

Abstract—We developed a habitat suitability index (HSI) model to understand and identify the optimal habitat and potential fishing grounds for neon flying squid (*Ommastrephes bartramii*) in the Northwest Pacific Ocean. Remote sensing data, including sea surface temperature, sea surface salinity, sea surface height, and chlorophyll-*a* concentrations, as well as fishery data from Chinese mainland squid fleets in the main fishing ground (150–165°E longitude) from August to October, from 1999 to 2004, were used. The HSI model was validated by using fishery data from 2005. The arithmetic mean modeling with three of the environmental variables—sea surface temperature, sea surface height anomaly, and chlorophyll-*a* concentrations—was defined as the most parsimonious HSI model. In 2005, monthly HSI values >0.6 coincided with productive fishing grounds and high fishing effort from August to October. This result implies that the model can reliably predict potential fishing grounds for *O. bartramii*. Because spatially explicit fisheries and environmental data are becoming readily available, it is feasible to develop a dynamic, near real-time habitat model for improving the process of identifying potential fishing areas for and optimal habitats of neon flying squid.

A modeling approach to identify optimal habitat and suitable fishing grounds for neon flying squid (*Ommastrephes bartramii*) in the Northwest Pacific Ocean

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Two predominant currents, the warm Kuroshio Current and the cold Oyashio Current, meet in the Northwest Pacific Ocean. The interaction of these two currents between the subtropical and subarctic fronts forms a transition region (Roden, 1991). The dynamic of the physical oceanographic structures in this region, including meandering eddies and frontal zones, results in a highly productive habitat, which serves as a favorable feeding ground for various commercially important species, such as neon flying squid (*Ommastrephes bartramii*), Pacific saury (*Cololabis saira*), anchovy (*Engraulis japonicus*), and albacore (*Thunnus alalunga*) (Pearcy, 1991; Zainuddin et al., 2006).

The neon flying squid (*O. bartramii*) is an important oceanic squid, which has been commercially harvested by the Japanese since 1974, and later by South Koreans and the Chinese (including Taiwanese) (Wang and Chen, 2005). There are four stocks of

O. bartramii (Bower and Ichii, 2005). Of the four stocks, the western winter-spring cohort of neon flying squid is a traditional fishing target for the Chinese mainland squid jigging fleet in the area of 39–46°N latitude and 150–165°E longitude from August to November (Chen and Tian, 2005), with Chinese mainland jigging representing from 75% to 84% of the total catch (Chen et al., 2008a).

The biology and distribution of *O. bartramii* have been the subject of several studies in recent decades (Yatsu and Watanabe, 1996; Yatsu and Mori, 2000; Watanabe et al., 2004; Wang and Chen, 2005). The western winter-spring cohort of neon flying squid can be found from subtropical waters to the subarctic boundary during the first half of the summer and then migrates northward into the subarctic domain from August to November. *Ommastrephes bartramii* gradually mature in fall and are thought to begin their spawning

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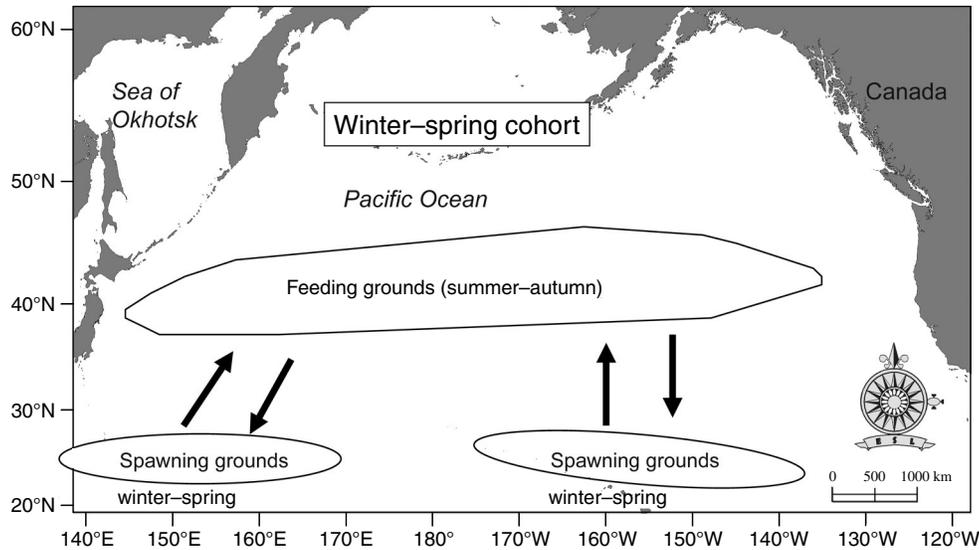


Figure 1

Migration pattern of the winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) in the North Pacific Ocean (Ichii et al., 2006).

migration in October and November (Fig. 1; Ichii et al., 2006). For a short-lived, single year-class population and opportunist species, the biophysical environment plays an important role in controlling the distribution and abundance of *O. bartramii* (Chen, 2004; Wang and Chen, 2005).

Many studies have shown that environmental variables such as sea surface temperature (SST), sea surface salinity (SSS), sea surface height anomaly (SSHA), chlorophyll-*a* (chl-*a*) concentrations, and current can strongly influence the distribution and availability of neon flying squid to fisheries (Chen, 1997; Chen and Chiu, 1999; Wang et al., 2003; Chen and Tian, 2005; Tian, 2006; Chen et al., 2007). Chen (1997) reported that monthly preferred SSTs for this squid species varied with seasons and areas, and the monthly preferred SST tended to decrease gradually from west to east. In the waters between 150°–165°E longitude, the monthly favorable SSTs were 12–14°C, 14–17°C, 15–19°C, 14–18°C, 10–13°C, and 12–15°C, respectively, for the months of June to November (Chen, 1997; Chen and Tian, 2005; Tian, 2006). While in the waters of 165–180°E longitude, the favorable SST in June and July ranged from 11–15°C (Chen and Tian, 2005; Tian, 2006). Yatsu and Watanabe (1996) reported that catch per unit of effort (CPUE) for the driftnet fishery near the Subarctic boundary in July was highest during years with a strong gradient between the 11 and 15°C SST isotherms. Chen and Chiu (1999) found that the distribution and abundance of *O. bartramii* in the central North Pacific Ocean were strongly influenced by water temperature and salinity, with temperature having a higher predictive power for estimating stock abundance. Tian (2006) reported that the monthly favorable SSSs for squid were 33.8–34.3, 33.3–34.4,

33.0–34.2, 33.0–33.7, 33.0–33.8 and 33.3–33.8 from June to November, respectively, in the north Pacific. Chen et al. (2007) discussed the influence of large-scale oceanic phenomena such as the Kuroshio Extension and El Niño Southern Oscillation (ENSO) events on squid distribution and recruitment. They concluded that these phenomena influence squid by affecting the SST and SSS of the spawning and feeding grounds.

From July to November, *O. bartramii* migrate north to feed. The presence of plankton also is a basic necessity for the presence of this squid (Chen, 2004). Wang et al. (2003) reported that a skewed distribution function could be used to describe the relationship between chlorophyll-*a* concentration and *O. bartramii* catch in the waters of 150–165°E longitude and 41–45°N latitude from August to October, and that the area with chlorophyll-*a* content ranging from 0.15 to 3 mg/m³ produced 95% of the total catch. Xu et al. (2004) found that in the waters of 152°E–171°W longitude and 39°–42°N latitude during June and July, *O. bartramii* tended to aggregate near areas with the highest abundance (50–100 ind/m³) of crustaceans (mainly Copepoda and Thaliacea).

Sea surface height anomaly (SSHA) is an important marine environmental variable that is closely related to the distributions of some fish species (Zhang et al., 2001) and is also considered an important environmental indicator for finding fishing grounds (Chen, 2004). Tian (2006) reported that *O. bartramii* is mainly distributed in the areas where the value of SSHA is below or near zero from August to November. Lu and Chen (2008) found that the squid *Illex argentinus* preferred habitats with zero or negative values of SSHA in the southwest Atlantic Ocean. This phenomenon also existed in the study of habitat suitability for chub

mackerel (*Scomber japonicus*) in the East China Sea (Chen et al., 2009) and in the study of the distribution of fishing grounds for purpleback flying squid (*Symlectoteuthis oualaniensis*) in the northwest Indian Ocean (Chen and Shao, 2006).

Based on the previous results, it was found that *O. bartramii*, as a short-lived (1-year) species, is usually aggregated in the waters with favorable ranges of SST, SSS, SSHA, and chl *a*. Although the favorable ranges of these environmental variables for *O. bartramii* are known, a robust method to predict where *O. bartramii* will aggregate in the traditional fishing grounds from these variables is not yet available. It is important to develop a model to predict the occurrence of aggregations of *O. bartramii* to reduce bycatch of untargeted species, reduce fuel costs, and improve efficiency of the fishery.

Habitat suitability index (HSI) modeling can be used in combination with the geographic information system (GIS) technology to create maps important to fisheries management (Eastwood et al., 2001). HSI models are based on suitability indices that reflect habitat quality as a function of one or more environmental variables. Recently, HSI modeling methods have been successfully used to identify and forecast potential fishing grounds for bigeye tuna (*Thunnus obesus*) (Feng et al., 2007; Chen et al., 2008b) and chub mackerel (Chen et al., 2009). Because near real-time environmental variables such as SST, chl *a*, and SSHA can be easily measured by remote sensing, an HSI modeling approach has great potential for estimating abundance (which will be used for resource management), and for forecasting fishing grounds.

The objectives of this study were to develop an HSI model to detect the potential fishing grounds for neon flying squid by using remote sensing data in combination with fisheries data, and to find the optimal habitat for *O. bartramii* on their feeding grounds to provide a scientific basis for the management of this species. The environmental variables considered in this study included SST, SSS, SSHA, and chl *a*, all of which have been identified as critical to the distribution and abundance of *O. bartramii* in previous studies (e.g., Chen, 1997; Wang et al., 2003; Xu et al., 2004; Tian, 2006).

Methods and materials

Fishery data

The area of 39–46°N latitude and 150–165°E longitude is an important traditional fishing ground for *O. bartramii* from August to November (Chen and Tian, 2005). Between 75% and 84% of the total catch has been landed in this area by Chinese mainland squid jigging fleets during the last decade (Chen et al., 2008a). Fishery data from 1999 to 2005 from this area were compiled monthly (Chinese Mainland Squid Technical Group, Shanghai Ocean University, Shanghai, China). These data, including squid catch per fishing day and fishing

position, were georeferenced and grouped into a unit of 0.5°×0.5° latitude and longitude.

We assumed no bycatch in the squid fishery (Wang and Chen, 2005) and that catch per unit of effort (CPUE) (tons [t]/day [d]) of the squid jigging vessels is a good indicator of stock abundance on the fishing grounds (Chen et al., 2008c). The nominal CPUE in one fishing unit of 0.5°×0.5° was calculated as follows:

$$CPUE_{ymi} = \frac{C_{ymi}}{F_{ymi}}, \quad (1)$$

where $CPUE_{ym}$ = monthly nominal CPUE(t/d) at *i* fishing units in month *m* and year *y*;

C_{ymi} = monthly catch (t) at *i* fishing units in month *m* and year *y*; and

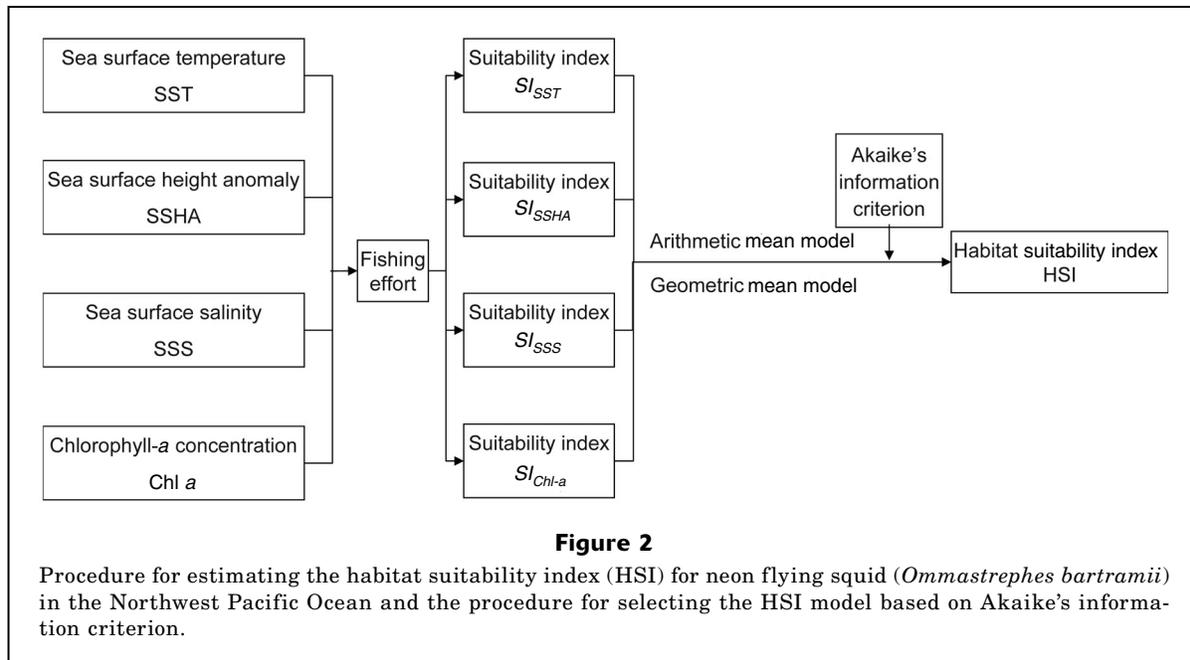
F_{ymi} = number of fishing days at *i* fishing unit in month *m* and year *y*.

Satellite remote sensing data

Physical and biological environmental data used to describe oceanographic conditions in our survey area included SST, SSS, SSHA, and chl *a*. Monthly SST data with a spatial resolution of 0.5°×0.5° were obtained from the Physical Oceanography Distributed Active Archive Center (PODAAC) of the National Aeronautics and Space Administration (NASA) website (http://podaac.jpl.nasa.gov/DATA_CATALOG/index.html, accessed October 2008). Monthly SSS and SSHA data sets, both with a spatial resolution of 0.5°×0.5°, were downloaded from the IRI/LDEO Climate Data Library (<http://iridl.ldeo.columbia.edu>, accessed October 2008). Monthly chl-*a* level-3 standard map images with a spatial resolution of 9 km, from the “sea viewing wide field of view sensor (SeaWiFS), were obtained from the Goddard Space Flight Center on the NASA website (<http://oceancolor.gsfc.nasa.gov/SeaWiFS/>, accessed October 2008).

Establishment of the HSI model

The potential fishing grounds could be estimated through a habitat model combined with satellite-derived environmental factors. Fishing effort has been considered an index of fish occurrence or fish availability (Andrade and Garcia, 1999), and also successfully used in developing HSI models (Gillis et al., 1993; Swain and Wade, 2003; Zainuddin, et al., 2006; Tian et al., 2009). Therefore, we first analyzed fishing effort in relation to the above four environmental variables to identify the probability of *O. bartramii* availability. The probability, expressed as a suitability index (SI), was defined from the relationships between fishing effort and environmental variables. The highest probability value (SI=1) is associated with the fishing effort in a given interval of the environmental variables, which represents the most favorable environmental condition (Brown et al., 2000). The lowest probability value (SI=0) indicates the lowest fishing



effort (i.e., equal to 0) in the presence of fishing. The SI values between 0 and 1 were assigned to the ranges of the corresponding environmental variable (Table 1; Brown et al., 2000).

The SI values derived from each variable were then combined into the empirical HSI model (Fig. 2). Two empirical HSI models, the arithmetic mean model (AMM) and the geometric mean model (GMM) are commonly used to estimate habitat availability (U.S. Fish and Wildlife Service, 1980a, 1980b; Hess and Bay, 2000; Lauver et al., 2002; Chen et al., 2009). The HSI is a univariate variable also having a value between 0 and 1

(Brooks, 1997). The two empirical HSI models were described as follows:

AMM (Hess and Bay, 2000; Chen et al., 2009):

$$HSI_{AMM} = \frac{1}{n} \sum_{i=1}^n SI_i; \quad (2)$$

and GMM (Lauver et al., 2002; Chen et al., 2009):

$$HSI_{GMM} = \left(\prod_{i=1}^n SI_i \right)^{1/n}; \quad (3)$$

where SI_i = the SI for i^{th} environmental variable;

n = the number of environmental variables used in the model;

$i = 1, 2, \dots, \text{and } n.$

On the basis of previous studies on the relationship between environmental variables and squid catch, we considered SST as the primary variable for identifying habitat for *O. bartramii* and used different combinations of one (SST), two (SST and one other variable), three (SST and two other variables), and four (SST, SSS, SSHa, and chl a) variables as habitat data. The SI values derived from different combinations of habitat variables were then combined into the HSI model (Fig. 2).

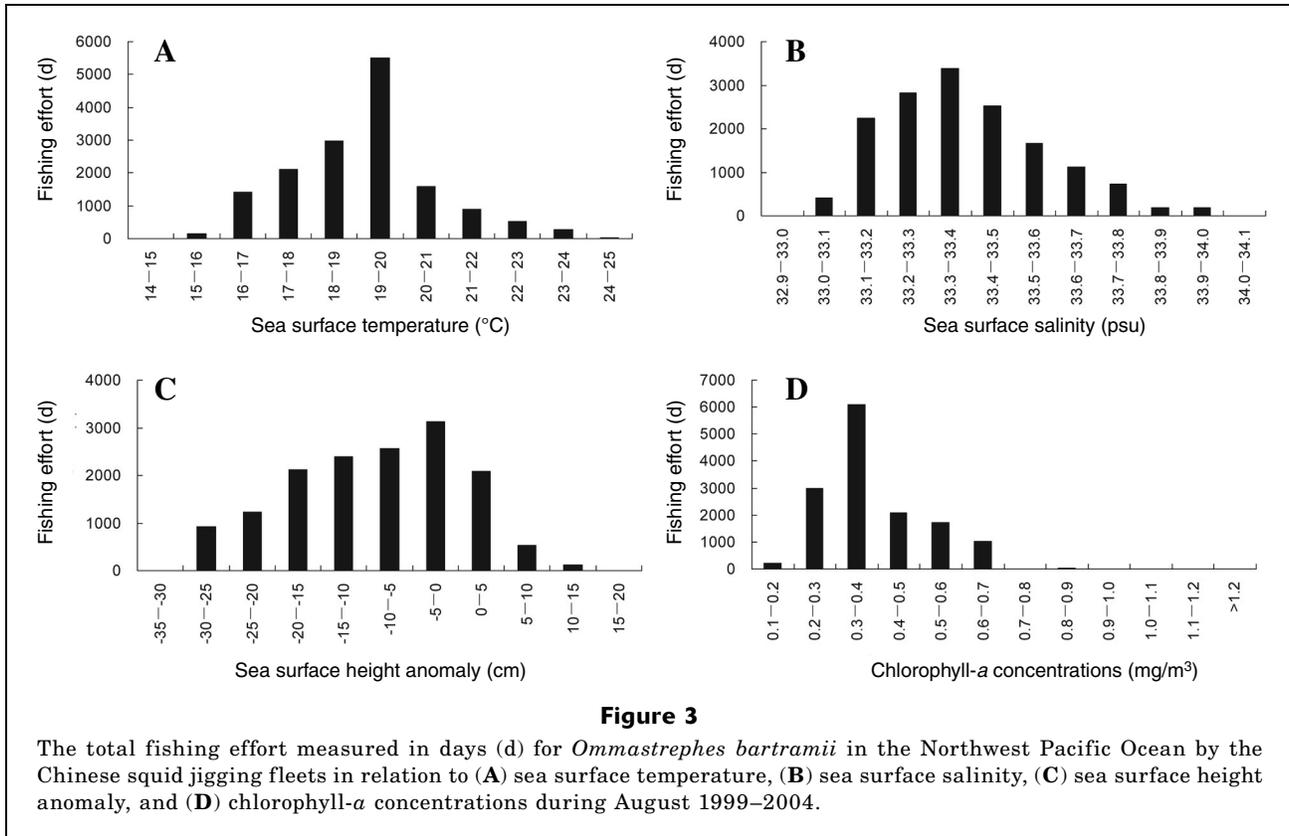
Selection of HSI model and validation

The monthly HSI values from August to October of 1999–2004 were estimated by the approach described above. The percentages of total fishing effort from 1999

Table 1

Definitions of suitability index values for *Ommastrephes bartramii* based on the fishing effort of Chinese squid jigging fleets in one fishing unit of 0.5° latitude \times 0.5° longitude in the Northwest Pacific Ocean.

Suitability index value	Description of habitat use
1	The highest fishing effort in the Chinese squid jigging fishery
0.5	Common occurrence or average fishing effort in the Chinese squid jigging fishery (between 2000 fishing days and the highest fishing effort)
0.1	Rare occurrence or low fishing effort in the Chinese squid jigging fishery (fewer than 2000 fishing days)
0	Fishing effort is zero in the Chinese squid jigging fishery (0 fishing days)



to 2004 were also produced according to ranges of calculated HSI values (i.e., HSI = [0–0.2]; [0.2–0.4]; [0.4–0.6]; [0.6–0.8]; and [0.8–1.0]). Therefore, we assumed that a positive linear relationship exists between the value of HSI and fishing effort. The model can be written as

$$Y = a + bX,$$

where Y = the percentage of the fishing effort corresponding to different HSI values calculated for the same time;

X = the HSI value; and

a and b are the two parameters to be estimated.

The performance of different HSI models with one, two, three, and four environmental variables were evaluated and compared to identify the most suitable HSI model based on the Akaike's information criterion (AIC; Akaike, 1981).

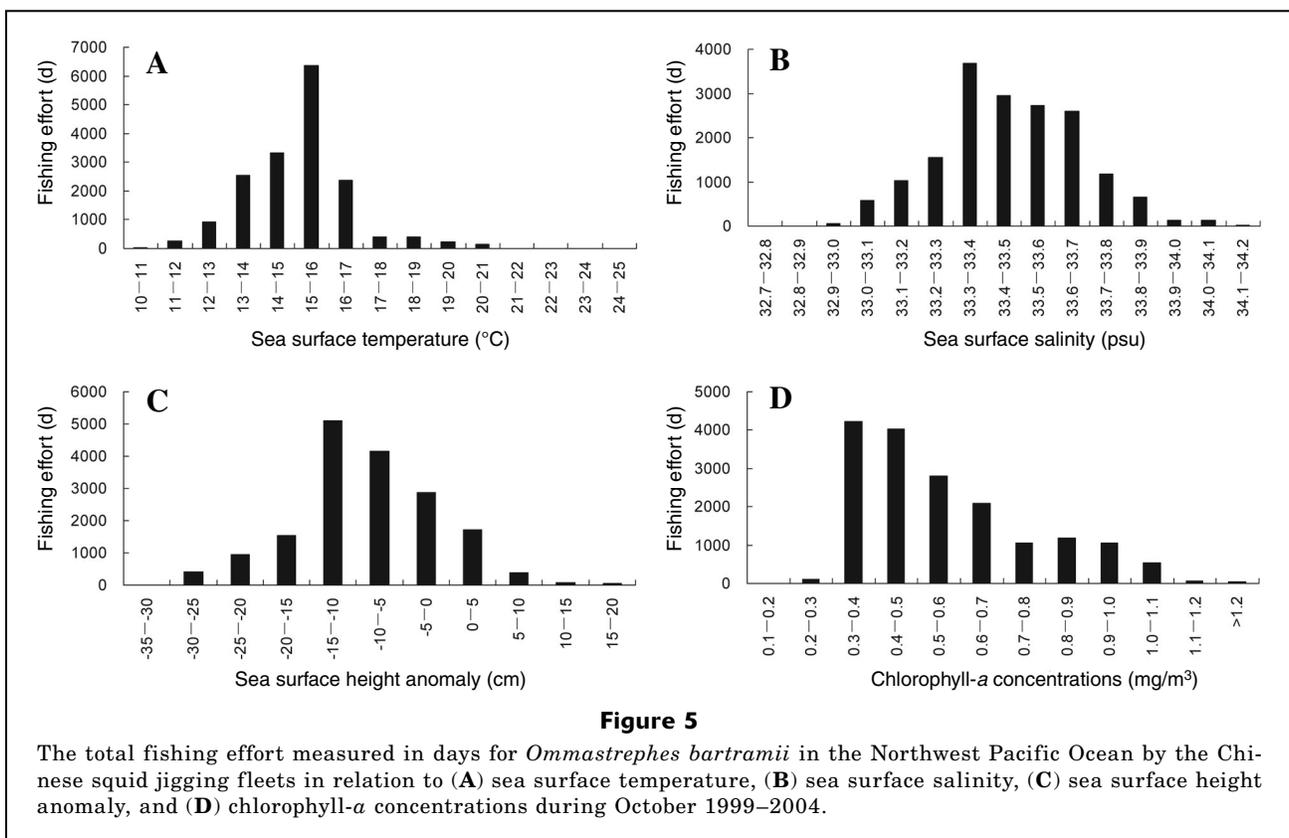
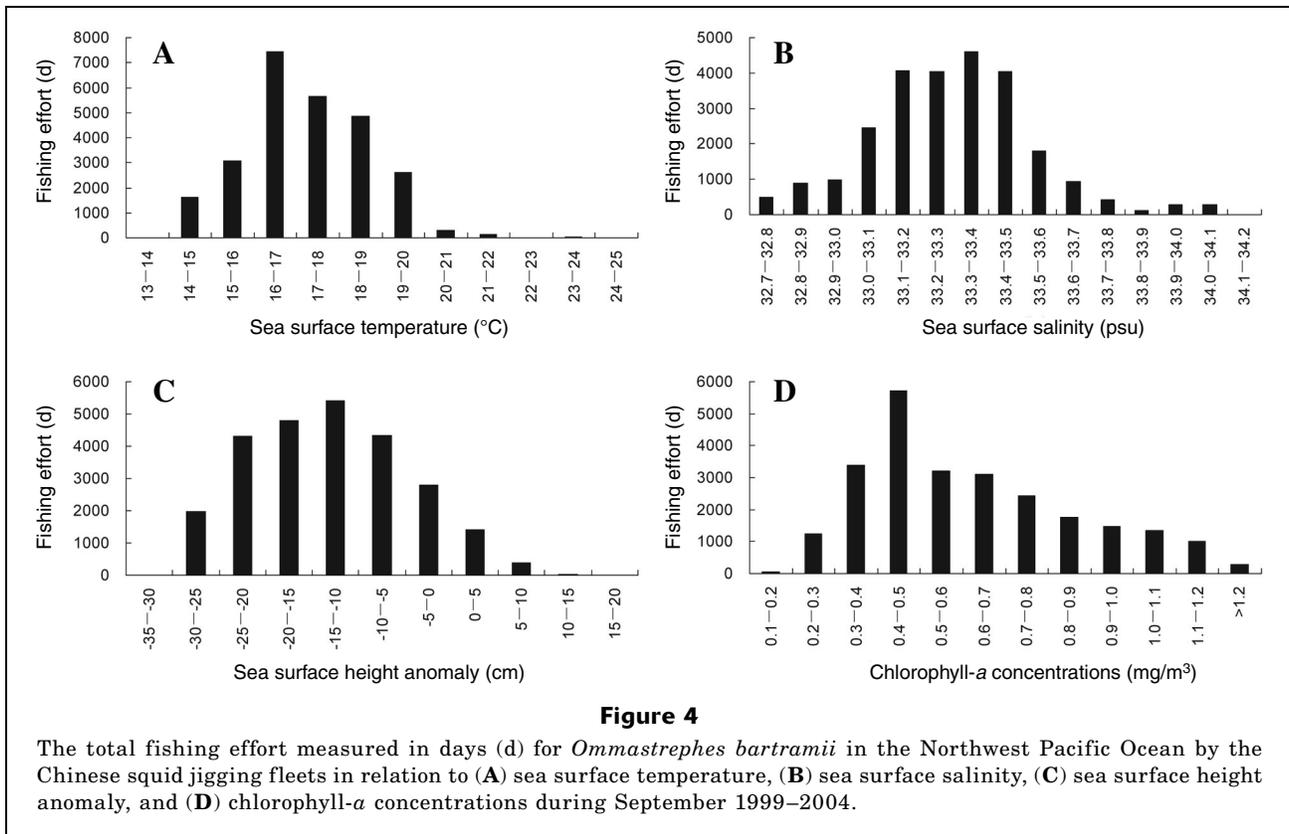
The model that yielded the minimum AIC value was selected as the best model. This model was then used for model testing and validation. The spatial distributions of HSI values derived from the above selected HSI model in 2005 were mapped with Marine Explorer, vers. 4.0 (Environmental Simulation Laboratory Co, Ltd, Saitama, Japan) for forecasting potential fishing grounds and were compared with the actual fishery data from the Chinese squid jigging fleets in 2005.

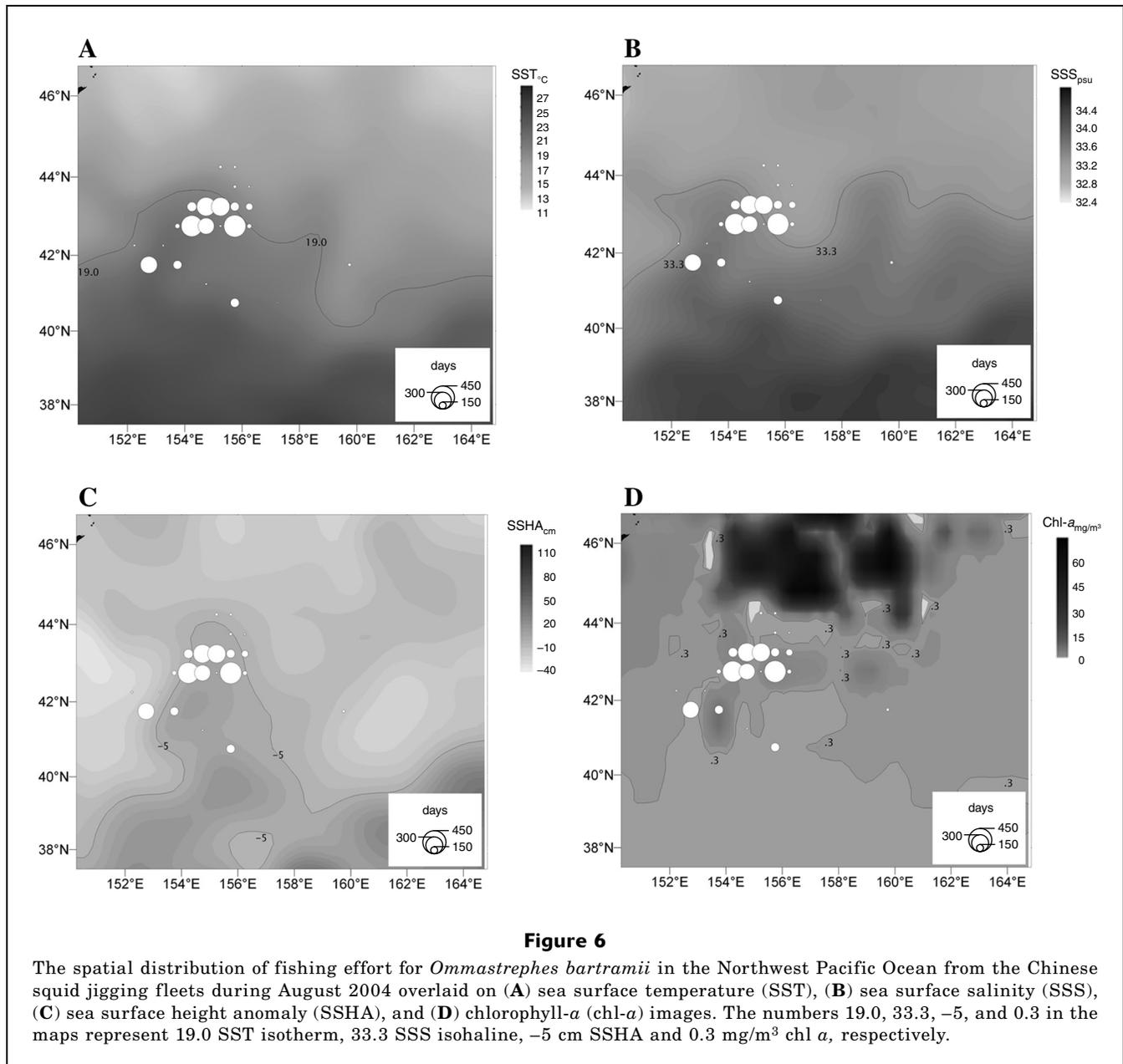
Results

Squid catch in relation to environmental variables

During August, fishing effort was highest in waters with SSTs ranging from 17° to 20°C (Fig. 3A), and the preferred SST tended to be centered at 19–20°C. High fishing effort (>2000 days) with respect to SSS occurred in areas where sea surface salinity (SSS) varied from 33.1 to 33.5 (Fig. 3B), and where the preferred SSS was between 33.3 and 33.4. We also found that high fishing effort (>2000 days) related to SSHA and chl *a* occurred in waters with SSHA ranging from –20 cm to 5 cm and with chl-*a* values between 0.2 and 0.4 mg/m³. The optimum SSHA and SSS tended to be between –5 and 0 cm and between 0.3 and 0.4 mg/m³ (Fig. 3, C and D). Similar results were shown for September and October (Figs. 4 and 5).

The spatial distribution of fishing effort for *O. bartramii* from August of 2004 is presented in Figure 6 to show its relationship with environmental variables SST, SSS, SSHA, and chl *a*. The center of fishing areas with a high aggregation of squid occurred in the waters of 42°–44° N latitude and 154°–157° E longitude (Fig. 6). The environmental maps of four variables indicated that squid were aggregated mostly in warm water near the 19°C SST isotherm (Fig. 6A) and 33.3 psu SSS isohaline (Fig. 6B), in the edge of a cold ring near the –5 cm SSHA (Fig. 6C), and in relatively high





chl-*a* concentration of about 0.3 mg/m³ (Fig. 6D) during August in 2004.

Because these four environmental variables are closely related with *O. bartramii* distribution, we rescaled them with SI values (ranging from 0 to 1) based on histogram distributions (Figs. 3, 4, and 5). On the basis of the SI definition (Brown et al., 2000; Table 1), the highest fishing effort was given an SI value of 1, the total fishing effort below 2000 days was given an SI value of 0.1, and the total fishing effort between the highest fishing effort and 2000 days was given an SI value of 0.5. The definitions of SI values for the four environmental variables are shown in Table 2.

HSI model selection

The different HSI models with one, two, three, and four environmental variables were evaluated for the most parsimonious HSI model. The HSI model with one variable (SST) was the best for predicting the percentage of fishing effort in an area when the GMM was applied (Table 3), whereas the HSI model with three variables (SST, SSHA, and chl *a*) was the best when the AMM was applied (Table 3). When the same sets of environmental variables were used for the two empirical HSI models, respectively, the AMM model yielded better results in predicting the fishing effort because its AIC value was less than that of the GMM model.

Therefore, we determined that the AMM model with three variables, SST, SSHA, and chl *a*, was the most parsimonious HSI model (Table 3).

To further compare the performances of AMM and GMM, we estimated the average actual percentage of fishing catch, average actual percentage of fishing effort, and average CPUE of *O. bartramii* according to the grouped HSI values from AMM and GMM with three

variables, SST, SSHA, and chl *a*, from August to October, 1999–2004. From August to October, the area with the HSI value >0.6 had 58.8% of the total catch, 56.63% of the total fishing effort for the AMM model (Fig. 7, A and B), but 51.46% of the total catch and 46.56% of the total fishing effort based on the GMM model (Fig. 7, A and B). The area with the HSI value of less than 0.4 yielded 15.48% and 38.58% of the total catch according

Table 2

Definition of suitability index (SI) values for the four environmental variables—sea surface temperature (SST), sea surface salinity (SSS), sea surface height anomaly (SSHA), and chlorophyll-*a* (chl-*a*) concentrations—used to develop a model to predict occurrences of *Ommastrephes bartramii* aggregations from August to October in the Northwest Pacific Ocean.

Month	SI	SST (°C)	Chl <i>a</i> (mg/m ³)	SSHA (cm)	SSS (psu)
August	1	≥19 and <20	≥0.3 and <0.4	≥-5 and <0	≥33.3 and <33.4
	0.5	≥17 and <19	≥0.2 and <0.3	≥-20 and <-5	≥33.1 and <33.3
		≥20 and <21	≥0.4 and <0.6	≥0 and <5	≥33.4 and <33.6
September	0.1	≥15 and <17	≥0.1 and <0.2	≥-30 and <-20	≥33.0 and <33.1
		≥21 and <25	≥0.6 and <0.9	≥5 and <15	≥33.6 and <34.0
	0	<15 and ≥25	<0.1 and ≥0.9	<-30 and ≥15	<33.0 and ≥34.0
	1	≥16 and <17	≥0.4 and <0.5	≥-15 and <-10	≥33.3 and <33.4
		0.5	≥15 and <16	≥0.3 and <0.4	≥-25 and <-15
	0.1	≥19 and <20	≥0.5 and <0.8	≥-10 and <0	≥33.4 and <33.5
		≥14 and <15	≥0.1 and <0.3	≥-30 and <-25	≥32.7 and <33.0
≥20 and <23		≥0.8 and <1.3	≥0 and <15	≥33.5 and <34.1	
0	<14 and ≥23	<0.1 and ≥1.3	<-30 and ≥15	<32.7 and ≥34.1	
October	1	≥15 and <16	≥0.3 and <0.4	≥-15 and <-10	≥33.3 and <33.4
	0.5	≥13 and <15	≥0.4 and <0.7	≥-10 and <5	≥33.4 and <33.7
		≥16 and <17			
	0.1	≥10 and <13	≥0.2 and <0.3	≥-30 and <-15	≥32.9 and <33.3
≥17 and <21		≥0.7 and <1.3	≥5 and <20	≥33.7 and <34.1	
0	<10 and ≥21	<0.2 and ≥1.3	<-30 and ≥20	<32.9 and ≥34.1	

Table 3

Parameters of linear regression model between the percentage of fishing effort and habitat suitability index (HSI) and AIC value for the two HSI models, geometric mean model (GMM) and arithmetic mean model (AMM), under different combinations of environmental variables, sea surface temperature (SST), sea surface salinity (SSS), sea surface height anomaly (SSHA), and chlorophyll-*a* (chl-*a*) concentrations. The linear regression model can be written as $Y=a+bX$, where Y and X represent the percentage of fishing effort and HSI, respectively. Δ AIC is the difference in Akaike's information criterion (AIC) values between that model and the best model.

Environmental variables	GMM				AMM			
	<i>a</i>	<i>b</i>	AIC	Δ AIC	<i>a</i>	<i>b</i>	AIC	Δ AIC
SST	7.01	44.97	64.78	0	7.01	44.97	64.78	3.81
SST, SSS	13.05	13.47	71.06	6.28	8.64	15.68	76.65	15.68
SST, SSHA	6.19	27.62	76.54	11.76	4.26	31.47	75.77	14.8
SST, chl <i>a</i>	17.42	5.17	75.99	11.21	11.80	16.41	68.61	7.64
SST, SSHA, chl <i>a</i>	19.57	0.87	80.03	15.25	6.53	26.94	60.97	0
SST, SSS, SSHA	11.18	17.64	84.64	19.86	-2.01	44.03	77.24	16.27
SST, SSS, chl <i>a</i>	19.08	1.84	77.16	12.38	2.58	34.85	62.26	1.29
SST, SSS, SSHA, chl <i>a</i>	18.39	3.23	71.60	6.82	1.11	37.78	70.00	9.03

to the AMM and GMM models, respectively (Fig. 7A), and produced 16.02% and 41.39% of the total fishing effort according to the AMM and GMM models accordingly (Fig. 7B).

Moreover, the monthly CPUEs from 1999 to 2004 were compiled and calculated according to the grouping of AMM-based and GMM-based HSI values estimated from the three environmental variables (SST, SSHA, and chl *a*). The CPUE values were found to increase with the AMM-based HSI value, but the CPUE was not the same for the GMM-based HSI value (Fig. 7C). When the AMM-based HSI values for an area ranged from 0 to 0.2, the average CPUE was only equal to 1.44 ± 0.34 t/d (mean \pm standard deviation). For the areas with HSI values ranging between 0.6 and 0.8 and higher than 0.8, the average CPUEs were 2.50 ± 0.26 t/d and 3.01 ± 0.59 t/d, respectively (Fig. 7C). All the results from the fishery data from 1999 to 2004 indicated that the AMM model was more suitable than the GMM model for estimating the HSI for *O. bartramii*, as we assumed.

HSI model validation

With the HSI value estimated from the AMM model in 2005, we mapped the spatial distribution of monthly HSI values, fishing locations, and CPUEs (Fig. 8). The HSI values >0.6 were mainly found in the areas of $152^{\circ}30' - 156^{\circ}30'$ longitude and $42^{\circ}30' - 44^{\circ}00'$ latitude, and $156 - 159^{\circ}$ longitude and $40^{\circ}30' - 42^{\circ}30'$ latitude (Fig. 8A), in which the catch and fishing effort occupied 78.17% and 65.17% of the total catch and total effort, respectively (Fig. 9, A and B) and the average CPUE was 3.51 t/d in August (Fig. 9C). In September, the HSI values >0.6 were widely distributed in the waters of $150^{\circ}30' - 151^{\circ}30'$ longitude and $40^{\circ}30' - 41^{\circ}30'$ latitude, and $152 - 165^{\circ}$ longitude and $40^{\circ}30' - 43^{\circ}30'$ latitude (Fig. 8B), in which the catch and fishing effort were 96.36% and 93.19% of the total catch and effort, respectively (Fig. 9, A and B) and the average CPUE was 3.77 t/d (Fig. 9C). However, there was no fishing activity in the area between $156 - 160^{\circ}$ longitude and $40^{\circ}30' - 42^{\circ}$ latitude, and $160 - 165^{\circ}$ longitude and $40^{\circ}30' - 43^{\circ}30'$ latitude (Fig. 8B). In October, the HSI values >0.6 were located in the areas of $152^{\circ}30' - 156^{\circ}$ longitude and $42^{\circ}30' - 44^{\circ}30'$ latitude, $156 - 157^{\circ}45'$ longitude and $42^{\circ} - 43^{\circ}$ latitude, $158^{\circ} - 160^{\circ}$ longitude and $41^{\circ} - 43^{\circ}$ latitude, and $162^{\circ} - 163^{\circ}30'$ longitude and $43 - 44^{\circ}30'$ latitude (Fig. 8C), where the catch and fishing effort were 68.90% and 68.16% of the total catch and efforts (Fig. 9, A and B), respectively, and the average CPUE was 3.10 t/d (Fig. 9C). These results indicate that AMM can yield a reliable prediction of the potential fishing ground for *O. bartramii*.

Discussion

The biophysical environments in the transition zone region of North Pacific Ocean have been hypothesized to influence the migration, distribution, and abundance

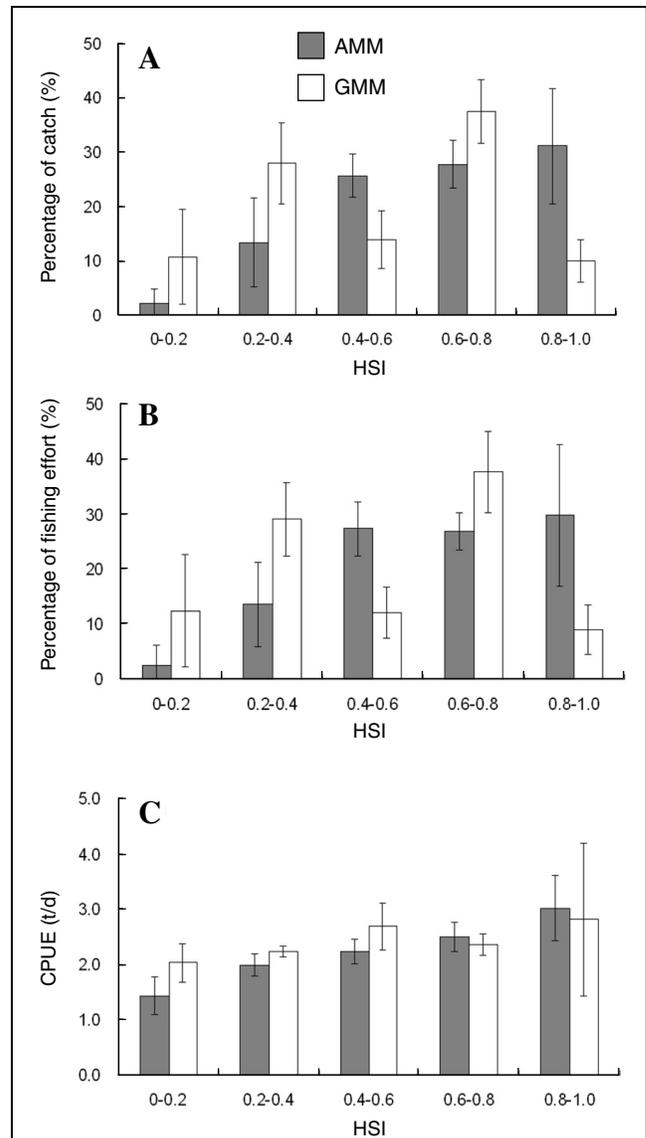
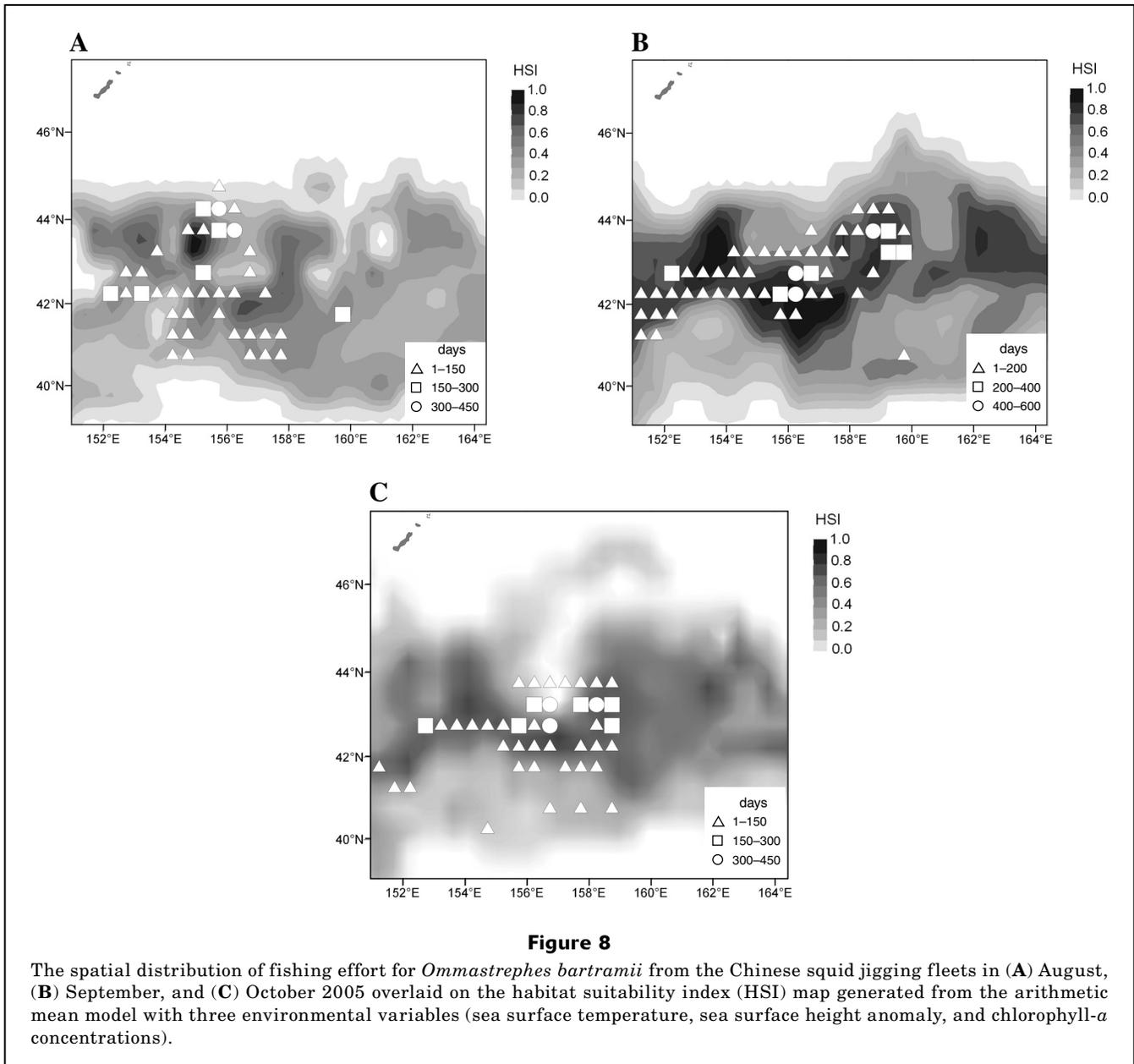


Figure 7

The relationship between the habitat suitability index (HSI) values estimated from the arithmetic mean model (AMM) and the geometric mean model (GMM), and (A) actual percentage of catch, (B) actual percentage of fishing effort, and (C) catch per unit of effort (CPUE) for *Ommastrephes bartramii* from 1999 to 2004 in the Northwest Pacific Ocean.

of *O. bartramii* (Tian, 2006; Ichii et al., 2009). Within more specific ranges, the highest density of *O. bartramii* was found in waters with favorable ranges of SST, SSS, SSHA, and chl *a* (Table 2). These ranges can be considered indicators of areas with the highest probability of finding *O. bartramii*. The highest squid abundance or optimum habitat were concentrated around the $19 - 20^{\circ}$ C SST isotherm, the $33.3 - 33.4$ psu SSS isohaline, and the 0.3 mg/m^3 chl-*a* isopleth in August; $16 - 17^{\circ}$ C SST, $33.3 - 33.4$ psu SSS, and $0.4 - 0.5 \text{ mg/m}^3$ chl *a* in September;



and 15–16°C SST, 33.3–33.4 psu SSS, and 0.3–0.4 mg/m³ chl *a* in October. The results are the same as those in previous findings (Chen and Chiu, 1999; Chen, 1997; Tian, 2006) and indicate that the dynamics of high *O. bartramii* aggregations were influenced by the progression of seasonal cooling (thermal and SSS front), and that the movement of the chl-*a* front can be predicted by using the specific levels of the proxy variables. These proxy indicators appear to play a critical role in formulating and patterning potential *O. bartramii* habitat and migration routes.

The SSHA field is coupled with the dynamics (currents) and thermodynamics (heat balance) of the upper ocean. Convergences and divergences of the water mass transport in the surface layer of the ocean result in

positive and negative sea level anomalies, respectively (Zagaglia et al., 2004). Variations in water density, which are dominantly controlled by changes in temperature or in heat storage (changes in the mixed layer depth or its temperature), also give rise to sea level anomalies (Polito et al., 2000). It is natural, therefore, to expect that changes in SSHA can be related to variations in the CPUE and *O. bartramii* distribution. Each species has a salinity preference and congregates at vertical salinity breaks, as at horizontal salinity “fronts” (Chen, 2004). We found that *O. bartramii* distribution is closely related to the environmental variables, SST, SSS, SSHA, and chl *a*. Of the four environmental variables considered in this study, SST, SSHA, and chl *a* can be easily obtained in near real-time from remote

sensing, and they are more important than SSS in forecasting *O. bartramii* habitat. Although the chl *a* and SST data obtained from remote sensing have limitations (Arrigo et al., 1998; Santos, 2000) and errors may occur in areas where the cloudy weather is frequent, these environmental data are commonly used in marine fisheries (Santos, 2000; Wang et al., 2003; Zagaglia et al., 2004; Zainuddin et al., 2006; Chen et al., 2008b). Moreover, because *O. bartramii* undertake vertical diel movements, inhabiting water depths of 0–40 m during night and 150–350 m during the day (Wang and Chen, 2005), other environmental variables, such as water temperature at the different depths and the vertical structure of water temperature, need to be considered in future analyses.

Fishing effort is a good indicator in estimating SI values when commercial fishery data are used. In the squid jiggling fishery of North Pacific Ocean, Chinese mainland fisherman first determine the fishing area with the help of near real-time SST and SSHA data from remote sensing and then locate the fishing position by using an echo-sounder (Chen, 2004; Wang and Chen, 2005). Therefore, fishing effort can be considered an index of squid occurrence. Although the nominal CPUE is affected by fishing boats, fishing technology, light power, and other environmental factors in the commercial fishery, CPUE is not suitable for estimating SI values. Tian et al. (2009) also reported that a fishing effort-based HSI model performed better than the CPUE-based HSI model in defining optimal habitats for neon flying squid, whereas the CPUE-based HSI model tended to overestimate the range of optimal habitats and underestimate monthly variations in the spatial distribution of optimal habitats.

Clearly, we found that *O. bartramii* are not randomly distributed in relation to environmental conditions. Outputs produced from HSI modeling can indicate the spatiotemporal variation of squid habitat conditions. Many fish habitat models have been developed by using combined empirical and GIS-based spatial modeling techniques (Rubec et al., 1999; Brown et al., 2000; Feng et al., 2007; Chen et al., 2008b). These approaches differ in their assumptions, inputs, and outputs. This study indicates that the HSI modeling approach, which is relatively simple and straightforward, may be an appropriate method for pinpointing optimal habitats and potential fishing grounds of squid. Because nearly every commercially important marine species is sensitive to SST and has a seasonal optimum SST range, and because the near real-time SST can be obtained from remote sensing, SST is usually considered a basic input variable in developing an HSI model (Eastwood et al., 2001; Le Pape et al., 2003; Zagaglia et al., 2004; Zainuddin et al., 2006).

Different HSI models with one to four variables tended to yield varying results. For the same set of environmental variables, the AMM model performed better than the GMM model because its AIC value was smaller (Table 3). The AMM model with three variables, SST, SSHA, and chl *a*, had the lowest AIC value for fishing

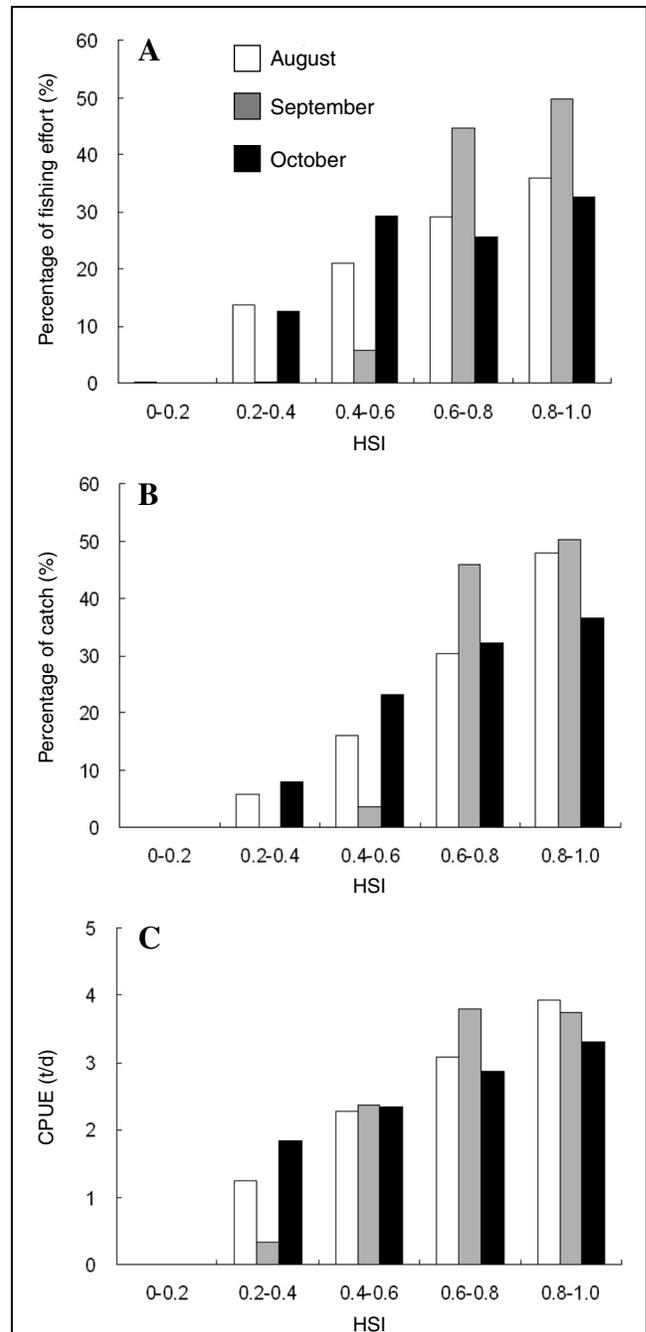


Figure 9

The relationship between the habitat suitability index (HSI) values estimated from the arithmetic mean model with three environmental variables (sea surface temperature, sea surface height anomaly, and chlorophyll-*a* concentrations), and (A) actual percentage of the total catch, (B) percentage of fishing effort, and (C) catch per unit of effort (CPUE) for *Ommastrephes bartramii* from August to October 2005.

effort. To further evaluate the performance of the AMM models, we compared their outputs with corresponding abundance density (CPUE). We found that the average

CPUE of *O. bartramii* increased from 1.44 t/d (0–0.2 of HSI) to 3.01 t/d (0.8–1.0 of HSI) and that the improvement in HSI occurred from August to October, 1999–2004. This approach, however, is not equivalent to testing the accuracy of the HSI model for predicting the quality of habitat for a species (Wakeley, 1988). In the evaluation of habitat quality, it is important to capture both the habitat characteristics and habitat selection in the linkage between physical environments and habitat preference of target species because only a precise HSI model can yield a reliable assessment (Chen, et al., 2008b). However, the uncertainty associated with the HSI model predictions usually results from the degree of reliability of the SI curve, input data, and the HSI model structure (Chen et al., 2009).

The AMM-based HSI modeling approach used in the present study was generally successful for its intended use in mapping habitat and forecasting fishing grounds when the three environmental variables (SST, SSHA, and chl *a*) were used, whereas GMM may be appropriate for determining potential fishing grounds when only one environmental variable (SST) is used. This result shows that SST is the most important environmental variable in the HSI modeling for neon flying squid. Different structures of HSI models would lead to different results, and the optimum HSI is different when different combinations of environmental variables are considered. Chen et al. (2009) also selected the AMM model as the optimum HSI model combined with four environmental variables (SST, SSHA, SSS, and chl *a*) in studying habitat suitability for chub mackerel in the East China Sea. Other different approaches are also used in addressing fish-habitat modeling. Norcross et al. (1997) modeled habitat suitability for flatfish by using a regression tree analysis in Alaska, and Swartzman et al. (1992) and Stoner et al. (2001) used generalized additive models for modeling flatfish distribution in the Bering Sea and for winter flounder (*Pseudopleuronectes americanus*) in New Jersey, respectively. Le Pape et al. (2003) characterized the distribution of common sole (*Solea solea*), using a general linear model. Eastwood et al. (2001) applied regression quantiles and GIS procedures to model the spatial variations in spawning habitat suitability for *S. solea*. The model output better reflects theoretical findings on the spatiotemporal nature of the species' response to preferred environmental conditions. The AMM model with three environmental variables (SST, SSHA, and chl *a*) was considered to be the most parsimonious model in this study. However, we may need to conduct more studies for estimating HSI using other methods. Some of these methods may include allocating different weights for different environment variables in developing HSI models and considering more environmental variables that may influence *O. bartramii* distributions, such as water temperatures at different depths, vertical structure of water temperature, and currents.

HSI models can be applied to identify potential fishing grounds, but an optimal strategy for the squid fishermen in searching for fishing grounds would be to target an area with high habitat-suitability indices

(>0.6) yielded from the AMM model. A dynamic near real-time habitat model incorporating more environmental variables, such as currents, fronts, winds, and other environmental variables, may further improve the process of identifying potential fishing areas.

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