid-jigging fisheries data to estimate squid stock abundance in 2000-2005, and found that the annual maximum allowable catch ranged from 80000 to 100000 t, which was consistent with the estimation by Osako and Murata (1983) for the annual sustainable catch of the western stock. However, as a short-lived ecological opportunist, *O. bartramii* is also typically subject to large fluctuations in abundance, responding rapidly to changes in environmental conditions (Saito 1994, Hayase 1995, Bower 1996, Chen 1997, 1999, Bower and Ichii 2005, Chen and Tian 2005, Cao et al. 2009). Therefore, environmental variables are considered to play a critical role in regulating the dynamics of squid stocks and need to be considered in the squid stock assessment.

An environmentally dependent surplus production (EDSP) model has been developed from the traditional surplus production model. In surplus production models, fish population dynamics and fishing processes including natural mortality, growth, recruitment, and fishing mortality are assumed to be a function of a single aggregated measure of biomass (Zhan 1992). This approach may be suitable for species with a short-life span and/or limited availability of age/size composition data (Zhan 1992). Research has also shown that surplus production models, although simple, may provide more accurate and precise estimates of management-related quantities than complex models (Ludwing and Walters 1985, 1989). Therefore, a surplus production model incorporating environmental variables would be an appropriate approach for assessing the *O. bartramii* stock.

O. bartramii is a short-lived species with a lifespan of less than one year (Roper et al. 1984), whose yearly biomass is almost dependent on the recruitment (Yu et al. 2013). Thus, it is reasonable to consider the environmental indices in the assessment of the *O. bartramii* stock. However, the traditional surplus models treat the carrying capacity and intrinsic rate of growth as constant (Chen et al. 2008), which is inconsistent with the facts that carrying capacity and population growth rate for squid may fluctuate greatly over time as a result of changes in environmental condition on the spawning ground and feeding ground. In this study, we developed two environmental indicators including the proportions of the areas with favourable SST on the spawning ground (P_s) and feeding ground (P_f), which were assumed to influence carrying capacity (K) and intrinsic growth rate (r), respectively. We evaluated the traditional production models and several EDSP models with both indices, P_s only or P_f only, being incorporated. These models were compared and an optimal model was selected for estimating the squid stock abundance and reference points. This study may provide a new insight into the assessment of *O. bartramii* stock.

MATERIALS AND METHODS

Fishery data

Data on daily catch (*t*), effort (days fished, *d*), fishing dates and fishing locations (longitude and latitude) were obtained from the Chinese mainland commercial jigging fleets operating in the areas between 35-45°N and 145-165°E in the northwest Pacific Ocean from July to December from 2003 to 2013. The western stock of the winter-spring cohort and the central-eastern stock of the winter-spring cohort are separated near 170°E (Bower and Ichii 2005). Thus, the Chinese commercial jigging fleet should target a unit stock. One unit of fishing area was defined as 0.5° latitude by 0.5° longitude.

We assumed no by-catches in the squid fishery (Wang and Chen 2005), and there would be little discard relative to annual catches. Chinese jigging vessels, about 200 in number from 2003 to 2013, were equipped with an engine of 120 KW×2, 112 KW squid attracting lights and 16 squid-jigging machines, and had almost identical fishing power and lighting operation. Therefore, catch per unit fishing day (CPUE, t d^{-1})

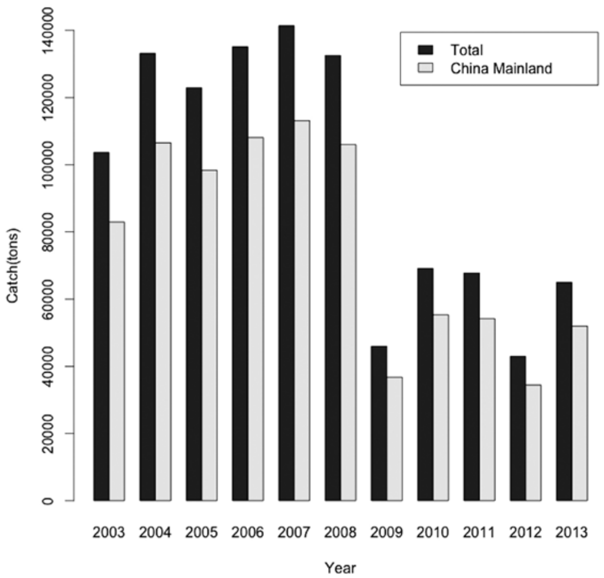

Fig. 1. – Annual total catch of the winter-spring cohort of *Ommastrephes bartramii* in the northwest Pacific.

of the squid-jigging vessels was a reliable indicator of stock abundance on the fishing ground (Chen et al. 2008). The monthly nominal CPUE in one fishing unit of 0.5°×0.5° is calculated as follows:

$$\mathrm{CPUE}_{ymi} = \frac{C_{ymi}}{F_{ymi}} \tag{1}$$

where CPUE_{ymi} is monthly CPUE at *i* fishing unit in month *m* and year *y*; C_{ymi} is monthly catch (*t*) at *i* fishing unit in month *m* and year *y*; and F_{ymi} is number of fishing days at *i* fishing unit in month *m* and year *y*.

Because the annual catch of *O. bartramii* by Chinese mainland accounted for about 80% of the total catches of this species (Cao 2010), we modified the annual total catch of *O. bartramii* from 2003 to 2013 in the northwest Pacific for our estimation (Fig. 1). Although the total annual catch estimated using this approach may have some issues for some years, the focus of this study is to develop and demonstrate a modelling framework which incorporates critical habitat information in the stock assessment for environmentally-sensitive species, and this data set is sufficient to serve this purpose.

Environmental data

Environmental variables SST, SSH and Chl-*a* concentration were used to obtain the standardized yearly CPUE based on the generalized additive model (GAM). Monthly SST, SSH and Chl-*a* concentration data from 2003 to 2013 on the presumed spawning (20°-30°N, 130°-170°E) and fishing grounds (38°-46°N, 150°-165°E) were obtained from the Live Access Server of National Oceanic and Atmospheric Administration OceanWatch (http://oceanwatch.pifsc.noaa.gov/las/servlets/dataset). The spatial resolution of SST, SSH and Chl-*a* concentration data were 0.1°×0.1°, 0.25°×0.25°, and 0.05°×0.05°, respectively. All the environmental data were then converted to a 0.5°×0.5°

grid by the method of averaging for each month in order to correspond to the spatial grid of CPUE. For instance, averaging 25 points of SST can convert to a 0.5°×0.5° grid.

Standardizing yearly CPUE by generalized additive model

CPUE is commonly assumed to be proportional to stock abundance. Therefore, it is usually considered as a relative abundance index in the monitoring and assessment of a fish stock (Maunder and Punt 2004). The GAM model is previously employed to standardize yearly CPUEs, which represent the same proportional change in stock size of *O. bartramii* using data samples (Tian et al. 2009a). The CPUE is naturally ln-transformed with errors being assumed to be normally distributed in the GAM modelling. This assumption was evaluated using Q-Q plots. The functional relationships between CPUE and environmental variables are likely to be non-linear (Bigelow et al. 1999). Thus, GAM was used for the CPUE standardization in this study, which can be written as:

$$\mathrm{Ln}(\mathrm{CPUE}+c)=factor(\mathrm{year})+factor(\mathrm{month})+ +s(\mathrm{longitude})+s(\mathrm{latitude})+s(\mathrm{SST})+ +s(\mathrm{SSH})+s(\mathrm{Chl}\text{-}a)+\varepsilon \quad (2)$$

where s is a spline smoother function; and constant c is assumed to be 10% of mean CPUE (Campbell 2004); var $\varepsilon= \sigma^2$ and $E(\varepsilon)=0$.

Environmentally dependent surplus production models

The areas with the favourable SST (21-25°C) in the presumed spawning ground (20º-30ºN, 130º-170ºE) during the spawning season (January-April) play a critical role in determining the recruitment of *O. bartramii* (Saito 1994, Hayase 1995, Bower 1996, Bower and Ichii 2005), and the areas with favourable SST (15ºC-19ºC in August, 14-18°C in September, 10-13°C in October and 12-15°C in November) on the feeding ground (38°-46°N, 150°-165°E) during the feeding season (August-November) influence the distribution of *O. bartramii* in feeding activity (Chen 1997, 1999, Chen and Tian 2005). Annual environmental indices were averaged from monthly P_s and P_f which were calculated by the number of fishing units with the optimal SST divided by the total number of the fishing units on the spawning and feeding ground, respectively.

Schaefer's surplus production model (referred to as SP) can be written as

$$\log(B_t)\big|K,\sigma^2 = \log(K)+u_t$$

$$\log(B_t)\big|B_{t-1},K,r,\sigma^2 =$$

$$= \log\left\{B_{t-1}+rB_{t-1}\left(1-\frac{B_{t-1}}{K}\right)-C_{t-1}\right\}+u_t \quad (3)$$

$$\log(I_t)\big|B_t,q,\tau^2 = \log(q)+\log(B_t)+\upsilon_t \quad (4)$$

where B_t is the biomass in t year; K is the carrying capacity; r is the intrinsic rate of stock growth; q is the catch ability coefficient; and I_t is the CPUE in t year. I_t is assumed to be proportional to B_t, and u_t and υ_t are independent and identically distributed IID N (0, σ^2) and IID N(0, τ^2) random variables respectively.

We hypothesized that for a given year "effective" carrying capacity was in proportion to P_s and the "effective" intrinsic stock growth rate changed in proportion to P_f for *O. bartramii*. Therefore, the surplus production model with the parameter of P_s (referred to as P_s-EDSP) is given by:

$$\log(B_t)\big|K,\sigma^2 = \log(K)+u_t$$

$$\log(B_t)\big|B_{t-1},K,r,\sigma^2 =$$

$$= \log\left\{B_{t-1}+rB_{t-1}\left(1-\frac{B_{t-1}}{Ps_{t-1}K}\right)-C_{t-1}\right\}+u_t \quad (5)$$

The surplus production model with the parameter of P_f (referred to as P_f-EDSP) is given by:

$$\log(B_t)\big|K,\sigma^2 = \log(K)+u_t$$

$$\log(B_t)\big|B_{t-1},K,r,\sigma^2 =$$

$$= \log\left\{B_{t-1}+Pf_{t-1}rB_{t-1}\left(1-\frac{B_{t-1}}{K}\right)-C_{t-1}\right\}+u_t \quad (6)$$

The surplus production model with the parameters of both P_s and P_f (referred to as P_s-P_f-EDSP) is given by:

$$\log(B_t)\big|K,\sigma^2 = \log(K)+u_t$$

$$\log(B_t)\big|B_{t-1},K,r,\sigma^2 =$$

$$= \log\left\{B_{t-1}+Pf_{t-1}rB_{t-1}\left(1-\frac{B_{t-1}}{Ps_{t-1}K}\right)-C_{t-1}\right\}+u_t \quad (7)$$

Based on the results of Prager (1994) and Chen et al. (2011b), we assumed that the initial biomass of *O. bartramii* B_0 in 2003 was 400000 t. The likelihood function and prior distribution of the parameters in Bayesian inference were stated as follows:

- Likelihood function

We fitted Schaefer's surplus production models by Bayesian inference in R using the R2WinBugs library (Sturtz et al. 2005). A likelihood function was used to estimate the degree of fitting between the observation data and the data predicted by the surplus production models (Li et al. 2011). We assumed that the observation errors followed the ln-normal distribution, and the likelihood function is written as:

$$L(I\,|\,\theta)=\prod_{2003}^{2013}\frac{1}{I_t\sigma\sqrt{2\pi}}\exp\left\{\frac{[\log(I_t)-\log(qB_t)]^2}{2\sigma^2}\right\} \quad (8)$$

The σ was estimated to be 0.12 in the CPUE stanardization.

Table 1. – The fishery management reference points of *O. bartramii* in the northwest Pacific Ocean. BRP, biological reference point; SP, surplus production; EDSP, environmentally dependent surplus production models; P_s, proportion of favourable spawning habitat areas with sea surface temperature of 21-25°C; P_f, proportion of favourable feeding habitat areas with different sea surface temperature ranges in different months; MSY, maximum sustainable yield. Note: C_t is the catch in year t and B_t is the biomass in year t

Management reference point	Catch	Fishing mortality coefficient (F)	Biomass (B)
BRP in SP model	MSY=$rK/4$	$F_{MSY}=r/2$ $F_{0.1}=0.45r$ $F_t=C_t/B_t$	$B_{MSY}=K/2$
BRP in P_s-EDSP, P_f-EDSP, P_s-P_f-EDSP models	MSY=$P_f\ rP_s\ K/4$	$F_{MSY}=P_f\ r/2$ $F_{0.1}=0.45P_f\ r$ $F_t=C_t/B_t$	$B_{MSY}=P_s\ K/2$

- Setting prior distribution of model parameters

The parameters of r, K and q were assumed to be normally distributed as N(1.19, 0.6^2), N(75, 37.5^2) and N(1.5×10^{-5}, $(0.75\times10^{-5})^2$), respectively (Ichii et al. 2006, Cao 2010, Chen et al. 2011b).

- Calculating posterior distribution of parameters

The initial guess values for the parameters of models in the likelihood estimation were set as follows: the intrinsic rate of growth was 0.8, carrying capacity was 400000 t and the catchability coefficient was 0.5×10^{-5}. The posterior distribution of parameters of Schaefer models were calculated by the Markov Chain Monte Carlo (MCMC) method in R. Three MCMC chains were used and the number of MCMC iterations was 50000, and the first 10000 results of iterations were discarded. For the subsequent 40000 times, we saved the results every 40 times.

Fishery biological reference points, including maximum sustainable yield (MSY), fishing mortality at MSY level (F_{MSY}), biomass at MSY level (B_{MSY}), fishing mortality at target level (F_{tar}, fishing mortality at 0.1 level, $F_{0.1}$), fishing mortality at MSY level (F_{MSY}), and actual fishing mortality for year t (F_t) based on the SP and EDSP were estimated using mean values of posterior distribution of parameters of models (Table 1). The selection of models was based on the deviance information criterion (DIC), where the lowest DIC is selected to be the best model.

RESULTS

Comparing the nominal CPUE with the GAM-standardized CPUE

The GAM model was constructed based on temporal (year and month), spatial (latitude and longitude) and environmental (SST, SSH and Chl-*a* concentration) factors. The annual nominal CPUE was then compared with the GAM-estimated standardized CPUE from 2003 to 2013. The same variability trends were exhibited between the annual nominal CPUE and the GAM-standardized CPUE (Fig. 2). Large differences occurred in 2007: the nominal CPUE was highest with a value of 5.12 t d^{-1}, while the GAM-standardized CPUE in 2007 was extremely low with a value of 1.16 t d^{-1}. The production and abundance of western winter-spring cohort of *O. bartramii* fluctuated from year to year: both were high in 2003-2008 and low in 2009-2013 (Fig. 1).

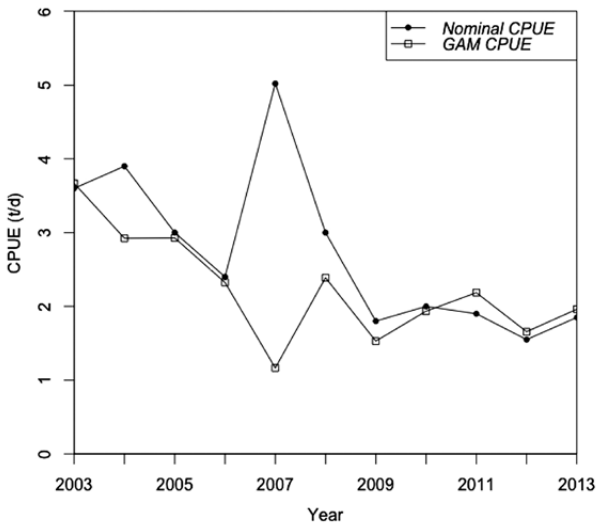

Fig. 2. – Nominal CPUE and GAM-standardized CPUE in 2003-2013.

Comparison of surplus production models

According to the samplings in MCMC and the posterior distribution of parameters (r, K, and q) of the four surplus production models (Fig. 3), there were large differences between the posterior distribution of parameters and their prior distributions. The mean posterior values of parameters (r, K, and q) for the four surplus production models were different. The ranges of r, K, and q were 1.71-1.90, 650000-950000 t, and 0.3-0.4×10^{-5}, respectively. The minimum values of r

Table 2. – Summary statistics for the parameters of Schaefer surplus production models of *O. bartramii*.

Models	r				K 10^4				q 10^{-4}				DIC
	Mean	SD	*Rhat*	*n.eff*	Mean	SD	*Rhat*	*n.eff*	Mean	SD	*Rhat*	*n.eff*	
SP model	1.77	0.65	1.00	580	65	0.17	1.00	1000	0.04	0.002	1.00	1000	55.9
P_s-model	1.71	0.69	1.00	1000	90	0.16	1.00	1000	0.03	0.002	1.00	290	30.7
P_f-model	1.90	0.78	1.00	420	80	0.17	1.00	1000	0.03	0.002	1.00	820	35.8
P_s-P_f-model	1.87	0.77	1.00	1000	95	0.17	1.00	1000	0.03	0.002	1.00	1000	40.1

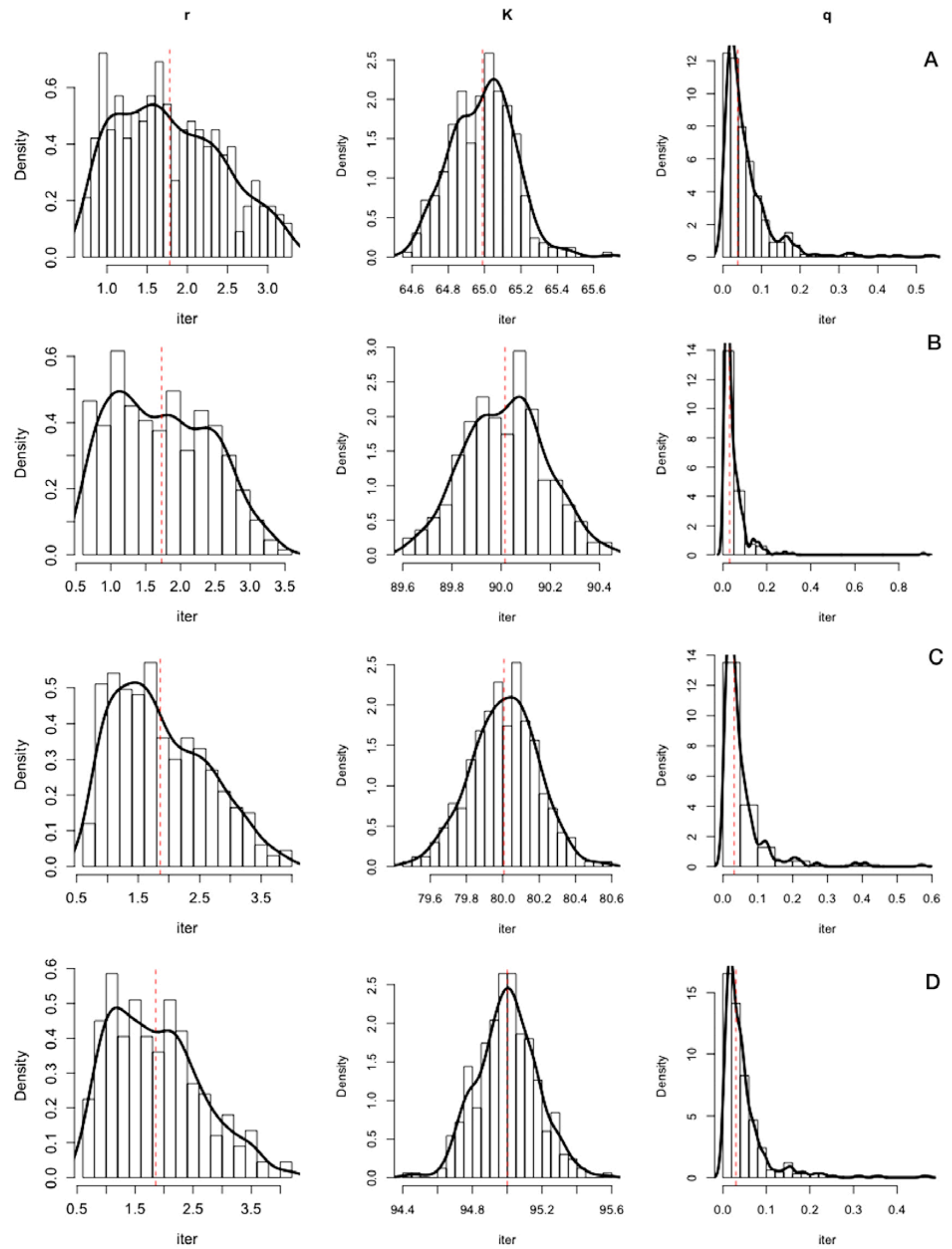

Fig. 3. – Density for *r, K, q* in (A) the SP model; B, the P_s-EDSP model; C, the P_f-EDSP model; D, the P_s-P_f-EDSP model.

and *K* occurred in the P_s-EDSP and SP model, and the maximum of *r* and *K* occurred in the P_f-model and P_s-P_f-model, respectively. The results suggested that the optimal fitted model was the P_s-EDSP with the minimum DIC value (Table 2).

The MSY and B_{MSY} were 289100 and 325000 t for the SP model, respectively (Table 3). The MSY varied from 210000 to 262500 t and its biomass ranged from 360000 to 450000 t for the P_s-EDSP model (Table 3). For the P_f-EDSP model, the MSY ranged from 245300 to 371600 t, and the B_{MSY} was approximately 400000 t (Table 3). For the P_s-P_f-EDSP model, the MSY was within the range of 254100 to 392400 t, and the B_{MSY} was from 380000 to 475000 t (Table 3).

Moreover, the values of F_{tar} and F_{MSY} in the SP model differed from those in other three models (Table 3). Of the four surplus production models, the indications were that the fishing mortality coefficient of *O. bartramii* from 2003 to 2013 was much smaller than the values of F_{tar} and F_{MSY}. Meanwhile, the annual catch of *O. bartramii* in 2003-2013 was also lower than the value of MSY (Table 3).

The results of the four surplus production models indicated that the biomass and development of the *O. bartramii* fishery are in a good state at present (Table 3; Fig. 4). The resource of this species was at a high level, with no sign of occurrence of overfishing based on the P_s-EDSP model (Fig. 4).

Table 3. – The fishery management reference points and stock assessment results estimated by the SP model (A), the P_s-model (B), the P_f-model (C) and the P_s-P_f-model (D) in 2003-2013.

Year	Biomass (10^4t) A	B	C	D	B_{MSY} (10^4t) A	B	C	D	B_{lim} (10^4t) A	B	C	D
2003	40.00	40.00	40.00	40.00	32.5	39.95	40.0	42.27	8.12	9.98	10.0	10.57
2004	54.41	63.56	60.11	63.53	32.5	42.30	40.0	44.65	8.12	10.58	10.0	11.16
2005	53.52	76.03	63.19	72.30	32.5	43.20	40.0	45.60	8.12	10.80	10.0	11.40
2006	54.97	63.01	71.76	71.91	32.5	38.70	40.0	40.85	8.12	9.68	10.0	10.21
2007	53.16	68.44	66.41	70.70	32.5	39.60	40.0	41.80	8.12	9.90	10.0	10.45
2008	52.70	56.64	63.83	59.61	32.5	36.00	40.0	38.00	8.12	9.00	10.0	9.5
2009	53.87	68.82	68.37	71.77	32.5	40.05	40.0	42.28	8.12	10.01	10.0	10.56
2010	64.53	91.14	76.67	90.79	32.5	45.00	40.0	47.50	8.12	11.25	10.0	11.87
2011	56.70	73.86	71.94	82.64	32.5	43.20	40.0	45.60	8.12	10.80	10.0	11.40
2012	61.10	71.26	72.50	73.00	32.5	38.71	40.0	40.85	8.12	9.67	10.0	10.21
2013	62.23	80.74	76.86	82.88	32.5	40.51	40.0	42.75	8.12	10.13	10.0	10.69

Year	MSY (10^4t) A	B	C	D	F_{tar} A	B	C	D	F_{MSY} A	B	C	D	F_t A	B	C	D
2003	28.91	23.37	37.16	39.24	0.8	0.78	0.84	0.84	0.88	0.87	0.92	0.93	0.32	0.32	0.32	0.32
2004	28.91	24.68	33.08	36.89	0.8	0.78	0.74	0.74	0.88	0.87	0.82	0.83	0.30	0.26	0.28	0.26
2005	28.91	25.20	26.37	30.05	0.8	0.78	0.60	0.59	0.88	0.87	0.66	0.66	0.29	0.20	0.24	0.21
2006	28.91	22.59	36.04	36.79	0.8	0.78	0.81	0.81	0.88	0.87	0.90	0.90	0.31	0.27	0.23	0.23
2007	28.91	23.10	31.22	32.60	0.8	0.78	0.70	0.70	0.88	0.87	0.78	0.78	0.33	0.26	0.27	0.25
2008	28.91	21.00	26.76	25.40	0.8	0.78	0.60	0.60	0.88	0.87	0.66	0.67	0.31	0.29	0.26	0.28
2009	28.91	23.37	32.70	34.54	0.8	0.78	0.74	0.74	0.88	0.87	0.82	0.82	0.11	0.08	0.08	0.08
2010	28.91	26.25	28.24	33.52	0.8	0.78	0.64	0.64	0.88	0.87	0.70	0.71	0.13	0.09	0.11	0.10
2011	28.91	25.20	24.53	27.94	0.8	0.78	0.55	0.55	0.88	0.87	0.61	0.61	0.15	0.11	0.12	0.10
2012	28.91	22.58	24.90	25.41	0.8	0.78	0.56	0.56	0.88	0.87	0.62	0.62	0.09	0.07	0.07	0.07
2013	28.91	23.63	28.62	30.56	0.8	0.78	0.64	0.64	0.88	0.87	0.70	0.71	0.13	0.10	0.10	0.10

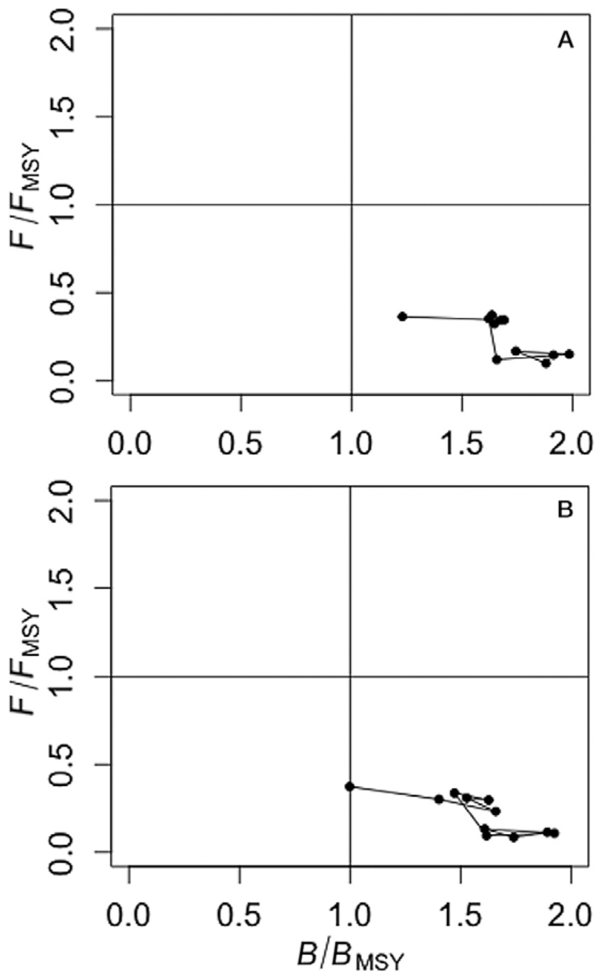

Fig. 4. – Development of the *O. bartramii* fishery from 2003 to 2013 based on the SP model (A) and the P_s-EDSP model (B).

DISCUSSION

There have been many attempts to explain variation in recruitment based on the relationship between some direct or indirect measures of year-class strength and environmental variables (Cushing 1982). The most commonly used environmental variables are temperature, salinity and wind (Leggett and Frank 2008). Temperature, because it regulates many physiological processes, has been considered to be an important explanatory variable of recruitment in the context of global warming (Cardinale and Hjelm 2006). Salinity has frequently been used as an indirect measure of nutrient flux, and the physical process by which wind may influence recruitment is thought to be primarily through effects on the egg and larval transportation and distribution (Leggett and Frank 2008). The significance of these variables identified in this study is consistent with their ecological roles in regulating the squid habitat quality and stock dynamics (Yu et al. 2015).

For a short-lived species, the role of environmental variables in regulating its population dynamics has received much emphasis and comprises an important research topic (Roberts 1998, Agnew et al. 2002). Most squid live for less than one year (Boyle 1987), and recruitment success is greatly influenced by the physical and biological environmental conditions on the spawning and nursery grounds, which contribute to the variability in the stock abundance (Sakurai et al. 2000). In addition, the abundance and distribution of squid populations on the fishing ground tend to be greatly affected by oceanographic conditions and respond quickly to changes in the environment (Wadley and Liu 1983, Waluda et al. 1999, 2001, 2006, Yatsu et al. 2000, Anderson and Rodhouse 2001, Rodhouse 2001, Bazzino et al. 2005). For instance, Waluda et al. (2001) suggested that about 55% of the variability in recruitment of the Falkland Island *Illex argentinus* fishery could be explained by variations in the total putative favourable SST areas on the spawning ground during the spawning season. Variability in the abundance of *Todarodes pacificus* in the Sea of Japan was found to be closely related to changes in their favourable SST areas for paralarvae development (Sakurai et al. 2000). Cao et al. (2009) and Cao (2010) suggested that February P_s and August to November P_f could account for about 60% of the variability in *O. bartramii* abundance between 1995 and 2004. February P_s was the most important factor influencing squid recruitment during the spawning season, and feeding ground P_f during the fishing season also had a strong influence on CPUE. Consequently, the SST is an important environmental indicator for predicting the recruitment of squid (Agnew et al. 2002), and should be considered in *O. bartramii* stock assessment.

In this study, the nominal CPUE in 2007 was extremely high, possibly due to the high concentrated fishing operation along the longitudinal direction during that year. This finding suggests that it is important to obtain the standardized yearly CPUE. Additionally, no significant correlations were identified between yearly CPUE and monthly P_s and P_f. However, Cao et al. (2009) and Cao (2010) evaluated the influences of SST on the spawning ground on the abundance of *O. bartramii*. These authors suggested that there was a significant positive relationship between the monthly proportion of favourable SST areas on the spawning ground and CPUE, but this relationship was not consistent with the results of our study. The reasons which caused this difference might be the use of a variety of resource abundance indicators (nominal or standardized CPUE) and different sources of fishery data. Therefore, the average P_s during spawning months and the average P_f during feeding months other than significant P_s and P_f were used to measure the "effective" K and r. The methods for estimating the parameters of the surplus production model can be divided into three types: equilibrium estimators, process-error estimators and observation-error estimators (Polacheck et al. 1993, Wang et al. 2014b). Each estimator has its own drawback. For example, the assumption of the equilibrium estimators is that they are suitable for applying to a fishery in equilibrium but not for an actual fishery. For process-error estimators, we usually obtain negative values of parameters (r, q) when converting the surplus production equation into a linear form fitted by a linear regression. Bayesian inference has been increasingly used for fisheries in recent years because it provides a systematic approach that explicitly incorporates both uncertainty and risk caused by uncertainty in the analysis (Hilborn et al. 1993, McAllister et al. 1994, Kinas 1996, Chen et al. 2000). Atypical errors should also be noted in the data. Mis-specification of prior distribution and the choice of an inappropriate likelihood function may result in unreliable posterior distribution for parameters in Bayesian inference (Berger 1994, Adkison and Peterman 1996, McAllister and Kirkwood 1998, Chen et al. 2000). In this paper, we used Bayesian inference to estimate the parameters of the four surplus production models, and attempted to interpret the data consistently by using standardized CPUE and modifying the yearly catch from 2003 to 2013. We also referred to some previous studies in order to set the prior distribution (normal distribution) of parameters and to select the likelihood function (Cao 2010, Chen et al. 2011b). According to the MCMC results, there were great differences in the posterior distributions of parameters (r, K, q) and prior distributions. It was shown that the fishery data for *O. bartramii* provided enough information to estimate the parameters in these four surplus production models.

Fishery statistics of the Chinese squid-jigging fleets (Fig. 1) suggest a large fluctuation in annual production of *O. bartramii*. In this study, the annual catches of *O. bartramii* are lower than the MSY. The current fishing mortality rates are also lower than F_{tar} in the four surplus production models, indicating that overfishing does not occur in the *O. bartramii* fishery (Fig. 4). The yearly biomass of *O. bartramii* in the four surplus production models is higher than B_{MSY}, suggesting that the resource of *O. bartramii* is not overfished and has been at a high level of abundance in recent years. Thus, we can conclude that overfishing does not occur and the stock is not overfished for the *O. bartramii* stock in the northwest Pacific. These findings are basically consistent with the previous results (Cao 2010, Chen et al. 2011b).

The DIC value of the original surplus production model was maximum in the four models, and the fitting level of the surplus production model with environmental factors was higher than that of the models without environmental factors (Table 3). Changes in environmental factors (P_s and P_f) have important impacts on carrying capacity (K) and intrinsic rate of growth (r). The particle-tracking experiment showed that paralarvae and juveniles aged <90 days remained on their spawning grounds and that Chl-*a* in this habitat, where 21°C<SST<25°C, had a significant positive correlation with the CPUE (Nishikawa et al. 2014), and P_s calculated by average optimal SST (21°C<SST<25°C) on the spawning ground would affect the survival of paralarvae and juveniles. Moreover, SST was the most important environmental factor in the formation of the fishing ground based on the HSI model and the neural network model (Tian et al. 2009b, Wang et al. 2014a). P_f is a measure of habitat quality of the fishing ground and would affect individual growth. Hence, environmental conditions, especially P_s and P_f, have significant influences on the spawning, hatching, growth, and even the whole life history of *O. bartramii*. We considered annual variability of environmental variables in estimating fishery management reference points (MRPs), resulting in temporal differences in reference points, which better reflect temporal changes in the habitat quality than the reference points assumed to be same over time in a traditional stock assessment. This can be useful to help adjust annual regulations in *O. bartramii* fisheries management.

The development status of the *O. bartramii* fishery from 2003 to 2013 based on the SP model and the P_s-EDSP model were plotted (Fig. 4). At present, the *O. bartramii* fishery development is still not fully exploited, and the advantage of the EDSP model is not obvious in this situation. However, with an increased intensity of exploitation, the EDSP model proves to be more conservative as the "B/B_{MSY}" in the P_s-EDSP model tended to be closer to "1" (the threshold of overfishing) than that in the SP model (Fig. 4). In summary, when there was low P_s and P_f, the "effective" r and K decreased, calling for a decline in fishing effort to avoid the overexploitation of *O. bartramii* resources.

The uncertainty of the models came mainly from (1) uncertainty associated with data because we only included the catch data from the Chinese fishery, although we standardized yearly CPUE and modified yearly catches; and (2) uncertainty of model parameters: we assumed the biomass in 2003 to be an initial value of 400000 t, and this may induce biases in the estimation of biomass of *O. bartramii*. In addition, we also assumed that the standard deviation of CPUE (σ) was equal to 0.12, and the effects of this assumed σ value on model selection and resource assessment need to be further investigated in future studies.

In summary, an estimated EDSP model fitted the data better than the conventional Schaefer surplus model without environmental factors in estimating the squid stocks. We found that the fishery MRPs largely depended on optimal spawning and feeding habitat areas. These findings suggest that environmental factors on the spawning and feeding grounds should be considered in squid stock assessment and management of *O. bartramii* in the northwest Pacific.

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