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ENSO Impacts on Jumbo Flying Squid Habitat Off Peru

China

ENSO impacts on jumbo flying squid habitat off Peru

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Executive summary

Dosidicus gigas is an ecologically and economically important squid species extensively distributed in the Eastern Pacific Ocean. Its habitat is extremely sensitive to climatic and environmental variability. The relationship between habitat pattern of *D. gigas* and El Niño-Southern Oscillation (ENSO, divided into the El Niño, ENSO-neutral and La Niña events) was assessed from 1950 to 2015, using a habitat suitability index (HSI) modelling approach including two crucial environmental variables: sea surface temperature (SST) and sea surface height anomaly (SSHA). On the basis of cross-correlation analysis, it showed that both SST anomaly (SSTA) and SSHA were significantly positively related to the ENSO index. Moreover, a significantly negative association was found between the HSI values and the ENSO index. Due to the El Niño events, water surface temperature off Peru became warmer and sea level rose, resulting in contracted areas of suitable SST and SSHA; consequently, suitable habitats for *D. gigas* dramatically decreased. In contrast, during the ENSO-neutral and La Niña years, the extent of suitable SST and SSHA increased due to the colder water and lower sea level, and suitable habitat for *D. gigas* expanded. Moreover, the latitudinal gravity centre of HSI (LATG_HSI) was significantly positively associated with the ENSO index. Relative to the ENSO-neutral and La Niña years, a southward movement of the monthly preferred SST isotherm for *D. gigas* during the El Niño years could explain the occurrence of more suitable habitats in southern waters off Peru. These findings suggested that the ENSO event plays an important role in regulating environmental conditions off Peru and further affected the spatio-temporal distribution of *D. gigas* habitat.

1. Introduction

It is widely accepted that climate variability at various spatio-temporal scales has significant impacts on global marine species, especially for climate-sensitive species or in sensitive regions in the oceanic waters worldwide (Brander, 2010). For instance, global warming creates a very high pressure on marine ecosystem structure and fisheries production in low- and middle-latitude areas of the ocean (Xu et al., 2016; Ben-Hasan & Christensen, 2019; Silva, Leiva & Lastra 2019). In general, the impacts of climate variability not only change the life history of marine species (e.g. growth rate, migratory route or reproduction time) but also affect the distribution of suitable habitat over their whole life stages (Stenseth et al., 2002; Alheit et al., 2012). Under a changing climate, marine habitats suffer degradation, fragmentation, enlargement, movement or even disappear (Chen et al., 2011; Yi et al., 2017). Without a good understanding of how habitat distribution patterns respond to climate variability it is difficult for fishermen to identify where the abundant fishing grounds occur (Lan, Evans & lee, 2013). Annual production of economically important species experience drastic fluctuations, challenging the sustained provision of high-quality protein for humans. Climate variability is truly a critical driver resulting in the fluctuation of habitat changes (Dueri, Bopp & Maury, 2014; Feyrer et al., 2015). Therefore, predicting the spatial and temporal distribution of species' habitats in a changing climate is important for adapting to climate variability and making correct and effective fisheries management decisions.

The Eastern Tropical Pacific Ocean (ETP) is a region with two major oceanic upwelling ridges (the countercurrent and equatorial ridges) (Waluda & Rodhouse, 2006). Consequently, the ETP provides comparatively high phytoplankton biomass and primary production (Fiedler et al., 1992), and supports large-scale important pelagic fisheries for many countries such as Peru, Chile, China, Japan and United States (Okamoto & Bayliff, 2003; Madigan et al., 2018; Xu et al., 2019). The Humboldt Current System (HCS) off Peru is one of the major Eastern Boundary Upwelling Systems existing in the ETP (Chavez et al., 2008 and its nutrient rich waters support a high biological productivity (Aronés et al., 2019). This makes this region one of the world's most productive fishing grounds for economically important pelagic marine species such as anchovies (*Engraulis ringens*), sardines (*Sardinops sagax*), and the jumbo flying squid *Dosidicus gigas* (Chavez et a., 2003; Chen, Liu & Chen, 2008).

*Dosidicus giga*s is an ommastrephid squid species extensively distributed in the ETP between California and southern Chile, and inhabits coastal waters off South and North America to oceanic waters 125°-140°W (Nigmatullin, Nesis & Arkhipkin, 2001). *D. giga*s occupies an important position in the food chain, serving as a bridge to connect large-size marine mammals with low trophic organisms, and also plays critical roles in distant-water fisheries (Markaida & Sosa-Nishizaki, 2003). Given that *D. giga*s has different geographical stocks (Argüelles et al., 2001), at present, major fishing grounds are exploited by hundreds of international fishing vessels inside and outside the exclusive economic zone off Peru and Chile, in the open sea at the equator bounded by 5°N-5°S and 90°W-130°W, off the Costa Rica Dome regions, and in the Gulf of California, Mexico (Liu, Chen & Chen, 2015). Among them, the fishing ground off Peru is the most important, yielding the highest production in the world. Because of the low catches of Argentina short-fin squid *Illex angentinus* in the Atlantic Ocean, in 2001 Mainland China changed its fishing strategy to exploiting *D. gigas*, which has subsequently expanded into a large-scale squid fishery off Peru (Chen, Liu & Chen, 2008). So far, approximately 250 Chinese fishing vessels are operating in the offshore waters. The highest commercial catch of *D. gigas* in China reached up to 300000 tonnes with an average output of 5 tonnes per day per vessel, accounting for about 70% of the total distant-water squid catches in China (Feng et al., 2017).

With only a short 1-year life cycle, *D. giga*s populations are extremely sensitive to climatic and environmental variability, showing interannual variations in its abundance and distribution (Frawley et al., 2019). A growing number of studies have concluded that the reason for the fluctuations in stock biomass and distribution shifts is the meso-scale climatic and regional environmental conditions at various spatial and temporal scales, such as the El Niño-Southern Oscillation (ENSO) event (Ichii et al., 2002; Waluda, Yamashiro & Rodhouse, 2006). The ENSO event can be divided into the El Niño, ENSO-neutral and La Niña. The abiotic and biotic factors in the ETP region are largely associated with the ENSO event, inevitably causing profound effects on fish species inhabiting in this area (Wang & Fiedler, 2006; Hernández-Miranda & Ojeda; 2006; Leung et al., 2019). For *D. gigas*, previous studies found that catches, habitat quality and latitudinal distribution of habitat hotspots showed large differences between El Niño and La Niña years between 2006-2013 (Yu et al., 2016, 2017). However, it is still unknown how the ENSO events affect environmental conditions off Peru and habitat pattern of the short-lived *D. gigas* over a long-term time scale.

This study employed two crucial environmental variables: sea surface temperature (SST) and sea surface height anomaly (SSHA), in combination with squid-jigging fisheries data, to develop a habitat suitability index (HSI) model and predict the spatial distribution of *D. gigas* in the South-east Pacific Ocean off Peruvian waters over the 1950-2015 period, and further evaluate the relationship between habitat pattern of *D. gigas* and ENSO events, which was divided into the El Niño, ENSO-neutral and the La Niña years. The objectives of this study were to (1) examine the responses of environmental conditions off Peru to different ENSO events over a long-term time scale using 66-year data; and (2) identify the differences in spatio-temporal distribution of favourable habitats of *D. gigas* off Peru under changing climatic and environmental conditions.

2. Materials and methods

2.1. Fisheries, environmental and climatic index data

In this study, Chinese commercial fisheries data for *D. gigas* were compiled by 0.5° longitude × 0.5° latitude and by month. Data were collected from National Data centres of Chinese distant-water fisheries, Shanghai Ocean University. Data included fishing date (year and month), fishing effort (days fished), fishing location (latitude and longitude) and catch (unit in tonnes). The study region was bounded by 8º−20ºS and 95−75ºW in the South-east Pacific Ocean off Peru (Figure 1).

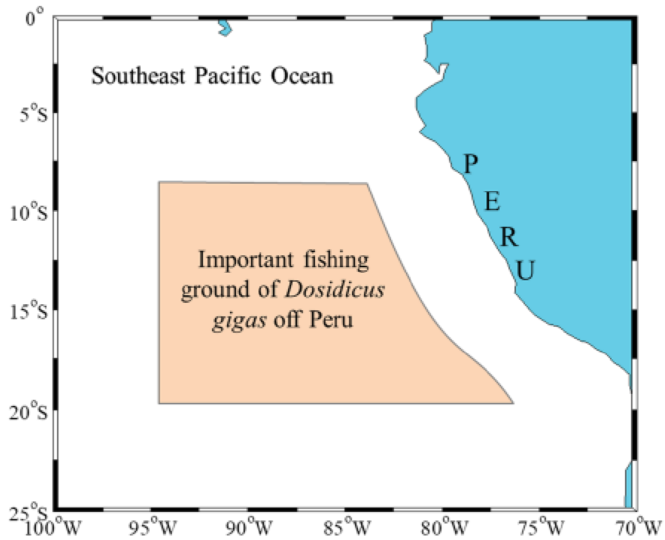

Figure 1 Geographical distribution of productive fishing ground with high catches of jumbo flying squid *Dosidicus gigas* outside the Exclusive Economic Zones (EEZ) off Peru.

Environmental data including SST and sea surface height (SSH) were obtained 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. The data covered the period from 1950 to 2015 on the *D. gigas* fishing ground off Peru.

The ENSO index was one standard measure to indicate the El Niño and La Niña events in the Pacific Ocean (Trenberth, 1997; An, 2004). In this study, the ENSO index was estimated using a 5-month running mean of SST anomaly (SSTA) in the Niño 3.4 region between 5ºN−5ºS and 120º−170ºW. Based on a threshold of +/− 0.5ºC for ENSO index, the warm and cold periods of above and below normal SSTs were defined as the El Niño and La Niña events, respectively, when the threshold was met for a minimum of 5 consecutive overlapping seasons. Periods where the ENSO index ranged from −0.5ºC to +0.5ºC were defined as the ENSO-neutral event. The definition for the El Niño and La Niña events was sourced from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center. The ENSO index from January to December during 1950−2015 was obtained from the website: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php.

2.2. Habitat suitability index calculation

To evaluate the spatial and temporal distribution of potential habitat for *D. gigas* off Peru, the habitat suitability index (HSI) value was calculated over the period 1950-2015. In general, developing the HSI model should follow three steps: (1) the first step was to examine the associations between the indicators of fish abundance (e.g. catch per unit effort, CPUE and/or fishing effort) and environmental variables, and then convert the relationship into a statistical-based suitability index (SI) model for each environmental variable (Tian et al., 2009; Li et al., 2016); (2) the second step was to combine all the SI models into an integrated HSI model based on different approaches such as the Arithmetic Mean Model (AMM), the Geometric Mean Model (GMM), the Continued Product Model (CPM), and the Minimum/Maximum Model (MINM/MAXM) (Li et al., 2014; Yen, Wang & Lu, 2017); (3) the third step was to compare the model performance and select the model with the best prediction performance to predict the HSI, and model validation was examined by different test analyses (Tanaka & Chen, 2016).

Many studies have already established the HSI model for *D. gigas* off Peru; thus, this study directly employed the SI models (SST and SSHA) sourced from a HSI prediction technique from Yu et al. (2016), which were rigorously statistically tested and assessed. Given that the AMM method was the best one to construct the HSI model for squid species (Yu et al., 2015), this method was applied to combine SST-based and SSHA-based SI models into the HSI model and to calculate the ultimate HSI values. Previous studies have already cross-validated the

SST-SSHA-based HSI model using actual fisheries data and proved that this model yielded a good prediction performance (Jin & Chen, 2014; Yu et al., 2015). The HSI model was not specifically validated in this study. The HSI values ranged from 0 to 1. The areas with HSI$\leqslant$0.2 and with HSI$\geq$0.6 were defined as poor habitat and suitable habitat, respectively, for the *D. gigas* fishery (Yu et al., 2015, 2016).

2.3. The linkage between habitat variations and environmental changes

Variability of the ENSO index, SSTA and SSHA within the study area from January to December during 1950-2015 were examined in the South-east Pacific Ocean off Peru. Cross-correlation associations between the ENSO index and environmental factors (SSTA and SSHA) were evaluated with a significant level of P<0.05 for time-lags of months. Through this analysis, the response of environmental variability to the ENSO event was detected.

Based on the ENSO index, the 66 years from 1950 to 2015 were divided into three types: the El Niño, ENSO-neutral and the La Niña years. Moreover, the months from September to December were the most important and productive fishing season for *D. gigas* off Peru. Thus, these months were chosen as the focused study period. Spatial distribution of 4-month averaged SSTA and SSHA from September to December on the fishing ground of *D. gigas* off Peru was examined and compared under the climatic conditions of the El Niño, ENSO-neutral and the La Niña events from 1950-2015. Boxplots were further drawn for 4-month average SSTA, SSHA, SI-SST and SI-SSHA to understand environmental changes and suitability variability for each factor under different climatic conditions.

Latitudinal distribution of fishing ground for *D. gigas* have exhibited large differences under changing environments (Yu et al., 2017). Therefore, to show how the latitude location of the fishing ground changed with the habitat distribution, monthly HSI values and latitudinal gravity centres of HSI (LATG_HSI) were calculated and used to indicate the habitat quality and distribution. Cross-correlation analysis was applied to evaluate the relationship between the ENSO index and HSI values, and between the ENSO index and LATG_HSI to understand the process whereby the ENSO event influenced the habitat pattern of *D. gigas* off Peru. Furthermore, the percentages of poor and suitable habitats within the whole study area were determined and compared under various climatic conditions as well as the spatial distribution of the 4-month averaged HSI. To exhibit how the habitat distribution shifted with the ENSO events, the LATG_HSI, occurrence of suitable habitats at latitude and the most preferred SST isotherm from September to December were exhibited under El Niño, ENSO-neutral and La Niña events. The preferred SST for *D. gigas* from September to December was sourced from Yu et al. (2016), which was defined by the SST ranges with the highest fishing effort that occurred in each month. Besides, the LATG_HSI, an indicator of spatial distribution of habitat hotspots for squid species, was determined based on the equation as follows (Yu et al., 2019):

$$\mathrm{LATG_{HSI}} = \frac{\sum (\mathrm{Latitude}_{(i,m)} \times \mathrm{HSI}_{(i,m)})}{\sum \mathrm{HSI}_{(i,m)}}$$

where $\mathrm{Latitude}_{(i,m)}$ is the latitude of the *i*th fishing grid in month *m*; $\mathrm{HSI}_{(i,m)}$ is the HSI value within the *i*th fishing grid in month *m*.

3. Results

3.1. Classification of the years from 1950 to 2015

Between 1950 to 2015, 20, 30 and 16 years were identified as the El Niño, ENSO-neutral and the La Niña years, respectively, based on the analysis of the ENSO index (Table 1). The number of the ENSO-neutral years was much higher than the other two types of years.

Table 1 The years with different climatic conditions during 1950-2015 according to the definition of the El Niño and La Niña events

ENSO types	Year
El Niño event	1951, 1953, 1957, 1963, 1965, 1969, 1972, 1976, 1977, 1982, 1986, 1987, 1991, 1994, 1997, 2002, 2004, 2006, 2009, 2015

ENSO-neutral	1950, 1952, 1956, 1958, 1959, 1960, 1961, 1962, 1966, 1967, 1968, 1974, 1978, 1979, 1980, 1981, 1984, 1985, 1989, 1990, 1992, 1993, 1996, 2001, 2003, 2005, 2008, 2012, 2013, 2014
La Niña event	1954, 1955, 1964, 1970, 1971, 1973, 1975, 1983, 1988, 1995, 1998, 1999, 2000, 2007, 2010, 2011

3.2. Environmental variability under changing climate conditions

Environmental conditions off Peru exhibited a significant change with the shift of the ENSO phase from an El Niño event to a La Niña event. It was clear that the variability trend of the ENSO index, SSTA and SSHA showed a similar pattern from 1950 to 2015 with dramatically annually fluctuations. The SSTA and SSHA increased/decreased with the increasing/decreasing ENSO index (Figure 2). Cross-correlation analysis suggested that a statistically significant positive relationship was found between the ENSO index and SSTA at a time lag of -9-9 months, and between the ENSO index and SSHA a time lag of -8-10 months ($P<0.05$). The highest correlation occurred at 0 and 1 month with a correlation coefficient value of 0.5942 for SSTA and 0.5647 for SSHA, respectively (Figure 2), suggesting that the environmental conditions off Peru almost changed concurrently when an anomalous ENSO event occurred.

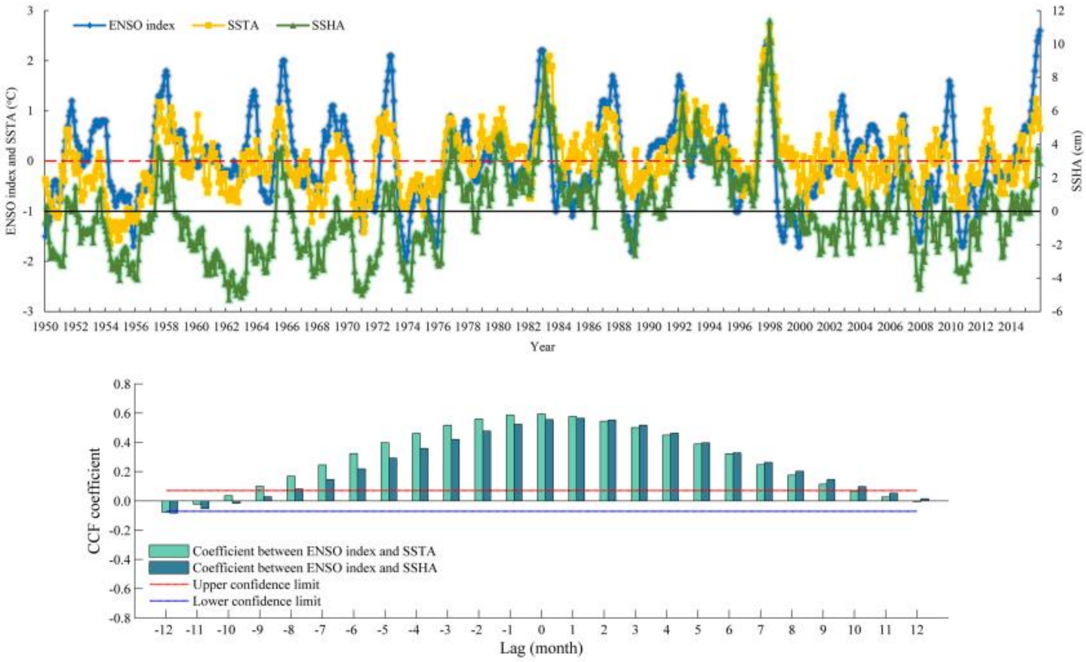

Figure 2 Interannual variability of the ENSO index, sea surface temperature anomaly (SSTA) and sea surface height anomaly (SSHA) on the fishing ground of *Dosidicus gigas* in the South-east Pacific Ocean off Peru during 1950–2015 (Upper panel). Cross correlation coefficients between the ENSO index and SSTA, and between the ENSO index and SSHA (Lower panel).

During the El Niño years, anomalous warm waters widely occurred off Peru, particularly a much warmer water mass distributed in the north-east regions off Peru (Figure 3). Correspondingly, the SSHA tended to be higher due to the El Niño events. In contrast, when the climatic conditions shifted into the La Niña events, the waters typically became cool, in particular extensive cooler waters occurred in the coastal areas off Peru combined with lower SSHA. The SSTA and SSHA during the ENSO-neutral years were clearly in the middle between the El Niño and La Niña years. Under changing ENSO phases from 1950 to 2015, the yearly 4-month averaged SSTA and SSHA clearly increased with the El Niño events and dramatically decreased with the ENSO-neutral and La Niña events (Figure 4). However, the suitability index of each environmental variable (SI-SST and SI-SSHA) for *D. gigas* showed an inverse variability trend, which clearly increased from the El Niño mode to the La Niña mode.

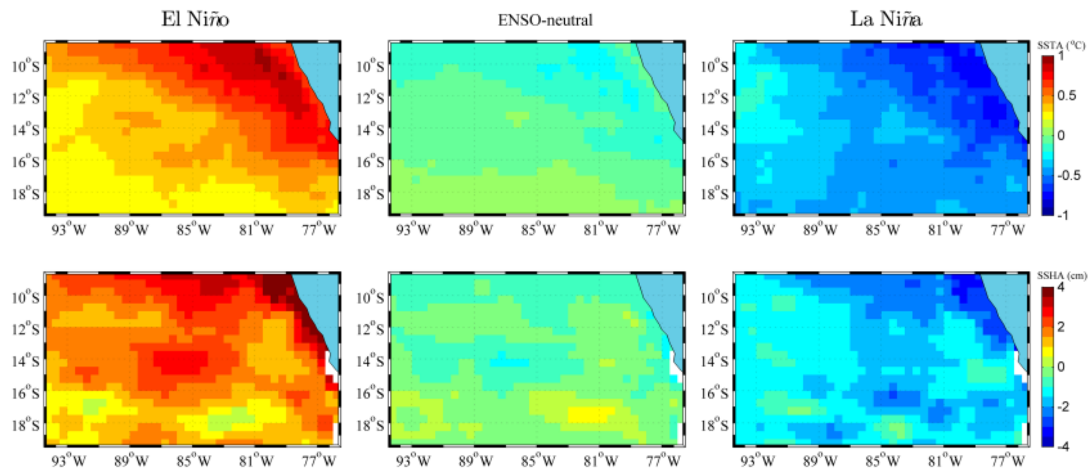

Figure 3 Spatial distribution of 4-month averaged sea surface temperature anomaly (SSTA, upper panel) and sea surface height anomaly (SSHA, lower panel) on the fishing ground of *Dosidicus gigas* in the South-east Pacific Ocean off Peru under the

climate condition of El Niño, ENSO-neutral and La Niña events from September to December 1950-2015.

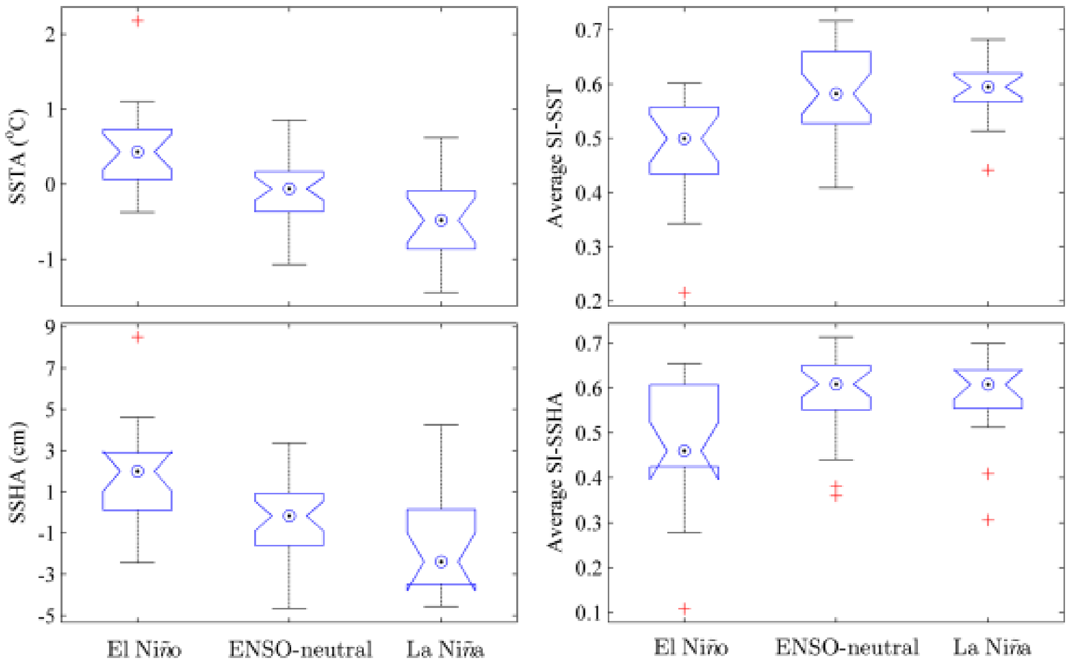

Figure 4. Variation of 4-month averaged sea surface temperature anomaly (SSTA), average suitability index (SI) of SST (SI-SST), sea surface height anomaly (SSHA) and average SI of SSHA (SI-SSHA) on the fishing ground of *Dosidicus gigas* in the South-east Pacific Ocean off Peru under the climate condition of El Niño, ENSO-neutral and La Niña events from September to December over 1950-2015. The blue point and red plus sign in the box-whisker plot indicated median and outliers, respectively.

3.3. Climate-driven spatio-temporal variations in the habitat pattern of *D. gigas*

Interannual variability and cross-correlation between the ENSO index and 5-month running mean his are shown in Figure 5. These results suggest that they had a totally different trend of which the low ENSO index generally corresponded to high HSI values. The cross-correlation analysis revealed a significant negative association between them with a time lag of -6-10 months ($P<0.05$). The highest correlation occurred at 1 month with a correlation coefficient value of -0.2656. Comparing the percentages of suitable and poor habitats for *D. gigas* occupying the whole study area from 1950 to 2015 (Figure 6), it was observed that the ranges of suitable habitats for *D. gigas* under the ENSO-neutral (45.6%) and La Niña events (36.4%) were much higher than that under the El Niño events (19.4%). Conversely, the poor habitats during the El Niño years were larger relative to the years under the other two climatic conditions. This result could also be seen from the spatial distribution of averaged HSI under the different ENSO phases (Figure 6). With the impacts of the El Niño events, the HSI values were relatively lower and suitable habitat occupied only 19.4% of the area in the south east of the fishing ground. Extensive poor habitats occurred in the north of the fishing ground. However, the occurrence of the ENSO-neutral and La Niña events yielded high HSIs, and large areas of suitable habitat occurred on the fishing ground with very small areas of poor habitat under these two climatic conditions.

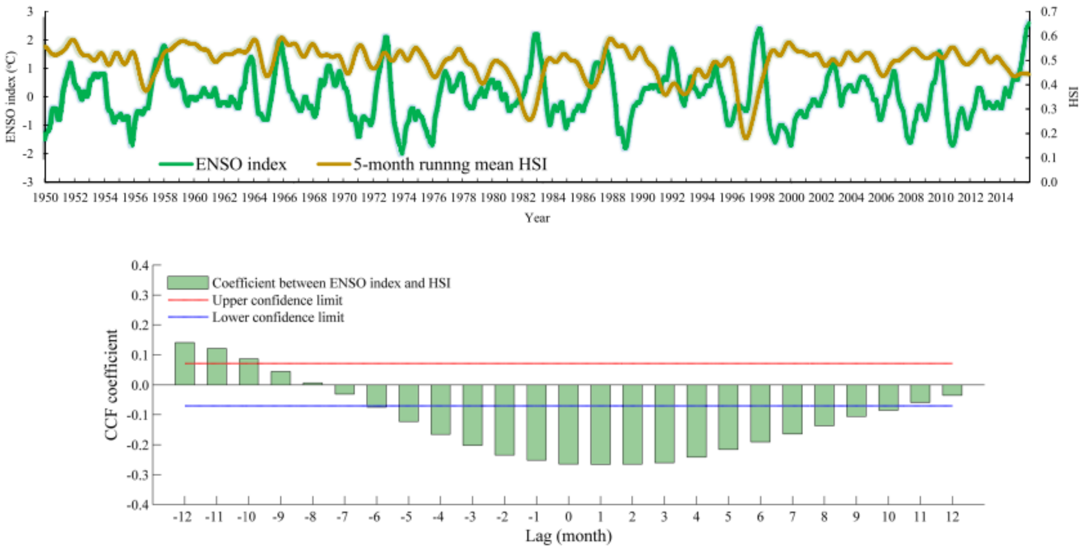

Figure 5. Interannual variability of the ENSO index and 5-month running mean habitat suitability index (HSI) on the fishing ground of *Dosidicus gigas* in the Southeast Pacific Ocean off Peru during 1950-2015 (Upper panel). Cross correlation coefficients between the ENSO index and 5-month running mean HSI (Lower panel).

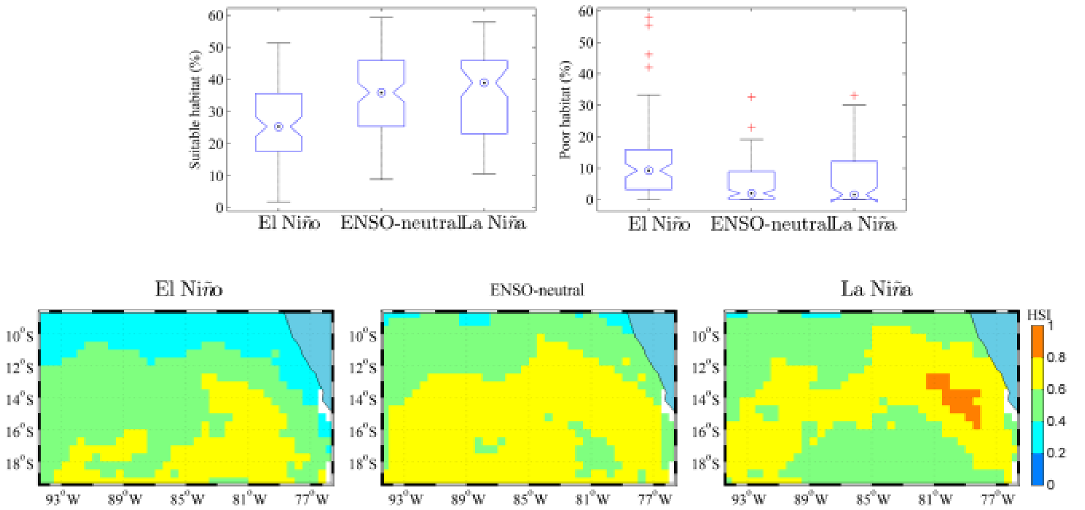

Figure 6. Variation of percentage of suitable habitat and poor habitat of *Dosidicus gigas* in the Southeast Pacific Ocean off Peru under the climate condition of El Niño, ENSO-neutral and La Niña events from September to December over 1950-2015 (Upper panel). Spatial distribution of 4-month averaged habitat suitability index (HSI) on the fishing ground of *Dosidicus gigas* in the Southeast Pacific Ocean off Peru from September to December during 1950-2015 (Lower panel). The blue point and red plus sign in the box-whisker plot indicated median and outliers, respectively.

Similarly, there was interannual variability of the latitudinal locations of habitat distribution and cross-correlation with the ENSO index (Figure 7). Results suggested that the variation of the ENSO index was consistent with the LATG_HSI, the latitude of LATG_HSI commonly increased with the ENSO index. The cross-correlation analysis indicated a significant positive relationship between them with a time lag of -7-8 months (P<0.05). The highest correlation occurred at 0 months with a correlation coefficient value of 0.3562. The monthly LATG_HSI from 1950 to 2015 was divided into three types based on the ENSO types. It was found that the LATG_HSI gradually decreased from the El Niño phase to the La Niña phase (Figure 8), suggesting that high-quality habitats of *D. gigas* were located in the southern regions (the median latitude was about 15ºS) on the fishing ground during the El Niño years, while favourable habitats shifted northward under the ENSO-neutral and La Niña conditions.

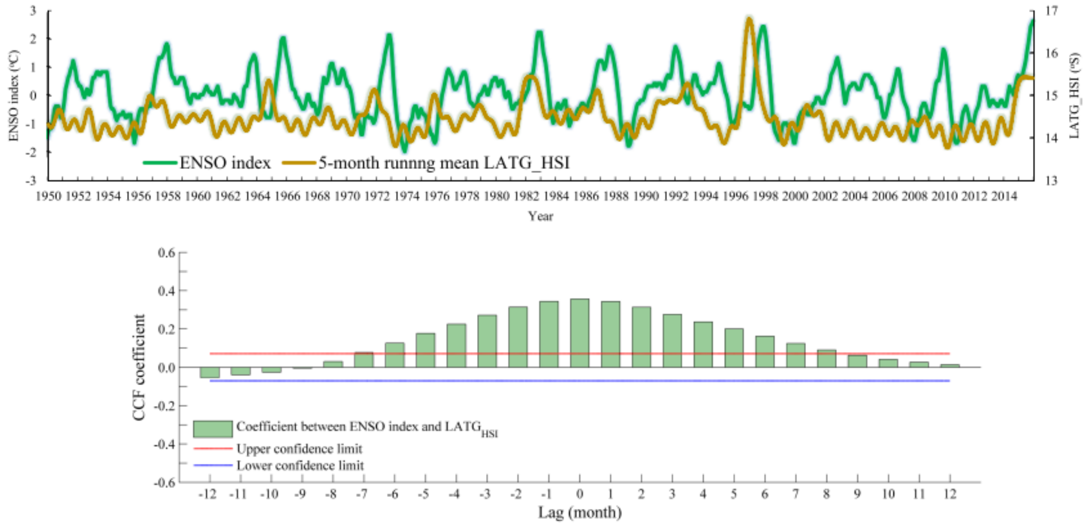

Figure 7. Interannual variability of the ENSO index and 5-month running mean LATG_HSI (latitudinal gravity centers of habitat suitability index) on the fishing ground of *Dosidicus gigas* in the Southeast Pacific Ocean off Peru during 1950-2015 (Upper panel). Cross correlation coefficients between the ENSO index and 5-month running mean LATG_HSI (Lower panel).

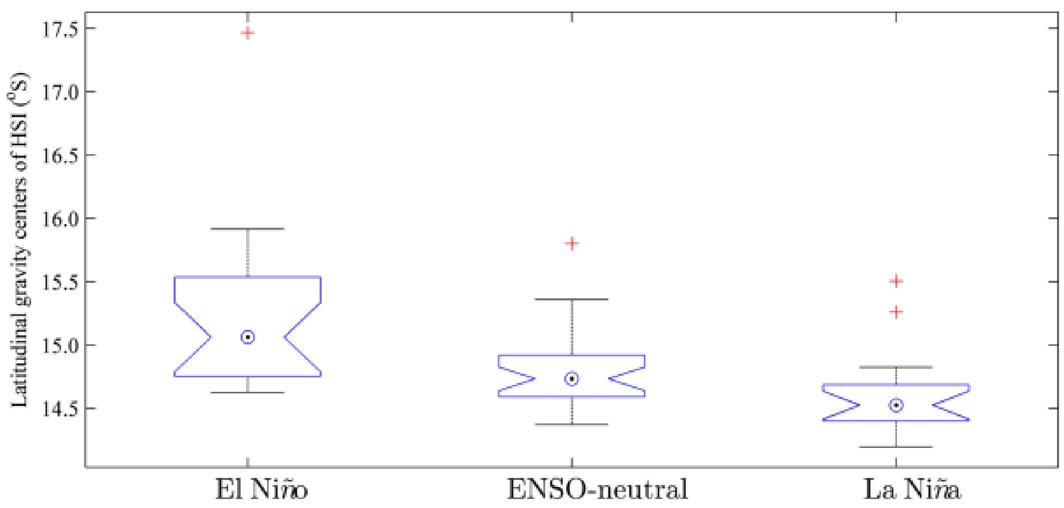

Figure 8. Variation of 4-month averaged LATG_HSI (latitudinal gravity centers of habitat suitability index) of *Dosidicus gigas* in the Southeast Pacific Ocean off Peru under the climate condition of El Niño, ENSO-neutral and La Niña events from September to December 1950-2015.

As regard to the latitudinal location of the suitable habitats of *D. gigas* on the fishing ground, the occurrence of the suitable habitats was examined and shown in

Figure 9. During the El Niño years, the suitable habitats occurred in the latitude from 13ºS to 19.5ºS, although only a few occurred between 13ºS and 16.5ºS and most occurred south of 17ºS. Nevertheless, during the years with the ENSO-neutral and La Niña events, the suitable habitats distributed over a range of 10.0ºS-19.5ºS with peaks between 13.0ºS-19.5ºS in ENSO-neutral conditions and peaks from 12.0ºS to 17.0ºS in La Niña conditions. The suitable habitat distribution pattern was in accordance with the latitudinal distribution of the most preferred SST isoline for *D. gigas* (Figure 10). Interestingly, the preferred SST for *D. gigas* moved northward in the El Niño years and migrated southward in the La Niña years, showing the same variability trend with the LATG_HSI and suitable habitat distributions.

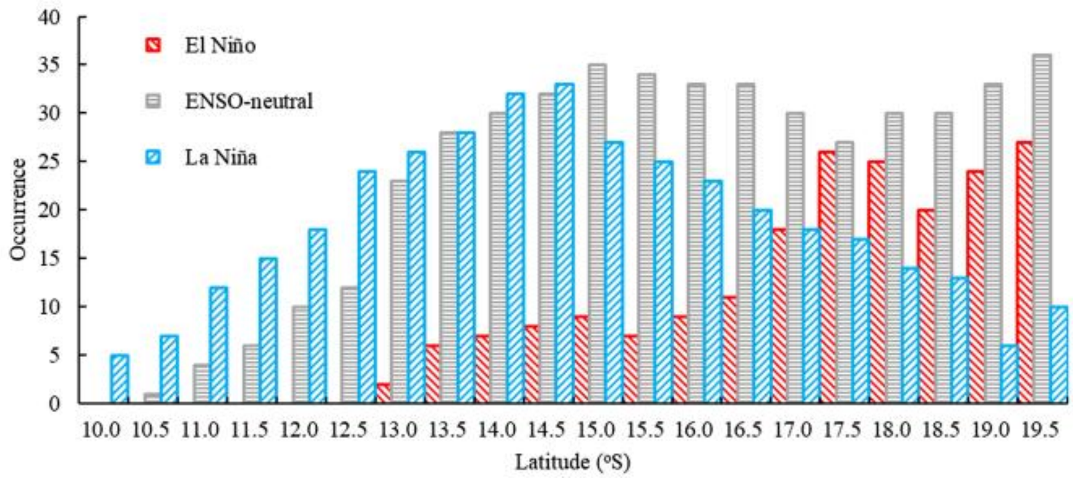

Figure 9. The occurrence of suitable habitats along the latitude within the study area in the Southeast Pacific Ocean off Peru under the climate condition of El Niño, ENSO-neutral and La Niña events from September to December 1950-2015.

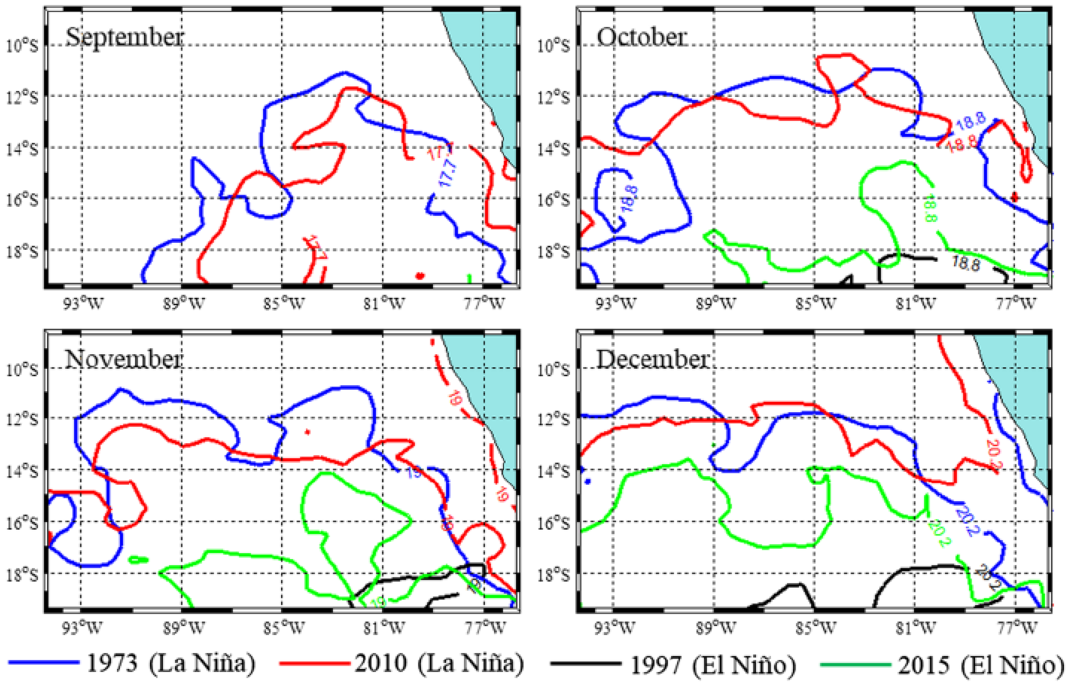

Figure 10. The most preferred sea surface temperature for *Dosidicus gigas* from September to December in the Southeast Pacific Ocean off Peru during the El Niño years of 1997 and 2015, and the La Niña years of 1973 and 2010.

4. Discussion

In this study, two important environmental variables (SST and SSHA) were selected as the prediction indicators in the construction of the HSI model developed for *D. gigas* in the South-east Pacific Ocean off Peru. Squid are heterothermic animals without the ability for temperature regulation (Pecl et al., 2004). Generally, water temperature could directly affect squid physiological metabolism, feeding and swimming behaviorus, migration and breeding (Robin & Denis; 1999; Yamaguchi et al., 2020). Fish reduce environmental stress from changing temperature through tolerance, resistance and habitat preference (Lu & Yuan, 2017). For short-lived ommastrephid squid, they preferred to inhabit suitable habitats with favourable conditions (Anderson & Rodhouse, 2001). Furthermore, *D. gigas* is a temperature-dependent squid species with its abundance closely associated to water temperature and has a variability and distribution shift (Medellín-Ortiz, Cadena-Cárdenas & Santana-Morales, 2016; Paulino, Segura & Chacón, 2016). Many studies suggested that SST was an important driver for the formation of abundant fishing ground and a reliable index for predicting squid habitats (Yu & Chen, 2018). Similar to SST, a strong linkage exists between SSHA and *D. gigas* stocks. Because of the complicated current systems off Peru, both horizontal and vertical oceanographical structure in the coastal and offshore waters drive the transport of nutrients and affect the regional marine ecosystem, playing an important role of fish dynamics (Penven et al., 2005; Montecino & Lange, 2009). SSH could be used to indicate the eddy activity and applied in the habitat models to evaluate its impacts on food availability for *D. gigas* (Yu et al., 2019). Therefore, taking SST and SSHA into account in HSI development was essential for predicting the habitats of *D. giga*s. Also, some other environmental factors such as chlorophyll-a (Chla) concentration and sea surface salinity in the HSI model were a necessary supplement for habitat prediction study (Li et al., 2014). However, relative to SST and SSHA, these factors contributed relatively little to spatial and temporal changes of *D. gigas* stocks. Thus, these factors were not included in the HSI model.

Many model-based approaches have been implemented to assess habitat patterns for pelagic fish species under changing climatic conditions in terms of biological and environmental variables (Brodie et al., 2015; La Mesa et al., 2015). The HSI model is one of the most efficient and popular tools widely applied to evaluate the impacts of climate variability on rapid changes of habitat in space and time (Gong et al., 2011). It can be employed to anticipate the possible impacts coming from different anomalous environments in the future and identify the key habitat (potential fishing ground) for marine species. For example, successful HSI models have been developed to predict the current and future suitable habitat distributions for the neon flying squid (*Ommastrephes bartramii*) in the North-west Pacific Ocean (Xu et al., 2016) and anchovy (*Engraulis ringens*) off central-northern Chile under the RCP (i.e. RCP2.6, RCP4.5, RCP6.0 and RCP8.5) emissions scenarios to explore the effects of global warming (Silva, Leiva & Lastra, 2019). In this study, given that previous studies established excellent SI models of different environmental conditions, an AMM-based integrated HSI model was directly applied by taking water surface temperature and

SSHA into account to predict the habitats of *D. gigas* off Peru. Other methods such as the GMM and CPM methods have never been used to construct the HSI model, however, their predictions would underestimate the habitat suitability (Gong et al., 2011). Comparing the various methods, the AMM method was considered as the best one.

The ENSO phenomenon is a dominant source of interannual climate variability in the tropical Pacific Ocean (Dijkstra, 2006). It has yielded significant changes in the tropical and subtropical environmental conditions and resulted in rapid variations in the marine ecosystem (Ampou et al., 2017; Possamai et al., 2018). The El Niño and La Niña events corresponded to the warm and cold phases of ENSO, respectively, with the appearance of basin-wide anomalously warming or cooling water appearing in the tropical Pacific (Philander, 1985). In this study, it was seen that the SST and SSHA in the coastal and offshore waters off Peru became higher during the El Niño years and lower during the La Niña years. Generally, in the period of the El Niño phase, the south-east trade winds weakened, thereby, the intensity of the equatorial undercurrent became strong which transported the warm equatorial surface water into the Peru regions. Besides, warm subtropical surface waters were further carried into the coast off Peru by the wind, reducing the strength of the upwelling (Wang & Picaut, 2004). The ENSO-driven environmental changes led to the cold waters and low sea level off Peru, as shown in our findings (Figure 3). During the La Niña periods, the trade winds strengthened and pushed the coastal warm water westward, the intensity of the equatorial undercurrent became weak, whereas the Peru current became strong as well as the upwelling. Deep cold water with high nutrient and productivity rose into the surface (Waluda & Rodhouse, 2006). Thus, the waters off Peru were cold with low sea level, which was consistent with our results.

Through the cross-correlation analysis, it was found that changes in the water temperature and sea level lagged the ENSO events only by 0-1 months, implying that environmental conditions on the fishing ground of *D. gigas* off Peru were sensitive and quickly responsive to the ENSO. Once the ENSO phase shifted from the El Niño mode to the La Niña mode, the climate-driven environmental changes subsequently drove variations in the suitability of each environmental factor for *D. gigas*. *D. gigas* preferred relatively cool water temperatures with low sea level in the South-east Pacific Ocean (Ichii et al., 2002; Waluda, Yamashiro & Rodhouse, 2006; Yu et al., 2016). Therefore, higher SI-SST and SI-SSHA were observed due to the cold-water temperature and low SSH during the ENSO-neutral and the La Niña years over the period of 1950-2015, implying that the environmental conditions in this climate mode were favourable for squid. With respect to the El Niño years, the condition was the opposite.

The large-scale ENSO phenomenon combined with regional environmental variability largely controlled stock dynamics of pelagic fish species as well as squids. For example, studies have shown that economically important marine species, such as Pacific saury *Cololabis saira* (Tian, Akamine & Suda, 2003), albacore tuna *Thunnus alalunga* (Zainuddin & Saitoh, 2004), tropical crab *Gecarcoidea natalis* (Shaw & Kelly, 2013) and *O. bartramii* in the Pacific Ocean (Chen, Zhao & Chen, 2007), have strong linkage with the ENSO events. For *D. gigas*, previous studies have stated that the ENSO-induced sudden temperature change possibly caused biological change (individual growth, forage community and population structure) during its one-year short life history (Keyl, Argüelles & Tafur, 2011; Arkhipkin et al., 2015; Portner et al., 2019). Furthermore, our studies demonstrated that habitat quality (suitability and range) and spatial distribution of *D. gigas* showed high correlations with the ENSO index. It was clear that the habitat suitability and its latitudinal location was vulnerable to the changing climate, both would quickly vary and shift in 0-1 months if the ENSO mode shifted. With the impacts from the El Niño events, water surface temperature off Peru became warmer and sea level rose, leading to contracted areas of suitable SST and SSHA. Consequently, the habitat quality and suitable habitats for *D. gigas* largely decreased. Conversely, during the ENSO-neutral and the La Niña years, the ranges of suitable SST and SSHA enlarged due to the colder water and lower sea level, resulting in the enlarged suitable habitat for *D. gigas*. Moreover, the latitudinal location of potential habitat for *D. gigas* was consistent with the movement of the ENSO-related SST isoline. The preferred SST isotherm for *D. gigas* moved southward during the El Niño years which could explain the occurrence of more suitable habitats in southern waters on the fishing ground relative to the ENSO-neutral and La Niña years. Our findings suggested that the ENSO event played an important role in regulating environmental conditions on the fishing ground of *D. gigas* and further affected the spatial-temporal distribution of *D. gigas* habitats.

Currently, the South Pacific Regional Fisheries Management Organization (SPRFMO), an inter-governmental international organization including 15 members from Asia, Europe, Americas and Oceania, has formally managed *D. gigas* stock of the South Pacific Ocean for long-term conservation and sustainable exploitation of this fishery (http://www.sprfmo.int/). Therefore, understanding the causes and consequences of changing climatic conditions on *D. gigas* habitats could provide the scientific basis for the development of management measures for *D. gigas* fisheries. There was an argument that the low catches of *D. gigas* in recent years from the coastal waters off Peru were largely attributable to high fishing pressures on the high seas and the *D. gigas* stock was overfished. This remains highly controversial. The distant-water *D. gigas* fisheries were largely affected by the ENSO phenomenon, particularly an El Niño event could cause a sudden decrease in the extent of *D. gigas* suitable habitat and *D. gigas* abundance, consequently the catch would decline (Waluda, Yamashiro & Rodhouse, 2006; Yu et al., 2016). The uncertainty associated with how *D. gigas* stock responded to climate variability at various spatio-temporal scales has hampered management. Based on our findings, there is urgent need to establish better measures to reduce the adverse effects of climate change (e.g. the El Niño event) on *D. gigas*, such as (1) accurate prediction of habitat hotspots in such a dynamic and changing climatic and environmental conditions in order to avoid wasting time, labour and fuel costs in identifying fishing grounds; (2) a reduction in the number of fishing vessels to prevent overfishing, especially in El Niño years due to the low habitat quality and contracted suitable habitats of *D. gigas*; and (3) designation of marine protected areas (MPA) to protect squid breeding stocks and recruitment. To achieve this, the detected spawning ground and the predicted habitat hotspots of *D. gigas* could be regarded as potential MPAs where fishing was not allowed. Additionally, *D. gigas* is important to regional pelagic marine food webs, and changes in habitat quality and distribution would induce significant variations of its preys or predators through the food chain. Long-term persistence of habitat patterns for *D. gigas* stock in the Southeast Pacific Ocean under changing ENSO variability could also have important implications for local fisheries and economies (Frawley et al., 2019).

References

Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M. et al. (2012). Climate variability drives anchovies and sardines into the North and Baltic Seas. *Progress in Oceanography*, 96(1), 128-139. https://doi.org/10.1016/j.pocean.2011.11.015

Ampou, E.E., Johan, O., Menkes, C.E., Niño, F., Birol, F., Ouillon, S. et al. (2017). Coral mortality induced by the 2015-2016 El Niño in Indonesia: The effect of rapid sea level fall. *Biogeosciences*, 14, 817-826. https://doi.org/10.5194/bg-2016-375

An, S.I. (2004). Interdecadal changes in the El Niño-La Niña asymmetry. *Geophysical Research Letters*, 31(23). https://doi.org/10.1029/2004GL021699

Anderson, C.I. & Rodhouse, P.G. (2001). Life cycles, oceanography and variability: Ommastrephid squid in variable oceanographic environments. *Fisheries Research*, 54(1), 133-143. https://doi.org/10.1016/S0165-7836(01)00378-2

Argüelles, J., Rodhouse, P.G., Villegas, P. & Castillo, G. (2001). Age, growth and population structure of the jumbo flying squid *Dosidicus gigas* in Peruvian waters. *Fisheries Research*, 54(1), 51-61. https://doi.org/10.1016/S0165-7836(01)00380-0

Arkhipkin, A., Argüelles, J., Shcherbich, Z. & Yamashiro, C. (2015). Ambient temperature influences adult size and life span in jumbo squid (*Dosidicus gigas*). *Canadian Journal of Fisheries and Aquatic Sciences*, 72(3), 400-409. https://doi.org/10.1139/cjfas-2014-0386

Aronés, K., Grados, D., Ayón, P. & Bertrand, A. (2019). Spatio-temporal trends in zooplankton biomass in the northern Humboldt Current System off Peru from 1961-2012. *Deep Sea Research Part II: Topical Studies in Oceanography*, 169, 104656. https://doi.org/10.1016/j.dsr2.2019.104656

Ben-Hasan, A. & Christensen, V. (2019). Vulnerability of the marine ecosystem to climate change impacts in the Arabian Gulf-an urgent need for more research. *Global Ecology and Conservation*, 17, e00556. https://doi.org/10.1016/j.gecco.2019.e00556

Brander, K. (2010). Impacts of climate change on fisheries. *Journal of Marine Systems*, 79(3-4), 389-402. https://doi.org/10.1016/j.jmarsys.2008.12.015

Brodie, S., Hobday, A.J., Smith, J.A., Everett, J.D., Taylor, M.D., Gray, C.A. et al. (2015). Modelling the oceanic habitats of two pelagic species using recreational fisheries data. *Fisheries Oceanography*, 24(5), 463-477. https://doi.org/10.1111/fog.12122

Chavez, F.P., Bertrand, A., Guevara-Carrasco, R., Soler, P. & Csirke, J. (2008). The northern Humboldt Current System: Brief history, present status and a view towards the future. *Progress in Oceanography*, 79, 95-105. https://doi.org/10.1016/j.pocean.2008.10.012

Chavez, F.P., Ryan, J., Lluch-Cota, S.E. & Ñiquen, M. (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science*, 299(5604), 217-221. https://doi.org/10.1126/science.1075880

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), 1024-1026. https://doi.org/10.1126/science.1206432

Chen, X.J., Liu, B.L. & Chen, Y. (2008). A review of the development of Chinese distant-water squid jigging fisheries. *Fisheries Research*, 89(3), 211-221. https://doi.org/10.1016/j.fishres.2007.10.012

Chen, X.J., Zhao, X.H. & Chen, Y. (2007). Influence of El Niño/La Niña on the western winter-spring cohort of neon flying squid (*Ommastrephes bartramii*) in the northwestern Pacific Ocean. *ICES Journal of Marine Science*, 64(6), 1152-1160. https://doi.org/10.1093/icesjms/fsm103

Dijkstra, H.A. (2006). The ENSO phenomenon: Theory and mechanisms. *Advances in Geosciences*, 6, 3-15. https://doi.org/10.5194/adgeo-6-3-2006

Dueri, S., Bopp, L. & Maury, O. (2014). Projecting the impacts of climate change on skipjack tuna abundance and spatial distribution. *Global Change Biology*, 20(3), 742-753. https://doi.org/10.1111/gcb.12460

Feng, Y.J., Cui, L., Chen, X.J. & Liu, Y. (2017). A comparative study of spatially clustered distribution of jumbo flying squid (*Dosidicus gigas*) offshore Peru. *Journal of Ocean University of China*, 16(3), 490-500. https://doi.org/10.1007/s11802-017-3214-y

Feyrer, F., Cloern, J.E., Brown, L.R., Fish, M.A., Hieb, K.A. & Baxter, R.D. (2015). Estuarine fish communities respond to climate variability over both river and ocean basins. *Global Change Biology*, 21(10), 3608-3619. https://doi.org/10.1111/gcb.12969

Fiedler, P.C., Chavez, F.P., Behringer, D.W. & Reilly, S.B. (1992). Physical and biological effects of Los Niños in the eastern tropical Pacific, 1986-1989. *Deep Sea Research Part A. Oceanographic Research Papers*, 39(2), 199-219. https://doi.org/10.1016/0198-0149(92)90105-3

Frawley, T.H., Briscoe, D.K., Daniel, P.C., Britten, G.L., Crowder, L.B., Robinson, C.J. et al. (2019). Impacts of a shift to a warm-water regime in the Gulf of California on jumbo squid (*Dosidicus gigas*). *ICES Journal of Marine Science*, 76(7), 2413-2426. https://doi.org/10.1093/icesjms/fsz133

Gong, C.X., Chen, X.J., Gao, F., Guan, W.J. & Lei, L. (2011). Review on habitat suitability index in fishery science. *Journal of Shanghai Ocean University*, 20(2), 260-269. doi: cnki:sun:ssdb.0.2011-02-017

Hernández-Miranda, E. & Ojeda, F.P. (2006). Inter-annual variability in somatic growth rates and mortality of coastal fishes off central Chile: An ENSO driven process?. *Marine Biology*, 149(4), 925-936. https://doi.org/10.1007/s00227-006-0249-9

Ichii, T., Mahapatra, K., Watanabe, T., Yatsu, A., Inagake, D. & Okada, Y. (2002). Occurrence of jumbo flying squid *Dosidicus gigas* aggregations associated with the countercurrent ridge off the Costa Rica Dome during 1997 El Niño and 1999 La Niña. *Marine Ecology Progress Series*, 231, 151-166. https://doi.org/10.3354/meps231151

Jin, Y. & Chen, X.J. (2014). Forecasting hotspots of *Dosidicus gigas* in the offshore waters of Peru using habitat suitability model. *Progress in Fishery Sciences*, 35(3), 19-26. doi: 10.11758/yykxjz.20140303

Keyl, F., Argüelles, J. & Tafur, R. (2011). Interannual variability in size structure, age, and growth of jumbo squid (*Dosidicus gigas*) assessed by modal progression analysis. *ICES Journal of Marine Science*, 68(3), 507-518. https://doi.org/10.1093/icesjms/fsq167

La Mesa, G., Annunziatellis, A., Filidei Jr, E. & Fortuna, C.M. (2015). Modeling environmental, temporal and spatial effects on twaite shad (*Alosa fallax*) by-catches in the central Mediterranean Sea. *Fisheries Oceanography*, 24(2), 107-117. https://doi.org/10.1111/fog.12093

Lan, K.W., Evans, K. & Lee, M.A. (2013). Effects of climate variability on the distribution and fishing conditions of yellowfin tuna (*Thunnus albacares*) in the western Indian Ocean. *Climatic change*, 119(1), 63-77. https://doi.org/10.1007/s10584-012-0637-8

Leung, S., Thompson, L., McPhaden, M.J. & Mislan, K.A.S. (2019). ENSO drives near-surface oxygen and vertical habitat variability in the tropical Pacific. *Environmental Research Letters*, 14(6), 064020. https://doi.org//10.1088/1748-9326/ab1c13

Li, G., Cao, J., Zou, X.R., Chen, X.J. & Runnebaum, J. (2016). Modeling habitat suitability index for Chilean jack mackerel (*Trachurus murphyi*) in the South East Pacific. *Fisheries Research*, 178, 47-60. https://doi.org/10.1016/j.fishres.2015.11.012

Li, G., Chen, X.J., Lei, L. & Guan, W.J. (2014). Distribution of hotspots of chub mackerel based on remote-sensing data in coastal waters of China. *International Journal of Remote Sensing*, 35(11-12), 4399-4421. https://doi.org/10.1080/01431161.2014.916057

Liu, B.L., Chen, Y. & Chen, X.J. (2015). Spatial difference in elemental signatures within early ontogenetic statolith for identifying Jumbo flying squid natal origins. *Fisheries Oceanography*, 24(4), 335-346. https://doi.org/10.1111/fog.12112

Lu, W.Q. & Yuan, M.Z. (2017). The literature review of temperature change effect on fish behavior. *Journal of Shanghai Ocean University*, 26(6), 828-835. https://doi.org/10.12024 /jsou.20150501459

Madigan, D.J., Baumann, Z., Carlisle, A.B., Snodgrass, O., Dewar, H. & Fisher, N.S. (2018). Isotopic insights into migration patterns of Pacific bluefin tuna in the eastern Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(2), 260-270. https://doi.org/10.1139/cjfas-2016-0504

Markaida, U. & Sosa-Nishizaki, O. (2003). Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the United Kingdom*, 83(3), 507-522. https://doi.org/10.1017/S0025315403007434h

Masumoto, Y., Sasaki, H., Kagimoto, T., Komori, N., Ishida, A., Sasai, Y. et al. (2004). A fifty-year eddy-resolving simulation of the world ocean: Preliminary outcomes of OFES (OGCM for the Earth Simulator). *Journal of Earth Simulator*, 1, 35-56. https://doi.org/10.32131/jes.1.35

Medellín-Ortiz, A., Cadena-Cárdenas, L. & Santana-Morales, O. (2016). Environmental effects on the jumbo squid fishery along Baja California's west coast. *Fisheries science*, 82(6), 851-861. https://doi.org/10.1007/s12562-016-1026-4

Montecino, V. & Lange, C.B. (2009). The Humboldt Current System: Ecosystem components and processes, fisheries, and sediment studies. *Progress in Oceanography*, 83(1-4), 65-79. https://doi.org/10.1016/j.pocean.2009.07.041

Nigmatullin, C.M., Nesis, K.N. & Arkhipkin, A.I. (2001). A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). *Fisheries Research*, 54(1), 9-19. https://doi.org/10.1016/S0165-7836(01)00371-X

Okamoto, H. & Bayliff, W.H. (2003). A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1993-1997. *Inter-American*

Tropical Tuna Commission Bulletin, 22(4), 221-431.

Paulino, C., Segura, M. & Chacón, G. (2016). Spatial variability of jumbo flying squid (*Dosidicus gigas*) fishery related to remotely sensed SST and chlorophyll-a concentration (2004-2012). *Fisheries Research*, 173, 122-127. https://doi.org/10.1016/j.fishres.2015.10.006

Pecl, G.T., Moltschaniwskyj, N.A., Tracey, S.R. & Jordan, A.R. (2004). Inter-annual plasticity of squid life history and population structure: Ecological and management implications. *Oecologia*, 139(4), 515-524. https://doi.org/10.1007/s00442-004-1537-z

Penven, P., Echevin, V., Pasapera, J., Colas, F. & Tam, J. (2005). Average circulation, seasonal cycle, and mesoscale dynamics of the Peru Current System: A modeling approach. *Journal of Geophysical Research: Oceans*, 110(C10). https://doi.org/10.1029/2005JC002945

Philander, S.G.H. (1985). El Niño and La Niña. *Journal of the Atmospheric Sciences*, 42(23), 2652-2662. https://doi.org/10.1126/science.248.4957.904

Portner, E.J., Markaida, U., Robinson, C.J. & Gilly, W.F. (2019). Trophic ecology of Humboldt squid, *Dosidicus gigas*, in conjunction with body size and climatic variability in the Gulf of California, Mexico. *Limnology and Oceanography*. 1-17. https://doi.org/10.1002/lno.11343

Possamai, B., Vieira, J.P., Grimm, A.M. & Garcia, A.M. (2018). Temporal variability (1997-2015) of trophic fish guilds and its relationships with El Niño events in a subtropical estuary. *Estuarine, Coastal and Shelf Science*, 202, 145-154. https://doi.org/10.1016/j.ecss.2017.12.019

Robin, J.P. & Denis, V. (1999). Squid stock fluctuations and water temperature: Temporal analysis of English Channel Loliginidae. *Journal of Applied Ecology*, 36(1), 101-110. https://doi.org/10.1046/j.1365-2664.1999.00384.x

Shaw, A.K. & Kelly, K.A. (2013). Linking El Niño, local rainfall, and migration timing in a tropical migratory species. *Global change biology,* 19(11), 3283-3290. https://doi.org/10.1111/gcb.12311

Silva, C., Leiva, F. & Lastra, J. (2019). Predicting the current and future suitable habitat distributions of the anchovy (*Engraulis ringens*) using the Maxent model in the coastal areas off central-northern Chile. *Fisheries Oceanography*, 28(2), 171-182. https://doi.org/10.1111/fog.12400

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, 297(5585), 1292-1296. https://doi.org/10.1126/science.1071281

Taguchi, B., Xie, S.P., Schneider, N., Nonaka, M., Sasaki, H. & Sasai, Y. (2007). Decadal variability of the Kuroshio Extension: Observations and an eddy-resolving model hindcast. *Journal of Climate*, 20(11), 2357-2377. https://doi.org/10.1175/JCLI4142.1

Tanaka, K. & Chen, Y. (2016). Modeling spatiotemporal variability of the bioclimate envelope of *Homarus americanus* in the coastal waters of Maine and New Hampshire. *Fisheries Research*, 177, 137-152. https://doi.org/10.1016/j.fishres.2016.01.010

Tian, S.Q., Chen, X.J., Chen, Y., Xu, L.X. & Dai, X.J. (2009). Evaluating habitat suitability indices derived from CPUE and fishing effort data for *Ommatrephes bartramii* in the northwestern Pacific Ocean. *Fisheries Research*, 95(2-3), 181-188. https://doi.org/10.1016/j.fishres.2008.08.012

Tian, Y., Akamine, T. & Suda, M. (2003). Variations in the abundance of Pacific saury (*Cololabis saira*) from the northwestern Pacific in relation to oceanic-climate changes. *Fisheries research*, 60(2-3), 439-454. https://doi.org/10.1016/S0165-7836(02)00143-1

Trenberth, K.E. (1997). The definition of El Niño. *Bulletin of the American Meteorological Society*, 78(12), 2771-2778. https://doi.org/10.1175/1520-0477(1997)078<2771:TDOENO>2.0.CO;2

Waluda, C.M. & Rodhouse, P.G. (2006). Remotely sensed mesoscale oceanography of the Central Eastern Pacific and recruitment variability in *Dosidicus gigas*. *Marine Ecology Progress Series*, 310, 25-32. https://doi.org/10.3354/meps310025

Waluda, C.M., Yamashiro, C. & Rodhouse, P.G. (2006). Influence of the ENSO cycle on the light-fishery for *Dosidicus gigas* in the Peru Current: An analysis of remotely sensed data. *Fisheries Research*, 79(1-2), 56-63. https://doi.org/10.1016/j.fishres.2006.02.017

Wang, C. & Fiedler, P.C. (2006). ENSO variability and the eastern tropical Pacific: A review. *Progress in Oceanography*, 69(2-4), 239-266. https://doi.org/10.1016/j.pocean.2006.03.004

Wang, C. & Picaut, J. (2004). Understanding ENSO physics-A review. Earth's Climate: The Ocean-Atmosphere Interaction. *Geophysical Monograph Series*, 147, 21-48. https://doi.org/10.1029/147GM02

Xu, H., Lennert-Cody, C.E., Maunder, M.N. & Minte-Vera, C.V. (2019). Spatiotemporal dynamics of the dolphin-associated purse-seine fishery for yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Fisheries research*, 213, 121-131. https://doi.org/10.1016/j.fishres.2019.01.013

Xu, J., Chen, X.J., Chen, Y., Ding, Q. & Tian, S.Q (2016). The effect of sea surface temperature increase on the potential habitat of *Ommastrephes bartramii* in the Northwest Pacific Ocean. *Acta Oceanologica Sinica*, 35(2), 109-116. https://doi.org/10.1007/s13131-015-0782-9

Yamaguchi, T., Takayama, K., Hirose, N. & Matsuyama, M. (2020). Relationship between empirical water temperature and spring characteristics of swordtip squid (*Uroteuthis edulis*) caught in the eastern Tsushima Strait. *Marine Biology Research*, 1-10. https://doi.org/10.1080/17451000.2020.1712420

Yen, K.W., Wang, G. & Lu, H.J. (2017). Evaluating habitat suitability and relative abundance of skipjack (*Katsuwonus pelamis*) in the Western and Central Pacific during various El Niño events. *Ocean & Coastal management*, 139, 153-160. https://doi.org/10.1016/j.ocecoaman.2017.02.011

Yi, Y., Cheng, X., Yang, Z., Wieprecht, S., Zhang, S. & Wu, Y. (2017). Evaluating the ecological influence of hydraulic projects: A review of aquatic habitat suitability models. *Renewable and Sustainable Energy Reviews*, 68, 748-762. https://doi.org/10.1016/j.rser.2016.09.138

Yu, W., & Chen, X.J. (2018). Ocean warming-induced range-shifting of potential habitat for jumbo flying squid *Dosidicus gigas* in the Southeast Pacific Ocean off Peru. *Fisheries research*, 204, 137-146. https://doi.org/10.1016/j.fishres.2018.02.016

Yu, W., Chen, X.J., Yi, Q., Chen, Y. & Zhang, Y. (2015). Variability of suitable habitat of western winter-spring cohort for neon flying squid in the Northwest Pacific under anomalous environments. *PloS One*, 10(4). https://doi.org/10.1371/journal.pone.0122997

Yu, W., Chen, X.J., Zhang, Y. & Yi, Q. (2019). Habitat suitability modelling revealing environmental-driven abundance variability and geographical distribution shift of winter–spring cohort of neon flying squid *Ommastrephes bartramii* in the northwest Pacific Ocean. *ICES Journal of Marine Science*, 76(6), 1722-1735. https://doi.org/10.1093/icesjms/fsz051

Yu, W., Yi, Q., Chen, X.J. & Chen, Y. (2017). Climate-driven latitudinal shift in fishing ground of jumbo flying squid (*Dosidicus gigas*) in the Southeast Pacific Ocean off Peru. *International Journal of Remote Sensing*, 38(12), 3531-3550. https://doi.org/10.1080/01431161.2017.1297547

Yu, W., Yi, Q., Chen, X.J. & Chen, Y. (2016). Modelling the effects of climate variability on habitat suitability of jumbo flying squid, *Dosidicus gigas*, in the Southeast Pacific Ocean off Peru. *ICES Journal of Marine Science*, 73(2), 239-249. https://doi.org/10.1093/icesjms/fsv223

Zainuddin, M., Saitoh, S.I. & Saitoh, K. (2004). Detection of potential fishing ground for albacore tuna using synoptic measurements of ocean color and thermal remote sensing in the northwestern North Pacific. *Geophysical Research Letters*, 31(20). https://doi.org/10.1029/2004GL021000