

The Climate Change Response of Pacific Ocean Squids

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Abstract

Climate change is proving to be a driving factor reshaping the distribution and altering the movement of marine species, dynamics of which are crucial for sustainable development and marine resources management. However, how Pacific Ocean squids – boasting the salient biological features of a one-year life span and strong adaptive abilities, and which support more than 25% of global squid catches – respond to climate change is overlooked. We address this knowledge gap by constructing spatio-temporal generalized additive mixed models based on hundreds of thousands of digitized Chinese squid-jigging logbooks covering three Pacific stocks of two squid species (*Ommastrephes bartramii* and *Dosidicus gigas*) spanning 2005 – 2018. Here we show the relationships between environmental variables and local abundance of squids (reflected by response curves) track changes in climate; the squid biomass peaks and troughs coinciding with La Niña and El Niño events, respectively are moderate in contrast to the effects of directional climate change. We find substantial poleward shifts by squids inhabiting low latitude and middle latitudes. These findings have broad implications both for food security and open ocean ecosystem dynamics.

Introduction

Climate change is modifying oceanic biological response patterns through a variety of ways, such as changing habitats' physical and chemical properties, and amplifying environmental fluctuations^{1,2,3,4}. Thereby, it has been established as an important driver of changes to marine fisheries through altering primary production, food web interactions, life history, and distribution⁵. Myriad studies have examined the variety of species' distributional responses to climate change and found that temperature tends to be among the largest limiting habitat factor for most poikilothermic organisms^{2,3}. Thus, global warming is predicted on balance to increase fisheries catch potential in higher latitudes while decreasing in tropical regions due to the poleward shift in the geographical distribution of fish stocks^{1,6}. Because of the unique biological characteristics of short-lived, semelparous, fast growing, highly fecund, gluttonous, and metabolically efficient *Ommastrephes* squids^{7,8}, it is unclear whether or to what extent ocean warming will result in distributional changes.

Here we fill gaps in our knowledge regarding how squids respond to altered marine environmental variables driven by climate change in the Pacific Ocean. We used 1) Chinese squid-jigging fisheries data covering three stocks of two species (*Ommastrephes bartramii* in the Northwest Pacific Ocean, *Dosidicus gigas* in the offshore regions of Peru and Chile, and *Dosidicus gigas* in the equatorial waters of the Southeast Pacific Ocean, Fig. 1a, digitized by the National Data Center for Distant-water fisheries of China in Shanghai Ocean University; 2) marine environmental data, including sea surface temperature (SST), chlorophyll a (Chl), and sea surface salinity (SSS) downloaded from NOAA OceanWatch (<https://oceanwatch.pifsc.noaa.gov/>), and 3) Oceanic El Niño indices (ONI), which characterize ENSO events in the Pacific Ocean, downloaded from Climate Prediction Center (<https://www.cpc.ncep.noaa.gov/data/indices/sstoi.indices>) spanning from 2005 – 2018, to quantify the

effects of climate change on the squids' distribution. The Ocean Niño Index (ONI) values were divided into five levels (fONIs) including "Strong La Niña", "Moderate La Niña", "Normal", "Moderate El Niño", "Strong El Niño"²⁰ During this period, strong La Niña and El Niño events both occurred twice (Fig. S1). A simulation study showed that the monthly aggregated catch in 0.5° longitude × 0.5° latitude cell can serve as a robust local abundance index to represent the dynamics of spatial distribution for squids⁹, thus, the original fisheries datasets were grouped into monthly 0.5° × 0.5° cells, and the environmental data were converted into 0.5° × 0.5° for each month to correspond to the spatial resolution of the fishery data. Finally, we modelled 6048 (Fig. 1B), 3334 (Fig. 1C), and 8878 (Fig. 1D) fished cells covering the three stocks across ten variables 'Year', 'Month', 'Longitude', 'Latitude', 'SST', 'SSS', 'Chl', 'ONI', 'fONI', 'Effort', and 'Catch' for each record.

Quantifying the preferred habitat distribution of squids

We developed a set of generalized additive mixed models (GAMMS) to quantify the preferred habitat distributions and to check whether poleward shifts in habitat distribution track climatic changes. Because squid is continuous (catch weight in metric tons), asymmetrical, with variances generally increasing with higher catches (Fig. S2), we used GAMMs with a gamma distribution and log-link. The models included Catch as response variable, Month, Longitude, Latitude, SST, SSS, Chl as fixed random effects, and fONI as random effect for each stock, respectively. Model structure was tested following a hierarchical approach with five types of smoother for each fixed variable²¹. The approach enabled us to examine factors that influenced the preferred habitat distribution of squids. We fitted the models using the 'mgcv' package version 1.8¹⁰ in the R software environment. We determined the best-fitting model using AIC values (Table S1). The preferred habitat distribution during 2005 – 2018 were hindcasted by the final model for each squid (see Supplementary materials).

Generally, the most obvious pattern is that La Niña events (such as, 2010 and 2011) tend to increase suitable habitat compared to El Niño events (such as 2015) (Fig. S3 – S5) for the three stocks. However, annual variability and habitat preferences varied among stocks. For two stocks of *D. gigas* in the Southeast Pacific Ocean, we found sinusoidal annual distribution patterns: the suitable areas increase from April to November, and then decrease from December to the following April, whereas the unsuitable habitat areas have the opposite seasonal changes (Fig. S4, S5).

Environmental response curves of squids

Environmental response curves were created by plotting the scaled catch against the predictor of interest while holding all other predictors at their median values based on the distribution models for each ONI level and squid¹¹. Most response curves were bell-shaped, or appeared as partially bell-shaped, limited by sampling data contrast. We found that the environmental response curves are both species and stock-dependent. Despite incomplete environmental sampling overlap, SST and Chl a response curve shapes were similar across *D. gigas* stocks (Fig. 2). Moreover, the estimated environmental response curves differed significantly across climate regimes. Scaled abundance indices for strong La Niña years were

typically 2-3 fold higher than strong El Niño events across all stocks, and all environmental variables. Interestingly, *O. bartramii* response curves were most clustered (similar) across regimes, but increased dramatically in strong La Niña years.

Evaluating the dynamics of habitat for squids under climate change

The contour of annual suitable habitat area (SUA, the area with scaled catch > 0.6) was depicted to reflect the long-term dynamics in fishing grounds (Fig. 1E, 1F and 1G). The annual gravitational center positions (LonG – longitude of gravity, LatG – latitude of the gravity) were calculated¹², then we fit linear models with LatG as the response variable and LonG as explanatory variable to observe whether a poleward shift occurred (Fig. 1H, 1I and 1J). The spatial response maps were made (similar to environmental response curves by changing longitude and latitude, simultaneously) to reflect basic distributional patterns under the five ONI levels (Fig. 1K, 1L and 1M).

The results show that *O. bartramii* annual SUAs are getting smaller and moving northwestward (Fig. 1E), the annual SUA are getting bigger with moving southeast for *D. gigas* in the equatorial waters (Fig. 1F), and the annual SUA are getting smaller with moving southwest for *D. gigas* in the offshore Peru and Chile (Fig. 1G). Similarly, the significant latitudinal moving occurred on three squid stocks in the Pacific Ocean ($p < 0.05$, Fig. 1H, 1I, and 1J). The spatial response maps demonstrate the preferred habitat distribution for each stock clearly, and La Niña event tend to produce more suitable habitat than El Niño event (Fig. 1K, 1L and 1M).

Discussion

This work integrated climate and Ommastrepe squid fisheries dataset located in the Pacific Ocean spanning 14 years to provide demonstrations of how short-lived squid species are responding to climate change. We hindcasted the spatio-temporal distribution and then the habitat metrics for *O. bartramii* in the Northwest Pacific Ocean and *D. gigas* in the Southeast Pacific Ocean using GAMMs with oceanic El Niño index considered as random effect. Our results show clear differences in distribution patterns and habitat metrics conditional on species. The apparent poleward shift in the geographical distribution by the three target stocks in the Pacific Ocean.

The nested structures or non-independence are ubiquitous in the study of ecology^{13, 14}. Mixed models with random effects are useful tools for inference and increasingly easy to build and customize for specific fisheries problems by controlling for dependence structure in the data^{15, 16}. One of questions is how to select predictor variables for use as a random factor. In practical application, variables are modelled as random effects if the primary interest lies in estimating variances, while fixed factors are used for estimating the mean effect of a treatment¹⁷. Ecologically, we are interested in the distribution pattern variances spanning different climate modes (ONI levels) for squids driven by local environmental variables, such as SST, SSS and Chl. If ONI is considered as a fixed variable, it would be very hard to explain the influences of multiple levels of ONI on squid distributions. Thus, we assume that the fONI

reasonably is treated as random variable which divides the fisheries data into multiple groups. Consequently, the results derived from mixed models, such as response curves and habitat distribution patterns would be more robust than those in past studies who did not consider this “grouped feature”^{18,19}.

The life cycle traits may have positive and negative effects on squid species in relation to environmental change, as they can be both sensitive (rapid response) and resilient (rapid recovery) to various uncertainties such as overfishing or climate variability⁷. Relative to long-lived species, we could quickly and flexibly inspect the effectiveness of alternative management options in a shorter period. However, to achieve this requires accurate knowledge of squid distribution and preferred habitat which could be obtained from our results.

Based on our exploration, there are several suggestions for squid management in the Pacific Ocean. Firstly, the accuracy and robustness of distribution models were improved substantially by incorporating ONI random effects, thus, where squid relative annual / monthly abundance derived from distribution models is used for stock assessment models, climate variability should be considered. Secondly, suitable habitat area changes associated with different climate phases may affect the hatching and growth of squid⁸, altering model spawner-recruitment relationships and growth curves. Research should prioritize developing predictive capability in this respect to facilitate implementation of ‘climate-ready’ integrated stock assessment models. Thirdly, the altered response curves and the ongoing poleward movement for squids inhabiting low latitude waters suggests movement patterns may be considered in future assessment models. Generally, the proportions SUA overlap with climate phases showed that the La Niña events tend to benefit the squid abundance by increasing the suitable habitat areas, while the El Niño events are less advantageous due to opposite drivers. As squid stock assessment models are developed, managers should be aware that the total allowable catches (TACs) could be improved in La Niña years and be reduced in El Niño years, and the extent should be assessed carefully and systematically.

In summary, the environmental response curves and the preferred habitat distribution patterns of squids were markedly influenced by the effects of climate change in the Pacific Ocean. During last two decades, we find clear poleward movement from squids. Such detected features in spatial distributions should be seriously considered as components of sustainable development and management for squid resources in the Pacific Ocean.

Declarations

I would like to declare on behalf of my co-authors including **R. Boenish**, **Y. Li**, and **X. Chen** that this work was original research that has not been published previously, and not under consideration for publication elsewhere. No conflict of interest exists in the submission of this manuscript, and manuscript is approved by all authors for publication.

Authors Contributions are as follow:

J. Wang: all processes, including conceptualization, methodology, and writing, and so on.

R. Boenish: methodology, and writing.

Y. Li: conceptualization.

X. Chen: conceptualization and funding.

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Figures

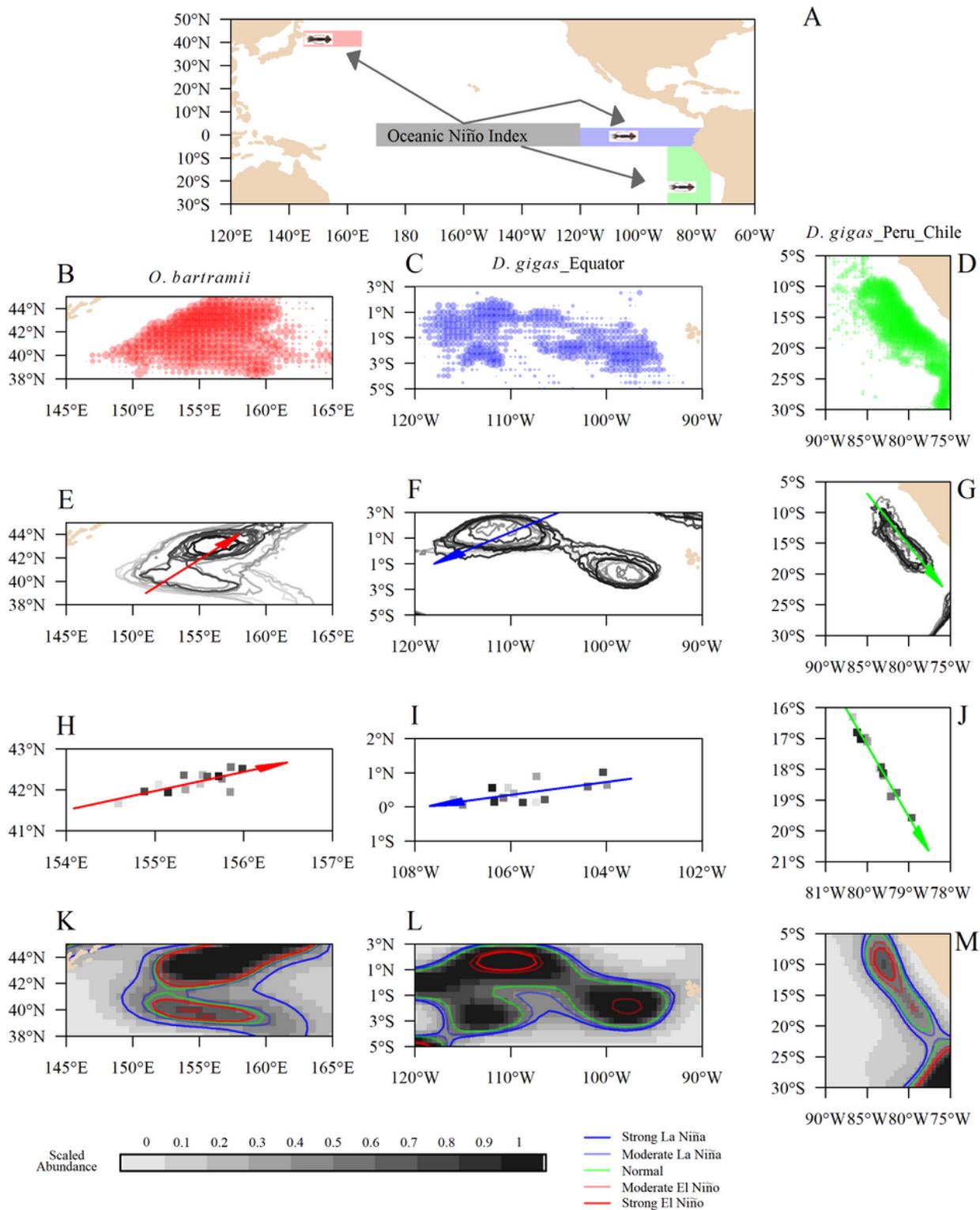


Figure 1

The fishing grounds, catch distributions, suitable habitat areas, and spatial response curves for squids in the Pacific Ocean. The catch distribution between 38° N – 45° N, 145° E – 165° E for *O. bartramii* in the Northwest Pacific Ocean (B), between 3° N – 5° S, 120° W – 90° W for *D. gigas* in the Equator of Southeast Pacific Ocean (C), between 5° S – 30° S, 90° W – 75° W for *D. gigas* in the offshore of Peru and Chile (D), was collected by Chinese squid-jigging fisheries. The size of circle on the feeding ground is proportional

to the catch of squids during 2005 – 2018. The contours of suitable habitat area for *O. bartramii* (E), *D. gigas* in the Equator of Southeast Pacific Ocean (F), and *D. gigas* in the offshore Peru and Chile (G) during 2005 – 2018, where years are represented consecutively from light to dark. Annual gravity centers for *O. bartramii* in the Northwest Pacific Ocean (H), *D. gigas* in the Equator of Southeast Pacific Ocean (I), and *D. gigas* in the offshore Chile of Southeast Pacific Ocean (J) during 2005 – 2018. The solid lines represent statistically significant latitudinal movement. Spatial response maps reflect the basic habitat distribution for *O. bartramii* (K), *D. gigas* in the Equator of Southeast Pacific Ocean (L), and *D. gigas* in the offshore Peru and Chile (M). The contours of SUA under different climate modes are shown overlaid a black-white gradient representing habitat distribution in normal years

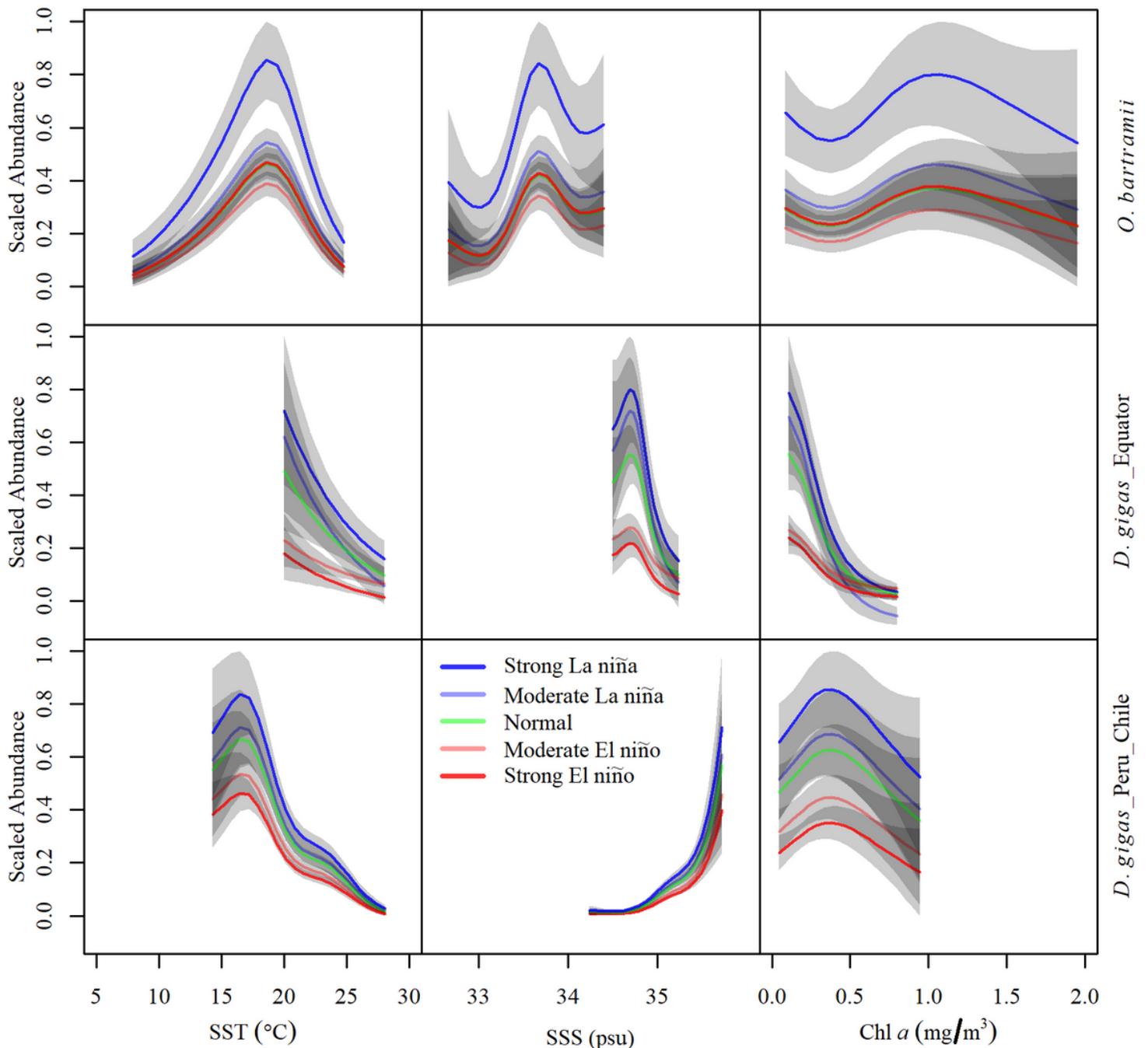


Figure 2

Response curves of sea surface temperature (left column), sea surface salinity (middle column), and Chl a (right column) for *O.bartramii* in the Northwest Pacific Ocean (up row), *D. gigas* in the equatorial waters in the Southwest Pacific Ocean (middle row), and *D. gigas* in the offshore Peru and Chile (down row) under five ONI effects.

Supplementary Files

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