Climate-related changes in seasonal habitat pattern of *Sthenoteuthis oualaniensis* in the South China Sea

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Introduction

The purpleback flying squid *Sthenoteuthis oualaniensis*, an ommastrephid squid species with fast growth rate, high reproductive capacity and short-lived lifecycle, is predominately distributed in the tropical and subtropical waters between 40°N and 40°S throughout Indo-Pacific regions (Nesis 1977; Dong 1991). Within the broad habitats in the worldwide oceans, *S. oualaniensis* has complex population structures. Its mantle length, spawning season, food, and other biology characteristics show large differences with different geographical distribution (Chen, Liu et al. 2007; Li et al. 2019). As with other ommastrephid squids, *S. oualaniensis* occupies an important position in the marine ecosystems and food webs, serving as a critical role of connecting large-size marine mammals and small fish as well as zooplankton and phytoplankton (Parry 2006, 2008). In the South China Sea, *S. oualaniensis* is one of the most abundant squids and contributes an important fishery for China and other neighboring countries (Fang et al. 2013). The population of *S. oualaniensis* from South China Sea usually performs horizontal and vertical migrations. This squid commonly migrates from offshore waters to coastal regions for breeding from March to May in spring. In the daytime, *S. oualaniensis* inhabits in the waters at depths deeper than 300 m and moves to the sea surface layer to feed at night (Harman et al. 1989; Young and Hirotta 1998). Due to its high economic values, *S. oualaniensis* has been commercially exploited by Chinese large-scale light falling-net fishery in the South China Sea (Zhang et al. 2010). The stock biomass of *S. oualaniensis* resources is at 3–4 million tons and 5–7 million tons in the Indian Ocean and in the Pacific Ocean, respectively (Zuyev, Nigmatullin, and Chesalin et al. 2002). The estimated stock biomass of *S. oualaniensis* in the South China Sea is up to 1.5 million tons using acoustic survey data and the logbook data (Zhang et al. 2014). Therefore, the *S. oualaniensis* resources in the South China Sea have important exploitation potentials.

The abundance and spatial distribution of Ommastrephid squids are strongly influenced by large-scale climate variability and regional environmental conditions (Anderson and Rodhouse 2001; Yu et al. 2015). Various anomalous climatic events occur will quickly induce the changes of local environments on the fishing and spawning grounds of squid species,
leading to the spatial shifts of breeding and feeding habitats and abundance variability (Cao, Chen, and Chen 2009; Postuma and Gasalla 2010). Consequently, squid abundance varies a lot and the locations of fishing ground undergo large movement with the changing environments, and annually squid catches for squid-jigging fisheries from different countries become fluctuant (Sakurai et al. 2002; Medellin-Ortiz, Cadena-Cárdenas, and Santana-Morales 2016; Igarashia et al. 2017). For example, in the western North Pacific Ocean, the neon flying squid Ommastrephes bartramii is dramatically affected by the El Niño-Southern Oscillation (ENSO) and critical environmental factors, such as sea surface temperature (SST), sea surface height anomaly (SSHA), and net primary production (NPP). Under different ENSO conditions, O. bartramii exhibits various densities and spatial distribution pattern. Climate-regulated environmental changes strongly dominate the O. bartramii fisheries in Mainland China, Japan, and Chinese Taipei (Chen, Zhao, and Chen 2007; Alabia et al. 2016). Additionally, the jumbo flying squid Dosidicus gigas in the Eastern Pacific Ocean has closely linkage with anomalous oceanographic and atmospheric conditions at various spatial and temporal scales. Climate variability, interannual oceanic oscillations and extreme events present a significant impact on D. gigas fisheries in the Gulf of California, Costa Rica, Equator, Peru, and Chile (Waluda, Yamashiro, and Rodhouse 2006; Ichii et al. 2002; Frawley et al. 2019). Given the importance of Ommastrephid squid in the global fisheries, assessing the impacts of changing environments can have significant implications for fisheries management.

The South China Sea is a deep semi-enclosed rhombus-shaped ocean basin and is the largest marginal sea of the western Pacific (Peng et al. 2018). It connects with the Pacific Ocean through the Luzon Channel (Nan, Xue, and Yu 2015). The local physical, chemical, and biological environmental conditions in the South China Sea are very complex and are associated with the El Niño phenomenon (Wang et al. 2006). For S. oualaniensis stock in the South China Sea, most studies focus on its biology characteristics including age, growth, stomach content, population structure, breeding, and so on (Fang et al. 2013). Regarding to the relationship between S. oualaniensis stock and marine environments, previous studies have concluded that environmental changes in Xisha-Zhongsha waters present a critical role in regulating spatio-temporal distribution of S. oualaniensis, especially showing strong correlations with SST, Chlorophyll-a concentration (Chla), and sea surface height (SSH) anomaly (Xu et al. 2016; Yu et al. 2017; Fang et al. 2019). However, up to now, seasonal habitat pattern of S. oualaniensis in the South China Sea and its relationships with some critical environmental variables are still unknown. Especially, how the large-scale climate variability such as the El Niño event affects the local environments on the fishing ground and further spatial and temporal distribution of suitable habitats of S. oualaniensis are still unclear. It is essential to evaluate the habitat quality for this squid on a seasonal timescale and connect it to some critical environmental factors.

At the present study, a habitat suitability index (HSI) modeling approach was applied to examine seasonal habitat pattern of S. oualaniensis in the South China Sea from spring to autumn using three critical environmental factors including SST, Chla, and SSH. Suitable habitats of S. oualaniensis were detected for each season and its formation mechanism was explored. The impacts of the El Niño event on habitat variations of S. oualaniensis were also evaluated. The objectives of the present study were to (1) identify the seasonal habitat pattern of S. oualaniensis from spring to autumn; (2) explore the relationship between spatio-temporal distribution of habitat and regional environments; (3) assess the impacts of changing climate conditions (i.e., the El Niño event) on habitat variations of S. oualaniensis in the South China Sea.

Materials and methods

Fisheries and environmental data

The fisheries data of S. oualaniensis in the South China Sea were obtained from the South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences. The spatial and temporal resolution of the data was 0.5°×0.5° and month. All the sampling data located in the main fishing ground between 5°–16°N and 110°–119°E in the offshore waters of South China Sea from 2014 to 2017 (Figure 1). Data information included fishing time (year and month), fishing location (longitude and latitude) and fishing effort (defined as number of fishing vessels per day). Fishing vessels that applied fishing lamps mainly located in waters with abundant fish, and fishermen were likely to leave when the catch rate decreased, which implied that an area with high fishing efforts indicated the occurrence of a certain suitable habitat for fish species (Chang et al. 2018). Thus, fishing effort was used to build the habitat model.

Data was aggregated into seasonal resolution inclusive with spring (March to May), summer (June to August) and autumn (September to November). Most of the Chinese light falling-net fishing vessels targeted S. oualaniensis in the South China Sea had the total tonnage of about 420 t with the length of 40–50 m, the width of 10–15 m and the depth of 4–6 m. Each fishing vessel was equipped with a main engine power of 280 KW × 2 and squid-attracting lamp power of 2000 W × 230. The main size of the net was about 281.60 m × 81.76 m with the maximum mesh size of
variables, the probability of squid occurrence (referring to the observed suitability index, SI) in various environmental ranges were calculated (Chen et al. 2010; Yen, Wang, and Lu 2017).

Then, the observed SI values combined with the class interval were applied to fit the SI curves for each environmental variable. The SI models were fitted by the following equations (Yu et al. 2016):

\[ SI_{\text{SST}} = \exp \left[ a \times (\text{SST} - b)^2 \right] \]
\[ SI_{\text{Chla}} = \exp \left[ a \times (\text{Chla} - b)^2 \right] \]
\[ SI_{\text{SSH}} = \exp \left[ a \times (\text{SSH} - b)^2 \right] \]

where a and b were the model parameters: SST, Chla, and SSH was the value of each class interval. The observed SI was drawn as well as the fitted SI curve to compare the model performance. Each SI model was statistically analyzed. Suitable environmental ranges for \textit{S. oualaniensis} in the South China Sea were identified as SI>0.6.

The next step was to establish the integrated HSI model for \textit{S. oualaniensis} in the South China Sea by combining all the SI models based on the Arithmetic Mean Method (AMM). The equation of the HSI model in this study was developed as (Li et al. 2014):

\[ HSI = \frac{1}{n} \sum_{i=1}^{n} (SI_{\text{SST}} + SI_{\text{Chla}} + SI_{\text{SSH}}) \]

where \( SI_{\text{SST}}, SI_{\text{Chla}} \), and \( SI_{\text{SSH}} \) were the predicted SI values on the fishing ground for SST, Chla, and SSH, respectively; n was the number of environmental factors in the HSI model. The HSI values ranged from zero to one. Zero indicated the most unfavorable habitats, whereas one indicated the most favorable habitats for \textit{S. oualaniensis} stock. In addition, the area with HSI<0.2, with 0.2≤HSI<0.6 and with HSI≥0.6 was defined as poor, common, and suitable habitat, respectively, for \textit{S. oualaniensis} stock in the South China Sea (Yu and Chen 2018).

Finally, the HSI model from spring to autumn was tested and validated by the following three steps. First, the fisheries and environmental data from 2014 to 2016 were used to develop the HSI model. All the SI models were statistically evaluated. Second, the actual fisheries data in 2017 were used to validate the HSI model. The predicted HSI values on the fishing ground of \textit{S. oualaniensis} stock in the South China Sea in 2017 were drawn overlapped with fishing efforts. Third, in order to examine the HSI model performance, the percentage of fishing effort and number of grids were determined within different HSI class interval (0.0–0.2; 0.2–0.4; 0.4–0.6; 0.6–0.8; 0.8–1.0) from spring to autumn.

**HSI model development, test, and validation**

The relationship between fishing efforts from spring-autumn and environmental variables was initially examined using histogram analysis. SST, Chla, and SSH was divided into class interval of 0.3°C, 0.02 mg/m³ and 4 cm, respectively. Based on the total number of fishing efforts in each class interval of different fishing vessels operated at night with few bycatch. In addition, due to winter was not the main fishing time, thus, this season was not included in the analysis in this study.

The environmental variables included SST, Chla, and SSH, which yielded strong impacts on \textit{S. oualaniensis} abundance and distribution. The monthly SST and Chla concentration data from the Moderate Resolution Imaging Spectroradiometer (MODIS) on the satellite Aqua platform were obtained from the Asia-Pacific Data Research Center (http://apdrc.soest.hawaii.edu/data/data.php). The MODIS Aqua nighttime SST data was acquired due to all the squid-jigging fishing activity occurred at night. Both SST and Chla Level-3 composite data were from 2014 to 2017 at 9-km of spatial resolution covering the whole fishing ground of \textit{S. oualaniensis} in the South China Sea. The SSH data were sourced from the eddy-resolving Ocean General Circulation Model for the Earth Simulator (OFES) model (Masumoto et al. 2004; Taguchi et al. 2007). Spatial and temporal resolution of environmental data was 0.1°×0.1° grid cell and month, respectively. All the environmental data were compiled into 0.5°×0.5° and season resolution to match with the fisheries data.

Seasonal variation of habitat pattern and its relationship with El Niño event

To examine the habitat pattern of *S. oualaniensis* in the offshore waters in the South China Sea, the HSI values from 2014 to 2017 were predicted and averaged by season, spatial distribution of HSI values in each season was drawn to compare the areas of poor, common, and suitable habitats. The occurrences of suitable habitats of *S. oualaniensis* by latitude and longitude from spring to autumn during 2014–2017 were further determined to figure out the seasonal spatial variations of favorable habitats. Furthermore, seasonal contour maps of $S_{SST}$ >0.6 overlain with the contour lines of $S_{Chl_a}$>0.6 and $S_{SSH}$>0.6 on the fishing ground of *S. oualaniensis* were mapped to explore the linkage between the favorable environmental conditions and the range and spatial distribution of the suitable habitats for each season. Spatial correlation analysis was performed between the HSI values and each environmental variable (SST, Chla, and SSH) on the fishing ground, and seasonally spatial distribution of correlation coefficients were also drawn.

The El Niño events significantly affected tropical and subtropical oceanic marine animal habitats (Possamai et al. 2018). In order to evaluate the impacts of the El Niño event on potential habitat of *S. oualaniensis* in the South China Sea, there years (spring 2014, 2015, and 2016) were selected to compare the environmental conditions and habitat patterns. Based on the definition of El Niño from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (CPC) (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php), the spring 2014 was a normal climate year, whereas spring 2015 and 2016 were the El Niño years. However, spring 2015 was an El Niño year with very strong intensity, while spring 2016 was El Niño year with relatively weak intensity. Differences in SST, Chla concentration and SSH between 2014 and 2015, and between 2014 and 2016 were initially determined to examine how environmental conditions changed on the fishing ground of *S. oualaniensis* in the South China Sea under different climate conditions. Then, suitable ranges of SST, Chla, and SSH for 3 years on the basis of suitability index higher than 0.6. Spatial distributions of suitable habitat of *S. oualaniensis* were finally compared in spring 2014, 2015, and 2016.

Results

Seasonal variations of environmental conditions

Environmental conditions for SST, Chla, and SSH on the fishing ground of *S. oualaniensis* in the South China Sea exhibited significant seasonal variations (Figure 2). It was observed that SST was the highest in summer and the lowest in winter. And SST in the coastal waters off Vietnam was lower relative to the waters in the high seas for each season. Especially in spring and winter, the waters were lower than 25°C in the nearshore areas off Vietnam. Chla was relatively high in winter comparing to other seasons. Additionally, the Chla density in the coastal regions was much higher than that in the open seas. Regarding to SSH, it was high in spring,
summer and autumn, and low in the winter. Waters with much lower SSH concentrated in the northern regions on the fishing ground of *S. oualaniensis* in comparison with the southern regions from spring to winter.

**Analysis of HSI models**

The SI curve for each environmental factor (SST, Chla, and SSH) was statistically evaluated and drawn in Figure 3. It was found that most SI models from spring to autumn had low Root Mean Square Errors (RMSE) and high correlation coefficient, indicating that the fitted SI models exhibited good model performance and could truly reflect squid-environment relationships. The suitable and optimal SST, Chla, and SSH ranges for *S. oualaniensis* showed dramatically seasonal variations.

The percentages of fishing occurrence and number of grids under each HSI class interval from spring to winter were shown in Figure 4 using data during 2014–2016. Within the HSI class interval between 0.0 and 0.2 (i.e., the poor habitat of *S. oualaniensis*), the fishing efforts and grids accounted for the lowest percentages in the three seasons. Most fishing efforts occurred in the normal and suitable habitats with the HSI class interval higher than 0.2. The suitable habitat (HSI higher than 0.6) yielded the highest fishing efforts, suggesting that most fishing operations occurred in the favorable habitats.

The HSI values from spring to autumn in 2017 were predicted and overlaid with the actual fishing efforts (Figure 5). Clearly, most fishing efforts were distributed in the regions with higher HSI values, especially in the waters with HSI>0.6. In spring 2017, only small percentages of fishing efforts occurred in the western regions of the fishing ground. Based on the above-mentioned analyses, it indicated that the HSI model in this study could yield reliable prediction capacity due to the well consistency between spatial distribution of fishing effort and fishing activity and the quality of the habitat.

**Figure 3.** Seasonal fitted suitability index (SI) curves inferred from the associations between fishing effort and sea surface temperature (SST), Chlorophyll-a (Chla) concentration and sea surface height (SSH) from spring to autumn over 2014–2016.
Spatial and temporal variations in *S. oualaniensis* habitats

Habitat patterns of *S. oualaniensis* in the South China Sea showed significant seasonal and spatial variations in spring, summer and autumn (Figure 6). The poor habitats mainly occurred in spring and summer, and were largely distributed in the coastal waters of Vietnam. In autumn, very few low-quality habitats located in the fishing ground. Relative to the suitable habitat, its range was highest in spring, followed by autumn and lowest in summer. In spring, suitable habitats were mostly bounded within two geographical regions between 5°-13°N, 108°-116°E (the northern part) and between 13°-16° and 113°-119°E (the southern part). However, the suitable habitats in summer became discontinuity, particularly the southern part of favorable habitats contracted and shifted southeastward relative to the spring. Suitable habitats in autumn further moved to the southeastern regions, but its range relatively enlarged.

The longitudinal and latitudinal distributions of suitable habitats from spring to autumn were shown in Figure 7. Suitable habitats were extensively distributed in the latitude between 4.5°-16.0°N and in the longitude between 107.0°-119.5°E but with seasonal variations. The occurrence of suitable habitats by latitude was divided into southern and northern parts with 12° N as the boundary line. Comparing to the summer and autumn, most suitable habitats occupied the southern waters on the fishing ground in spring. With respect to the longitudinal distribution, suitable habitats were largely located in the eastern waters of 108°E. However, favorable habitats of *S. oualaniensis* in spring mostly concentrated in the area between 109°E and

Figure 4. The percentage of fishing occurrence and number of grids under each habitat suitability index (HSI) class interval from spring to winter using data during 2014–2016.
115ºE, then shifted eastward in the regions between 113.5ºE and 119.5ºE.

The spatial distributions of favorable SST, Chla, and SSH were exhibited in Figure 8 on the fishing ground of S. oualaniensis in the South China Sea. The suitable SST was extensively distributed from spring to autumn, while the suitable Chla range was large in spring and low in summer and autumn. In addition, favorable SSH
was obviously divided into northern and southern parts in spring and summer. It was clear that the spatio-temporal pattern of the overlapping regions by the three favorable environmental conditions were consistent with the distribution of suitable habitats of *S. oualaniensis*. Moreover, significant positive correlation was found between SST and HSI, whereas negative relationship was revealed between HSI and Chla as well as SSH on the main fishing ground of *S. oualaniensis* on the basis of spatial correlation analysis (Figure 9).

### Impacts of the El Niño event on *S. oualaniensis* habitats

Large difference was found in the environmental conditions between 2014 and 2015, and between 2014 and 2016 (Figure 10). Comparing to normal climate condition in spring 2014, the El Niño events in spring 2015 yielded much lower SST. The SST in spring 2016 was a little bit higher than that in 2014. Both Chla and SSH in 2015 and 2016 were much higher than those in 2014, which were unfavorable for the formation of high-quality habitats for *S. oualaniensis*. Furthermore, it was observed that the favorable ranges of each environmental variable, especially the suitable SST areas, expanded in spring 2014 comparing to the two years (Figure 11). Consequently, the quality of habitat was high in 2014, but was relatively low in 2015 and 2016. Further, the suitable habitats of *S. oualaniensis* in spring 2014 enlarged, however, it largely contracted and became discontinuity in spring 2015 and 2016 (Figure 12).

### Discussion

Habitat modeling approach has been widely applied to examine species-habitat relationship, identify habitat hotspots and evaluate the impacts of climate variability and oceanographic conditions on spatio-temporal of habitat pattern for pelagic fish species (Tanaka and Chen 2016; Yi et al. 2017; Yu et al. 2019). However, the model prediction performance largely depends on the model inputs, structure, and other factors (Gong et al. 2011; Xue et al. 2017). Therefore, the HSI model accuracy and reliability should be carefully evaluated. Regarding to the HSI model in this study, some issues on the HSI model should be clarified.
Figure 8. Seasonal contour maps of SI_SST>0.6 (suitability index of sea surface temperature (SI_SST) higher than 0.6) overlain with the contour lines of SI_Chla>0.6 (suitability index of Chlorophyll-a (SI_Chla) higher than 0.6) and SI_SSH>0.6 (suitability index of sea surface height (SI_SSH) higher than 0.6) on the fishing ground of Sthenoteuthis oualaniensis from spring to autumn in the South China Sea.

Figure 9. Seasonally spatial distribution of correlation coefficients between the habitat suitability index (HSI) on the fishing ground of Sthenoteuthis oualaniensis and sea surface temperature (SST), Chlorophyll-a (Chla) concentration and sea surface height (SSH), respectively, from spring to autumn in the South China Sea.
First, the selection of SST, Chla, and SSH as the input variables of the HSI model was based on their significant influences on *S. oualaniensis* stock in the South China Sea. Many studies supported the conclusions that the above-mentioned three factors played an important role in regulating the abundance and distribution of *S. oualaniensis* (Xu et al. 2016; Yu et al. 2017, 2019a; Fang et al. 2019). *S. oualaniensis* was a warm water and temperature-sensitive oceanic squid species, its habitat range and distribution was closely associated with SST (Xu et al. 2016). Chla concentration could be regarded as a critical index to indicating the food availability and distribution of *S. oualaniensis* (Yu et al. 2017). As an ocean’s dynamic environmental parameter, SSH could reflect various warm-cold water mass and eddy structure, affecting the formation of *S. oualaniensis* fishing ground (Fang et al. 2013, 2019). Therefore, the three crucial variables were chosen to establish the HSI model.

Second, the relationship between fishing effort of *S. oualaniensis* and each environmental factor was employed to determine the SI values. The fishing effort was not randomly distributed, it followed the distribution range of suitable habitats with high abundance of fish population. Therefore, this study applied the fishing effort to construct the HSI model and predict the probability of squid occurrence with three key environmental factors. Previous studies also stated that fish effort could be used to estimate the SI for other pelagic fish species such as Pacific saury *Cololabis saira* in the Northwest Pacific Ocean (Hua et al. 2020) and chub mackerel *Scomber japonicus* in the East China Sea (Li et al. 2014). For Chinese squid fisheries, large amounts of fishing efforts in a certain area implied lots of fishing vessels concentrated in fishing ground with abundant squids, namely, this area might be a suitable habitat for the targeted squid species (Chen, Liu, and Chen 2008). In addition, CPUE-based (catch per unit effort) HSI model performance was ever compared with fishing

Figure 10. Differences in sea surface temperature (SST) (Upper panel), Chlorophyll-a (Chla) concentration (Middel panel) and sea surface height (SSH) (Lower panel) between 2014 and 2015 in spring (Left panel), and between 2014 and 2016 in spring (Right panel).
effort-based HSI model, results suggested the former model underestimated squid habitat quality, while the latter model yielded reliable habitat prediction ability (Tian et al. 2009). Thus, fishing effort was a better proxy to determine the SI than CPUE.

Third, different environmental factors contributed various influences to habitat variations of S. oualaniensis in the South China Sea. In fact, their importance commonly was different (Fang et al. 2016). There was one conclusion that SST was the most important factor, followed by Chla and SSH, for S. oualaniensis (Yu et al. 2019bb). Actually, it was very difficult to quantify their importance using the fisheries data with finite time series and limited research area (Gong et al. 2011). Therefore, the empirical arithmetic average method was considered as the best method to determine the ultimate HSI value, which showed obvious superior relative to other methods, such as continued product model or maximum/minimum model (Li et al. 2014; Silva et al. 2016). And the HSI model was tested and validated by three methods, our model has good model performance and yield reliable predictions for the habitat suitability for S. oualaniensis.

Fourth, due to the limited in data period and CPUE information, some uncertainties might be occurred in this analysis. For example, the HSI model should be

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**Figure 11.** Suitable ranges of sea surface temperature (SST), Chlorophyll-a (Chla) concentration and sea surface height (SSH) for *Stenoteuthis oualaniensis* in spring 2014 (the year with normal climate condition), 2015 (the El Niño year with very strong intensity) and 2016 (the El Niño year with weak intensity), based on the suitability index higher than 0.6.

**Figure 12.** Spatial distribution of suitable habitat (habitat suitability index higher than 0.6) of *Stenoteuthis oualaniensis* in spring 2014 (the year with normal climate condition), 2015 (the El Niño year with very strong intensity) and 2016 (the El Niño year with weak intensity) in the South China Sea.
compared between CPUE-based model and fishing effort-based model to improve the reliability and accuracy of the habitat prediction. By cooperating with other institutions or countries, future studies should involve more detailed fisheries data of *S. oualaniensis* with long-term time series to develop a comprehensive HSI model and clarify the impacts of the El Niño/La Niña events with different intensity.

Marine species habitat quality and distribution pattern on monthly, seasonal and interannual scale exhibited affinity to regional environmental variations. For example, spatial and temporal variability of habitat distribution of American lobster *Homarus americanus* presented large difference in spring and autumn off coastal waters of New Hampshire and Maine. Habitat suitability showed increasing trend for both sexes and stages (juvenile and adult) in the spring, while no significant trend was observed in the autumn (Tanaka and Chen 2016). Off Chile, geographic distribution of jack mackerel *Trachurus murphyi* habitat also showed seasonal variations and varied from year to year. Changes in the latitudinal gravity center of fishing ground of *T. murphyi* were consistent with latitudinal distribution of suitable habitat (Li et al. 2016). For short-lived squids such as *O. bartramii* in the western Pacific and *D. gigas* in the Eastern Pacific, environmental-related variability of habitat patterns on different scales were highly coincided with variations in CPUE and fishing ground distributions (Yu et al. 2019, 2020).

Habitat patterns of *S. oualaniensis* in the South China Sea including suitable and optimal range of each environmental variable, the ranges of poor/suitable habitat and their longitudinal and latitudinal distributions showed significant seasonal variations from spring to autumn. Firstly, the suitable range of SST was high in summer and low in spring and autumn. Generally, the near-surface waters were relatively warm in summer due to the low latitude and the equatorial current-driven warm waters into the South China Sea (Fang et al. 2016; Yu et al. 2019a, 2019b). With the season shifted, suitable Chla for *S. oualaniensis* was low in summer and relatively higher in spring and autumn, whereas the suitable ranges of SSH increased from spring to autumn. Then, the habitat quality of *S. oualaniensis* was poor in the coastal waters of the South China Sea during the three seasons, especially in spring and summer. *S. oualaniensis* was a pelagic squid species and preferred to inhabit in relatively deep waters rather than shallow areas (Fang et al. 2013). Besides, most of the fishing operations for *S. oualaniensis* occurred in the offshore waters, which might lead to the model biases. Third, seasonal changes in the range and spatial distribution of suitable habitats could be largely explained by the environmental changes of the three variables. The formation of suitable habitats for each season was driven by the overlapping areas of the favorable environmental conditions by the three variables. It was observed that the overlapping areas decreased in summer, thus, the range of suitable habitat of *S. oualaniensis* contracted in this season. Besides, the migration of suitable habitat in the longitudinal and latitudinal directions from spring to autumn was in accordance with the shift of preferred SSH and Chla (i.e., areas with SISSH > 0.6 and SIChla > 0.6). Squid usually preferred to inhabit in the areas with favorable environmental conditions. Once the environments surrounding the original habitat became unsuitable, squids would move to another more suitable habitat (Yu et al. 2015). Therefore, the southeastward shift of favorable environments for *S. oualaniensis* from spring to autumn determined the similar movement pattern of suitable habitat.

Significant associations were found between habitat quality of *S. oualaniensis* and environmental variables. Based on the relationships, it suggested that relatively warmer SST and lower Chla and SSH could yield higher habitat suitability of *S. oualaniensis* in this study. Previous study ever employed generalized additive model (GAM) to evaluate the relationship between the spring CPUE of *S. oualaniensis* in Xisha-Zhongsha waters of the South China Sea and environmental factors (Yu et al. 2019a). They stated that SST within the range of 24–28.5°C had a positive effect on *S. oualaniensis* CPUE. The majority of *S. oualaniensis* stock was mainly distributed in waters with Chla ranging from 0.05 to 0.15 mg/m³. CPUE generally increased with the Chla when the density was lower than 0.2 mg/m³. However, the relationship between Chla and CPUE shifted into negative when Chla density was higher than 0.2 mg/m³. In addition, linearly negative relation was found between *S. oualaniensis* CPUE and SSH anomaly. These conclusions were consistent with our findings. It was important note that squid generally preferred high prey density, but negative relationship was revealed between HSI and Chla in this study. This was not imply that the higher the Chla concentration, the better the squid habitat quality. Because *S. oualaniensis* inhabited the waters with specific suitable range of Chla. Based on previous studies, the suitable range of Chla was about 0.1–0.13 mg/m³ (Yu et al. 2017), which was consistent with our studies (see Figure 2). Though negative relationship was found between the Chla and HSI, however, the areas with enlarged suitable range of Chla, it was found that the HSI in this area would be high.

It is well known that climate variability presents an emerging challenge to the exploitation and sustainable management of squid fisheries in the worldwide oceans (Arkhipkin et al. 2020). In the Pacific Ocean, the El Niño and La Niña phenomena are important drivers of interannual variations of climate and marine ecosystems (Schwing et al. 2002). Recent spatial and temporal variations of habitat hotspots for ommastrephid squid
species are ascribed with high confidence to the El Niño/La Niña-driven regional environmental changes, such as *O. bartramii* and *D. gigas* (Chen et al. 2007; Alabia et al. 2016; Yu et al. 2016). But the impacts of the El Niño/La Niña events can be shown not only in the Pacific Ocean but also off the coastal waters of China. For example, the El Niño events were closely associated with biological and physical environmental changes in the East China Sea, dominating the habitat variations of *S. Japonicus* (Yu et al. 2018).

Detailed information about the impacts of the El Niño/La Niña events on *S. oualaniensis* in the South China Sea is scarce. Only two studies have reported that the La Niña event in early spring 2008 significantly affected temperature and feeding environments of *S. oualaniensis*, resulting in variations of squid stock size and fishing ground distribution (Yu et al. 2019a, 2019b). In this study, the impacts of the El Niño event on *S. oualaniensis* in the South China Sea were first estimated. Our finding revealed that such a climatic phenomenon played profound influences on habitat patterns of this squid. Relative to normal climate conditions in spring 2014, the El Niño events in spring 2015 and 2016 led to relatively cold water and high Chla and SSH. Due to the positive relationship between SST and HSI, and negative relationship between HSI and Chla as well as SSH, the environmental conditions under the El Niño conditions were unfavorable for squid growth and inhabitation and further the formation of high-quality habitats for *S. oualaniensis*, which consequently yielded contracted relatively low-quality of habitats in 2015 and 2016, and the range of suitable habitats largely contracted and became discontinuity. Although the El Niño event yielded a negative effect on habitat quality of *S. oualaniensis*, but the impacts showed difference because of the different intensity of El Niño events in the two years. A strong El Niño event occurred in spring 2015, but the intensity was weak in spring 2016. Therefore, it was found that the SST in 2016 was relatively higher than that in 2015, and the habitat quality was better in this year. The gigantic El Niño event yielded significant impacts on global fisheries. For example, the strong El Niño event occurred in 2015 dramatically changed the habitat patterns, abundance, and distribution of *S. Japonicus* in the East China Sea, *O. bartramii* in the Northwest Pacific Ocean and *D. gigas* in the Southeast Pacific Ocean (Guo et al. 2018; Chen et al. 2020; Wen et al. 2020). All the fishing efforts combined with the fishing vessels decreased as well as the catch in this year.

In summary, environmental conditions and habitat patterns of *S. oualaniensis* in the South China Sea showed significant seasonal and spatial variations. Spatial pattern of favorable environmental conditions played an important role in regulating the ranges and longitudinal and latitudinal distributions of suitable habitats (area with HSI≥0.6) of *S. oualaniensis* across seasons. Comparing to normal climate condition in spring 2014, the El Niño events in spring 2015 and 2016 yielded relatively lower SST and higher Chla and SSH, which were unfavorable for the formation of high-quality habitats for *S. oualaniensis*. Our findings suggested that seasonal habitat patterns of *S. oualaniensis* in the South China Sea were closely associated with local environmental conditions on the fishing ground. Importantly, the El Niño events strongly affected spatio-temporal variations of *S. oualaniensis* habitat.

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**Disclosure of potential conflicts of interest**

No potential conflict of interest was reported by the author(s).

**Data availability statement**

Data available on request from the authors.

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