Modelling the effects of climate variability on habitat suitability of jumbo flying squid, *Dosidicus gigas*, in the Southeast Pacific Ocean off Peru

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The jumbo flying squid *Dosidicus gigas* is a highly migratory species distributed throughout the Eastern Pacific Ocean. An integrated habitat suitability index (HSI) model was developed to evaluate the effects of climate variability (i.e. *El Niño*-Southern Oscillation) on the habitat suitability for *D. gigas* in the Southeast Pacific Ocean off Peru. The data used in the analysis included catch and fishing effort from the Chinese squid-jigging fishery over 2006–2013, as well as remotely sensed environmental data including sea surface temperature, chlorophyll *a* and sea surface height anomaly. Arithmetic mean HSI model was shown to have a better predictive performance and used to predict the HSI values and identify the suitable habitat for *D. gigas* over 2006–2012. Fishery and environmental data in 2013 was used to validate the model. The latitudinal location of suitable habitat was found to be important in determining the distribution of fishing efforts. Cross-correlation plot exhibited a significantly negative relationship between the average HSI values on the fishing ground and the *Niño* 3.4 indices with time-lags from 2 to 3 months, implying that the squid habitat responded quickly to the climate variability. Both suitable habitat areas and catches of *D. gigas* increased in *La Niña* periods and decreased in *El Niño* periods. The *La Niña* conditions tended to strengthen upwelling coupled with cool and nutrient-enhanced waters, which yielded favourable habitat conditions and high catches; whereas the *El Niño* conditions weakened upwelling coupled with warm and nutrient-depleted waters, which were unfavourable for squid habitat and reduced catches. Our findings indicated that large-scale climate variabilities could have great effects on squid habitat and such variabilities could be quantified by climate indices such as Oceanic *Niño* index.

**Keywords:** climate variability, *Dosidicus gigas*, habitat suitability index, southeast pacific ocean, spatial distribution, squid-jigging fisheries.

**Introduction**

The jumbo flying squid, *Dosidicus gigas* (d’Orbigny, 1835), is a large active squid with an extensive coastal and oceanic range between 40°N and 47°S throughout the Eastern Pacific Ocean (Nigmatullin et al., 2001). As a commercially important species, *D. gigas* sustains major fisheries in the Gulf of California (Morales-Bojórquez and Nevárez-Martínez, 2010), the coastal and oceanic waters of Peru and Chile (Taipe et al., 2001; Rocha and Vega, 2003; Keyl et al., 2011), and the offshore regions of the Costa Rica Dome (Chen et al., 2014), with exploitation extending westward to 120°W at the equator (Liu et al., 2015). Squid-jigging vessels from East Asia-Pacific countries such as Japan, Korea, Russia, and China have been attracted into the *D. gigas* fisheries in the Eastern Pacific Ocean (Ichii et al., 2002). Among them, Chinese squid-jigging fishing vessels began to target this squid in 2001 outside the exclusive economic zone (EEZ) off Peru, and subsequently China has developed a large squid fishery across the Southeast Pacific Ocean and maintained high catches of *D. gigas* in recent years (Chen et al., 2008a).
Climatic and environmental variations can strongly influence habitat range expansions and contractions of ommastrephid squid in the world ocean (Anderson and Rodhouse, 2001). The large-scale climate variability has great influences on local environments, forcing rapid responses of squid population (Rodhouse, 2013). For example, habitat condition of neon flying squid Ommastrephes bartramii was greatly affected by the El Niño-Southern Oscillation (ENSO) event in the Northwest Pacific Ocean, and fishing ground of O. bartramii tended to shift southward in El Niño years and northward in La Niña years (Chen et al., 2007). Additionally, negative North Atlantic Oscillation index was likely to yield favourable oceanographic conditions for short-finned squid Illex illecebrosus in the Northwest Atlantic Ocean, resulting in a large area of high productivity and high squid abundance (Dawe, 2000).

Dosidicus gigas has a lifespan of around 1–2 years (Argüelles et al., 2001). As for most squid species, the short-lived D. gigas tends to have highly variable abundance and distribution across years (Nevárez-Martínez et al., 2000; Litz et al., 2011). Such fluctuations in squid stocks can be primarily attributed to environmental variability at a range of spatial and temporal scales (Pierce et al., 2008). In the Gulf of California, Robinson et al. (2013) correlated interannual variability in the habitat quality of D. gigas with surface temperature (SST), chlorophyll a (Chl a) and coastal upwelling index. They found that the La Niña event in 1999 yielded favourable cold habitat and increased squid fishing landings due to cold SST and high Chl a with strong upwelling. Seasonal occurrences of D. gigas in the northern California Current System were considered to be driven by variable climatic phenomena such as ENSO and global warming, and oceanic conditions such as expansion and shoaling of the oxygen minimum zone in the eupelagic zone (Litz et al., 2011). In the coastal Peruvian waters, Waluda et al. (2006) related the squid fishing effort with SST (from 17 to 22°C) and ultimately with catch rates of commercial fleets. It was found that high catches of D. gigas occurred in 1994 with normal environmental condition, while low catches were observed during periods of cool or warm SST anomalies. Furthermore, squid abundance was found to be closely related to fishery-favourable SST range and significantly linked to ENSO events (Waluda and Rodhouse, 2006).

Habitats represent favourable environmental conditions for pelagic species and thus provide space-time envelopes of optimal conditions (Petitgas et al., 2014). Understanding the spatial and temporal dynamics of fish habitat can greatly improve ecosystem-based fisheries management and sustainable exploitation of fisheries resources (Valavanis et al., 2008). Increasing efforts have been conducted to model the habitat presence in relation to fish distribution and abundance by different methods, such as logistic regression model (Turgeon and Rodriguez, 2005), generalized additive model (Mugo et al., 2010), and habitat suitability index (HSI) model (Tian et al., 2009). HSI modelling is developed by the United States Environmental Protection Agency, and has gained more interests and been widely applied in habitat assessment (Hirzel et al., 2006). Because of inaccurate assessment of absence data, inadequate geographical sampling and sampling biases, HSI models, compared with other models, can generate superior model performance and reliable prediction in ecological studies (Jones et al., 2012; Li et al., 2014). Therefore, HSI models have been widely used to predict the spatio-temporal distribution of suitable habitats for both long-lived and short-lived fish species (Yen et al., 2012; Chang et al., 2013; Alabia et al., 2015). For example, Yu et al. (2015) developed an integrated HSI model to evaluate variability of habitat suitability for O. bartramii under anomalous environments during 1998–2009.

Dosidicus gigas supports the largest squid fishery in the world (Rocha and Vega, 2003). Understanding the process that D. gigas reacts to climate variability is an essential step towards their better management. However, to our knowledge, the interaction between the habitat of D. gigas and the large-scale climate change has not yet been examined. In this study, we apply an integrated HSI model to time-series fishing effort and landing data of D. gigas collected from the fishing ground in the Southeast Pacific Ocean off Peru to extract the main features of variability in the spatial distribution of their suitable habitat. The HSI model involves with three environmental variables including SST, Chl a and sea surface height anomaly (SSHA), which have been found to be strongly correlated with squid abundance in previous studies (Robinson et al., 2013). The objectives of this study are (i) to quantify the relationship between the key environmental variables and spatial distribution of D. gigas, (ii) to characterize and identify the squid suitable habitat over times, and most importantly (iii) to evaluate the effects of the large-scale climate variability (El Niño and La Niña events) on the variations of optimal habitat.

Material and methods

Fishery data

The fishery data of D. gigas from the fishing ground between 8°–20°S and 95°–75°W were available from the Chinese Squid-Jigging Technology Group of Shanghai Ocean University. Spatial resolution of the data was 0.5 × 0.5° latitude/longitude grid. Fishing operations were performed outside the EEZ off Peru. The fishery was operated from January 2006 to December 2013 with a monthly temporal resolution. Data included catch (tons), fishing effort (in fishing days), and fishing location (latitude and longitude). The nominal catch per unit effort (cpue) was calculated using the following equation (Chen et al., 2010):

\[ cpue_{ymij} = \frac{\sum \text{Catch}_{ymij}}{\sum \text{Effort}_{ymij}}, \]

where \( cpue_{ymij} \) was the monthly nominal cpue (tons [t] / days [d]) at longitude \( i \), latitude \( j \) in month \( m \), and year \( y \); \( \sum \text{Catch}_{ymij} \) was the total catch for all the fishing vessels within a fishing grid at longitude \( i \), latitude \( j \) in month \( m \), and year \( y \); and \( \sum \text{Effort}_{ymij} \) was the sum of fishing days of all the fishing vessels within a fishing grid at longitude \( i \), latitude \( j \) in month \( m \), and year \( y \).

Environmental data

The SST, SSHA, and Chl a data on the fishing ground off Peru were obtained from remotely sensed satellite database. The data covered period from January to December over 2006–2013. Monthly SST data derived from the composite Advanced Very High Resolution Radiometer (AVHRR) were sourced from the Live Access Server of National Oceanic and Atmospheric Administration (NOAA) OceanWatch as well as monthly SSHA data (http://oceanwatch.pifsc.noaa.gov/las/servlets/dataSet). Monthly MODIS Chl a data were obtained from the Asia-Pacific Data-Research Center, University of Hawaii (http://apdrc.soest.hawaii.edu/data/data.php). The spatial resolution was 0.1° × 0.1°, 0.25° × 0.25°, and 0.05° × 0.05°, respectively, for AVHRR SST, SSHA, and MODIS Chl a data. Before the environmental data were compiled for analysis, they were averaged on a 0.5 × 0.5° latitude/longitude grid to match the fishery data.
Climate index
In this study, we focused our analyses on the effects of the ENSO phenomenon (\textit{El Niño} and \textit{La Niña} events) on the suitable habitat of \textit{D. gigas}. The definition for \textit{El Niño} and \textit{La Niña} events was based on the 3-month running mean of SST anomalies in the Niño 3.4 region (\textdegree S–\textdegree S, 120°–170°W). The Oceanic Niño 3.4 indices over 2006–2013 were achieved from the NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoeyears.shtml). The \textit{El Niño} and \textit{La Niña} events were measured by the SSTs above or below a threshold of \( \pm 0.5 \)°C over at least 5 consecutive months, respectively. The intensity for each \textit{La Niña} and \textit{El Niño} event could be identified through the website (http://ggweather.com/ensoenoni.htm).

Developing the HSI model
Model assumptions
Model assumptions were given as follows: (i) the HSI model had considered most important environmental variables (SST, Chl \( a \), and SSHA); (ii) all the variables included in the model were independent and had equal influence in defining the suitable habitat for \textit{D. gigas}; (iii) fishing effort included in the HSI model was assumed to be proportional to squid distribution across the range of environmental conditions, which might not be the case if environments (e.g. SST) influenced squid catchability; and (iv) the relationship between the distribution of \textit{D. gigas} and the integrated influence of the three variables could be quantified by mathematical equations (Eastwood and Meaden, 2004; Song and Zhou, 2010).

Structure of HSI model
The first step in construction of the HSI model was to determine the suitability index (SI), which quantified the probability of species availability. We determined the SI model for each environmental variable as was explained in the study by Yu et al. (2015). For details in this study, refer to Supplementary material S1.

An integrated HSI model combined all the key environmental variables to describe the suitability of a given habitat of species. We then structured the integrated HSI model using two empirical algorithms: one was arithmetic mean model (AMM) (Hess and Bay, 2000; Chang et al., 2013) and the other was geometric mean model (GMM) (Lauer et al., 2002; Tomsic et al., 2007). Both models had been frequently used to estimate the habitat suitability. The equations were described as:

\[
\text{HSI}_{\text{AMM}} = \frac{S_{\text{Chl}a} + S_{\text{SST}} + S_{\text{SSHA}}}{3},
\]

\[
\text{HSI}_{\text{GMM}} = \sqrt[3]{S_{\text{Chl}a} \times S_{\text{SST}} \times S_{\text{SSHA}}},
\]

where \( S_{\text{Chl}a} \) was suitability value for Chl \( a \) concentration, \( S_{\text{SST}} \) was suitability value for SST, and \( S_{\text{SSHA}} \) was suitability value for SSHA. Fishery and remote sensing environmental data over 2006–2012 were used for HSI modelling. The HSI values ranged from 0 to 1, and the fishing grounds with HSI \( \geq 0.6 \) were considered as optimal-suitable habitat for \textit{D. gigas} in the Southeast Pacific Ocean off Peru (Tian et al., 2009).

HSI model selection and validation
All the HSI values were clustered into five HSI groups from 0.0 to 0.2, from 0.2 to 0.4, from 0.4 to 0.6, from 0.6 to 0.8, and from 0.8 to 1.0, respectively (Tian et al., 2009). We compared the percentage of total catches and fishing efforts in each HSI group obtained from the AMM-based and GMM-based HSI models from January to December during 2006–2012. A good HSI model would yield a high consistency between the optimally suitable habitat with HSI \( \geq 0.6 \) and productive catches and high fishing efforts, and low percentages of catches and fishing efforts would occur in poor habitat with HSI \( \leq 0.4 \) (Li et al., 2014). This criterion was used to evaluate and select HSI models to predict habitat suitability.

In addition to the criterion used above for comparing spatial distribution of HSI values and fisheries catches and efforts, environmental data in 2013 were used to predict the spatial distribution of HSI values derived with the AMM and GMM models for each month. Fishing effort frequencies were then overlaid on the predicted HSI maps to test and validate the HSI modelling results (Chang et al., 2013). Both the procedures described above for the HSI model selection and validation could guide us choose a more suitable HSI model to evaluate the effects of climate variability on habitat suitability for \textit{D. gigas} on the fishing ground off Peru.

Evaluating the effects of climate variability on habitat suitability
Annual spatial and temporal distributions of HSI values over 2006–2012 were predicted by the more suitable HSI model identified in this study. We then evaluate the effects of ENSO events on habitat suitability using the following procedures:

(i) Correlation analysis was conducted between the latitudinal gravity centre of fishing effort (LATG) and the average latitude of the areas with HSI \( \geq 0.6 \) on the fishing ground of \textit{D. gigas}. We attempted to examine how the fishing locations varied with the suitable habitat of \textit{D. gigas}. In this study, the LATG was expressed as (Chen et al., 2012):

\[
\text{LATG}_i = \frac{\sum (\text{Latitude}_i \times \text{Effort}_i)}{\sum \text{Effort}_i},
\]

where \( \text{Latitude}_i \) was the latitude of the \( i \)th fishing grid of 0.5 \times 0.5° in month \( m \); \( \text{Effort}_i \) was the total fishing efforts in the \( i \)th fishing grid in month \( m \).

(ii) Monthly HSI values on the fishing ground were averaged during 2006–2012. To identify the variability of HSI, we smoothed the monthly average HSI values with a 3-month running mean filter and compared with the Niño 3.4 indices. To determine whether or not there were time-lagged effects of ENSO events on the squid habitat, the relationship between the monthly average HSI values and Niño 3.4 indices was further evaluated using cross-correlation plots, with a significance level of \( p < 0.05 \) for time-lags of months (Postuma and Gasalla, 2010).

(iii) During 2006–2012, the oceanic environments experienced large fluctuations, two \textit{El Niño} and five \textit{La Niña} events were observed (Table 1). To have a spatio-temporal consistency to examine interannual changes of environmental conditions and squid suitable habitat, fishing months from January to March in 2006, 2008–2012 and from September to December in 2006, 2007, and 2009–2011 were chosen as our study time duration in this section. All the selected fishing months in these years corresponded to an anomalous environmental event (\textit{El Niño}/\textit{La Niña}) (Table 1). Monthly HSI contour maps in these years were created, as well as the evaluation of the suitable habitat areas (defined by the total fishing units with HSI \( \geq 0.6 \) occupying the waters on the fishing ground) and total catches for each month.
Table 1. The Oceanic Niño Index in the Niño 3.4 region (5°S-5°N, 120-170°W).

<table>
<thead>
<tr>
<th>Month</th>
<th>January</th>
<th>February</th>
<th>March</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
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<th>October</th>
<th>November</th>
<th>December</th>
</tr>
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<tbody>
<tr>
<td>2006</td>
<td>-0.9</td>
<td>-0.7</td>
<td>-0.5</td>
<td>-0.3</td>
<td>0.0</td>
<td>0.1</td>
<td>0.2</td>
<td>0.3</td>
<td>0.5</td>
<td>0.8</td>
<td>1.0</td>
<td>1.0</td>
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<tr>
<td>2007</td>
<td>-0.7</td>
<td>0.3</td>
<td>-0.1</td>
<td>-0.2</td>
<td>-0.3</td>
<td>-0.3</td>
<td>-0.4</td>
<td>-0.6</td>
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<td>-1.1</td>
<td>-1.2</td>
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<tr>
<td>2008</td>
<td>-1.5</td>
<td>-1.5</td>
<td>-1.2</td>
<td>-0.9</td>
<td>-0.7</td>
<td>-0.5</td>
<td>-0.3</td>
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<td>-0.1</td>
<td>-0.2</td>
<td>-0.5</td>
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<tr>
<td>2009</td>
<td>-0.8</td>
<td>-0.7</td>
<td>-0.5</td>
<td>-0.2</td>
<td>0.2</td>
<td>0.4</td>
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<td>2010</td>
<td>1.6</td>
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<td>-0.9</td>
<td>-1.2</td>
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<td>-1.5</td>
<td>-1.5</td>
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<tr>
<td>2011</td>
<td>-1.4</td>
<td>-1.2</td>
<td>-0.9</td>
<td>-0.6</td>
<td>-0.3</td>
<td>-0.2</td>
<td>-0.2</td>
<td>-0.4</td>
<td>-0.6</td>
<td>-0.8</td>
<td>-1.0</td>
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<tr>
<td>2012</td>
<td>-0.9</td>
<td>-0.6</td>
<td>-0.5</td>
<td>-0.3</td>
<td>-0.2</td>
<td>0.0</td>
<td>0.1</td>
<td>0.4</td>
<td>0.5</td>
<td>0.6</td>
<td>0.2</td>
<td>-0.3</td>
</tr>
</tbody>
</table>

Blue and red shading indicates La Niña and El Niño events, respectively. Green shading indicates normal climate condition. Boxes indicate fishing periods selected to evaluate the effects of climate variability on the habitat suitability for D. gigas in the Southeast Pacific Ocean.

Figure 1. Monthly variations of nominal cpue and fishing effort (in number of fishing days) of D. gigas for the Chinese squid-jigging fishery in the Southeast Pacific Ocean during 2006–2013.

Results

Temporal variability of cpue and fishing effort of D. gigas

Monthly cpue and fishing effort of D. gigas fluctuated in the Southeast Pacific Ocean off Peru (Figure 1), both decreasing gradually from January to March then increasing from April to December. Catch per unit effort was high in July to February, ranging from 4.40 to 6.64 t d⁻¹. The lowest cpue occurred in April with a value of 2.52 t d⁻¹. High frequencies of fishing effort were found through July to December. However, fishing efforts tended to be relatively low from April to June.

HSI model selection

The statistical assessments of each SI model were included in Supplementary material S2. Statistical analyses for these SI models were all significant (p < 0.05) mostly with high correlation coefficients of spline smooth regression models. This suggested that our modelling assumptions were satisfied. We further defined the optimal range of each environmental variable, which tended to vary with fishing months (see Supplementary material S3).

Results of comparison between the AMM- and GMM-based HSI models were provided in Supplementary material S4. Through the comparison, the AMM-based HSI model yielded a better model performance and was considered to be more appropriate to estimate the squid habitat suitability than the GMM-based HSI model.

We used both the AMM and GMM methods to predict of spatial distributions of HSI values from January to December in 2013 in the Southeast Pacific Ocean off Peru (see Supplementary material S5). The AMM model was found to yield more reliable predictions of the optimal habitat for D. gigas. Thus, we applied the AMM-based model to estimate the HSI values on the fishing ground of D. gigas over 2006–2012 in the subsequent analyses.

Distribution of fishing efforts in relation to squid suitable habitat

During 2006–2012, the monthly LATG fluctuated from 10.5°S in July 2007 to 19.1°S in April 2012, with relatively small variabilities in 2006 and 2011 (Figure 2a). Fishing efforts showed seasonal migrations in each year. Annual LATG initially moved southward during the early fishing months then shifted northward in the following months. Similar to the movement pattern of the LATG, the monthly average latitude of areas with HSI ≥ 0.6 varied from 13.5°S in January 2008 to 16.7°S in April 2008. Correlation analyses suggested a statistically significant positive relationship between the monthly average latitude of suitable habitat and the LATG over 2006–2012 (r = 0.453, p < 0.001).

Relationship between the Niño 3.4 indices and habitat quality

The average HSI value on the fishing ground was used to describe the habitat quality for D. gigas. It ranged from 0.38 in February 2010 to 0.74 in November 2010 and showed high-frequency variability (Figure 2b). We used a 3-month running mean filter to smooth this time-series data, which were then compared with the Niño 3.4 indices. High average HSI values were found to coincide with low Niño 3.4 indices. The cross-correlation analysis highlighted a significantly negative relationship between the average HSI values and Niño 3.4 indices with time-lags from −1 to 3 months. The highest correlation occurred at a 2-month time-lag with a correlation coefficient value of −0.31 (Figure 2c).

Variability in suitable habitat area and catch of D. gigas corresponding to different ENSO events

Contour maps of HSI values for D. gigas during January to March in 2006 and 2008–2012 were exhibited in Figure 3a. The predicted favourable habitats in January and March appeared to be larger than those in February. Suitable habitat tended to be shrunk in January 2008, February 2010 and 2012 and March 2010. Suitable habitat areas, measured as the total number of fishing cells, tended to increase in La Niña years (e.g. 2006, 2008, 2009, 2011 and 2012) and decrease in El Niño years (e.g. 2010) (Figure 4a). The El Niño event in 2010 resulted in a large decrease in the area of suitable habitat. Such variability directly influenced the catch of D. gigas, leading to extremely low catches in 2010 with 894 t in January, 906 t in February, and 867 t in March (Figure 4a). However, the catches in other years were generally higher than 1000 t. The largest catch was even up to 4153 t in January 2011.
The predicted suitable habitat during September to December showed a similar variability as fishing months from January to March. The La Niña events were likely to enlarge the suitable habitat area in 2007, 2010, and 2011 (Figures 3b and 4b). However, the habitat in 2006 and 2009 was affected by the El Niño events, resulting in a significant decline of suitable habitat areas (Figures 3b and 4b). Correspondingly, the La Niña events yielded high squid catches in 2007, 2010, and 2011, especially in 2010 and 2011 but with relatively low catches from September to November in 2007. Monthly catches in these years gradually increased. The highest catch was 4359 t in November 2011. On the contrary, the El Niño events in 2006 and 2009 led to poor catches with an exception in October 2009, the lowest catch was only 548 t in December 2009 (Figure 4b).

**Discussion**

The *D. gigas* stock was widely distributed in the study area which was well covered by Chinese squid-jigging vessels. Our study included monthly fishery and environmental data over a relatively long period from 2006 to 2013. Thus, the information included in this study could essentially present the key habitat characteristics and habitat selection of this squid stock and capture the linkage between squid habitat and environmental variables. Our dataset also included alternate positive and negative Niño 3.4 indices, covering several occurrences of El Niño and La Niña events, as well as the normal climate conditions (Table 1). This allowed us to evaluate the potential effects of interannual climatic and environmental variations on squid habitat by evaluating a few typical scenarios. We developed an integrated HSI model for *D. gigas* to identify optimal habitats in the Southeast Pacific off Peru. Our findings exhibited substantial plasticity of habitat suitability for *D. gigas* in response to climate variability (i.e. ENSO events), as shown by the fishing effort and catch data from the Chinese squid-jigging fishery (Figures 3 and 4). The La Niña events tended to increase suitable habitat for *D. gigas* and result in high squid catches; while the El Niño events were likely to reduce favourable habitat areas, consequently leading to great declines in catches. The HSI modelling method in this study improved our understanding of the
relationship between *D. gigas* distribution and habitat/climate change over broad geographical areas in the Southeast Pacific Ocean.

In this study, fishing effort data were used to estimate the probability of squid occurrence. From the *SI* curves, we could find that fishing efforts were not randomly distributed in relation to environmental conditions (see Supplementary material S3). High fishing efforts reflected that large amounts of fishing vessels were concentrated in an area, indicating that environmental conditions in the area were favourable for squid and consequently drove massive squid aggregations and attracted fishing vessels (Chen *et al.*, 2010). In fact, environmental conditions determined the spatio-temporal distribution of targeted species, and ultimately governed the dynamics of fisheries (e.g., for other squid species such as *Loligo plei*; Postuma and Gasalla, 2010). The rapid response of cephalopod to environmental cues made this group more susceptible to changes in habitat hotspots (Pierce *et al.*, 2008), which greatly

Figure 3. Spatial distribution of predicted *HSI* values based on the AMM-based *HSI* model (a) from January to March in 2006 and 2008–2012; (b) from September to December in 2006, 2007, and 2009–2011. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.
influenced the location of productive fishing ground and subsequent distribution of fishing vessels. Thus, fishing efforts could be identified as a reliable proxy indicator of squid abundance for detecting suitable habitat in HSI models.

The cpue was often considered as an abundance index for pelagic species and had wide applications in the HSI modelling (Chen et al., 2009; Yen et al., 2012). However, for ommastrephid squid, Tian et al. (2009) developed cpue-based and fishing effort-based HSI models for O. bartramii and compared their predictive performances. The cpue-based model tended to yield larger biases and uncertainties than the fishing effort-based model. Previous studies that developed HSI models for squid species did not consider cpue in analyses (Chen et al., 2010; Yu et al., 2015). Therefore, we did not embed the cpue data into the HSI model for D. gigas in our study.

We sourced the environmental variables with high spatial resolutions from the remote sensing satellite data, which provided temporally resolved synoptic views of broad ocean regions and could detect the potential oceanographic processes affecting squid stocks (Klemas, 2013). This study included SST, Chl a, and SSHA in the HSI model, largely depending on their critical roles in regulating squid habitats (Arkhipkin et al., 2015). From the SI curves (see Supplementary material S3), we found that the habitat characteristics for D. gigas in the Southeast Pacific off Peru might differ from various suitable ranges of environmental factors over time. There were some efforts evaluating the habitat preference for D. gigas. For example, Hu and Chen (2008) suggested that the monthly suitable range of SST for D. gigas off Peruvian waters tended to be from 21 to 23°C in June, from 19 to 21°C in July, from 18 to 20°C in August, from 18 to 21°C in September, from 18 to 21°C in October, and from 18 to 21°C in November, respectively. Fang et al. (2014) examined the fishing effort distributions in relation to Chl a concentration, and found that fishing operations for D. gigas in the high seas off Chile mostly took place in the regions with Chl a between 0.12 and 0.23 mg m⁻³ in March, between 0.20 and 0.37 mg m⁻³ in April and between 0.08 and 0.31 mg m⁻³ in May, respectively. These results were consistent with our findings. Although the SSHA field was characterized by the function of creating hydrodynamic trap of prey, which tended to be an important factor for habitat formation of pelagic species by yielding favourable feeding conditions (Zagaglia et al., 2004). However, few studies included it in studying D. gigas habitats. We suggested that the monthly suitable ranges of SST, Chl a, and SSHA synergistically formed suitable habitats and should be used for identifying and exploring the most optimal habitat for D. gigas.

Other than the AMM- and GMM-based models, there were many different empirical HSI models in ecological studies, such as the continued product model (CPM) (Chen et al., 2008b), the minimum model (MINM) (Van der Lee et al., 2006), the maximum model (MAXM) (Guo and Chen, 2009), the weighted mean model (Li et al., 2009), and the weighted geometric model (Vincenzi et al., 2006). Clearly, different HSI models would yield different spatial distribution of HSI values. For the CPM and MINM, their results tended to be too conservative, but for the MAXM, its results were overly optimistic (Gong et al., 2011). The AMM and GMM models were the most widely used aggregating methods to...
yield a composite $H_{SI}$. The AMM was based on the assumption that high $H_{SI}$ values on one variable could compensate for low $H_{SI}$ values on another one. Whereas the $S_I$ variables in the GMM model were assumed to be independent but also compensative (Chang et al., 2013). In this study, we identified a more suitable model between the AMM and GMM methods through two steps. The first step was to compare the performance of the AMM- and GMM-based $H_{SI}$ models in predicting monthly catch and fishing effort distributions within each $H_{SI}$ group over 2006–2012 (see Supplementary material S4). The second step was to validate and compare the two models in their prediction of the $H_{SI}$ values in 2013 (see Supplementary material S5). The AMM model was shown to perform better than the GMM model because of a strong agreement between the high $H_{SI}$ values and large proportions of fishing efforts and high catches (see Supplementary material S4 and S5). Therefore, the two steps help select a suitable $H_{SI}$ model and serve as a strong basis to predict habitat suitability in a changing climate.

We predicted the annual $H_{SI}$ values for 2006–2012. Significant positive relationship was found between the latitudinal gravity centre of fishing effort and the average latitude of suitable habitat (Figure 2a), suggesting that the model constructed in this study realistically reflected what were observed in the fishery. Monthly movement of suitable habitat tended to be consistent with changes in the location of fishing sites. This might be explained by the fishing behaviours of Chinese fishermen. Fishers fish in areas with high squid catch rates. Once the catch or the catch rates dropped, they quickly moved to another area with high squid density (i.e. habitat hotspots) (Li et al., 2014). Thus, fishing effort gravity centres closely followed the distribution of suitable habitat for high squid abundance. Cross-correlation analysis showed a significantly negative correlation between the average $H_{SI}$ on the fishing ground and the Niño 3.4 indices with time-lags of around 1 and 3 months (Figure 2c), indicating that the squid reacted quickly to climate variability. Variations in the SST anomaly in the Niño 3.4 region greatly affected the habitat of $D. gigas$ in the Southeast Pacific Ocean. High Niño 3.4 indices would yield poor squid habitat quality, while low Niño 3.4 indices were likely to sustain good habitat conditions. Climate indices such as the Niño 3.4 index and the Antarctic
Oscillation index could be used as crucial environmental parameters to predict squid habitat quality (Chen et al., 2007; Chang et al., 2015).

Outputs from the HSI model suggested that both suitable habitat areas and catches of *D. gigas* increased in the *La Niña* periods and decreased in the *El Niño* periods. This raised an interesting question: how did the critical environmental factors drive the variability in squid suitable habitat areas during a year corresponding to an *El Niño* or a *La Niña* event? To address this question, we took the fishing months with high squid abundance from September to December as an example to examine the variations in environmental conditions in the years of 2006, 2007, 2009, 2010, and 2010. Years 2006 and 2009 were *El Niño* years, while 2007, 2010, and 2011 were *La Niña* years. We found that cold surface waters and high Chl *a* extended to entire fishing grounds in the Southeast Pacific Ocean off Peru during 2007, 2010, and 2011. However, opposite patterns occurred in 2006 and 2009 (Figure 5). Furthermore, the SSHA was elevated in 2006 but reduced in 2007 (Figure 6). We combined these results to identify potential mechanisms to explain how large-scale climate variability might influence squid habitat by changing oceanographic processes in this study: the *La Niña* conditions resulted in weakened upwelling coupled with cool and nutrient-enhanced waters, which yielded favourable habitat conditions and high catches; whereas the *El Niño* conditions resulted in weakened upwelling coupled with warm and nutrient-depleted waters, which were unfavourable for the squid and reduced catches.

It was clear that changing climatic and environmental conditions affected the *D. gigas* stock levels. Variability in the upwelling and primary productivity was one of the most important factors contributing to the *D. gigas* population dynamics (Walada et al., 2006; Robinson et al., 2013). Identifying the critical factors influencing the spatial distribution of suitable habitat for *D. gigas* could help make effective fisheries management policies (Su et al., 2011). However, we found that significant importance of environmental drivers to squid distribution was generally ignored in stock assessment. Our study implemented a comprehensive evaluation of habitat of *D. gigas*. The thermal condition, food density, and SSHA field associated with large-scale climate variability (e.g. ENSO events) would result in strong shifts in the habitat distribution of this species. We suggested to use the HSI model to predict the optimal fishing ground of *D. gigas* and to explore habitat–environment interactions. However, inevitably, there were some biases in the HSI model. We did not differ the role of each environmental variable. Another issue was that the fishery data in the coast of Peru were not included, which limited the study area and reduced the contrast of environmental data. Further analysis was required in the future by considering the weights of environmental variables and collecting more fishery data through international cooperation.

**Supplementary data**

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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