

INTERANNUAL VARIABILITY OF HUMBOLDT SQUID (*DOSIDICUS GIGAS*) OFF OREGON AND SOUTHERN WASHINGTON

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ABSTRACT

Previous studies have shown that oceanographic conditions influence the distribution of range-expanding Humboldt squid (*Dosidicus gigas*), but broad-scale temporal and spatial distribution analyses are limited. Interannual variability in Humboldt squid occurrence is largely undocumented north of California. We combined annual occurrences noted by fishermen with fisheries-dependent and fisheries-independent data between 2002–11 from 42.0080°N, 131.0000°W to 46.7008°N, 131.0000°W. Humboldt squid more frequently occurred at a sea surface temperature range of 10.5°–13.0°C, sea surface height anomalies from –4.0–1.0 m, 0.26–3.00 mg m⁻³ chlorophyll *a*, and sea surface salinity range of 32.2–32.8 psu. Dissolved oxygen levels were bimodal, between 3.0–4.5 ml L⁻¹ and 6.0–7.0 ml L⁻¹ at 30 m depth. Maps of estimated likelihood of occurrence generated by non-parametric multiplicative regression were consistent with observations from fishermen. When Humboldt squid become abundant in northern California Current waters, research should include seasonal variability and oceanographic conditions at multiple depths.

INTRODUCTION

The Humboldt squid (*Dosidicus gigas*), also known as jumbo flying squid, is an opportunistic predator that has experienced episodic range expansions from the Eastern Tropical Pacific into South America and the California Current system. Humboldt squid sightings off of the South American coast have been documented since the 19th century and in 2002 they were seen as far south as Chiloe Island in southern Chile (Alarcón-Muñoz et al. 2008). In the northern California Current system, Humboldt squid were documented in the 1930s off California with increasing occurrences since 2002 (Field et al. 2007; Litz et al. 2011). Humboldt squid

have been seen as far north as Alaska (in 2004, Cosgrove 2005) and were first documented in southern Oregon in 1997 (Pearcy 2002). Peak density in Oregon occurred in 2009 (Litz et al. 2011); however, reported sightings in this area have decreased between 2009 and 2011 (Bjorkstedt et al. 2011; Marissa Litz, Oregon State University, pers. comm.).

Humboldt squid live 1–2 years, have rapid growth rates, and high-energy demands (Nigmatullin et al. 2001; Zeidberg and Robison 2007). As a large predator, there is concern that future Humboldt squid expansion will result in a decline in valuable commercial fishery stocks and impact coastal food webs in the California Current (Field et al. 2007). Humboldt squid have the ability to alter food sources and foraging strategies based on varied environmental conditions (Bazzino et al. 2010). These squid have been known to prey on Pacific herring (*Clupea pallasii*) (Field et al. 2007), mackerel (*Scomber japonicus*) (Sato 1976; Ehrhardt et al. 1983), sardines (*Sardinops sagax*) (Ehrhardt et al. 1983; Markaida and Sosa-Nishizaki 2003), hake (*Merluccius productus*) (Markaida and Sosa-Nishizaki 2003), rockfish (*Sebastes* spp.) (Field et al. 2007), and salmon (*Oncorhynchus* spp.). The valuable Pacific hake (*Merluccius productus*) fishery is of particular concern, as Humboldt squid are known to associate with hake schools and a decline in Chilean hake (*M. gayi*) biomass was attributed to an increase in Humboldt squid off the Chilean coast in 2001–06 (Alarcón-Muñoz et al. 2008). In Oregon, Humboldt squid presence coincided with a decline in juvenile Pacific hake, which was in contrast to recent abundance trends (Litz et al. 2011).

Previous research has indicated that oceanographic factors may contribute to the variable temporal and spatial population range of Humboldt squid (Gilly et al. 2006; Field et al. 2007; Zeidberg and Robison 2007),

and direct evidence of what is driving that expansion is still being actively researched (Bazzino et al. 2010). It has been proposed that warming oceans, the expansion of the oxygen minimum layer (OML), and large climatic processes such as the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) could influence Humboldt squid migration patterns through modifications of environmental conditions, community structure, and prey availability (Nigmatullin et al. 2001; Brodeur et al. 2006; Gilly et al. 2006; Bograd et al. 2008; Keyl et al. 2008; Mejía-Rebollo et al. 2008; Bazzino et al. 2010; Rosa and Seibel 2010; Litz et al. 2011; Stewart et al. 2012). Although changing ocean conditions (Stewart et al. 2012) and response to high productivity levels (Field et al. 2012) may enable expansion and seasonal migration into the northern California Current, Humboldt squid occurrence is limited by their ability to migrate to available spawning habitat (Staaf et al. 2011; Field et al. 2012).

In Oregon, there is no monitored fishery for Humboldt squid and their distribution is largely undocumented. Species distribution modeling (SDM), also known as habitat suitability modeling, may be able to aid in the understanding of Humboldt expansion off Oregon. Statistical habitat models investigate the relationship between species and their environments and can be utilized to further describe and predict potential habitat (Franklin 2009; McCune 2011). Squid fishery data have been analyzed using GIS (Valavanis et al. 2004; Sanchez et al. 2008; Chen et al. 2010), generalized additive models (GAMs) (Lefkaditou et al. 2008; Sanchez et al. 2008; Litz et al. 2011), and maximum entropy (Maxent) (Lefkaditou et al. 2008) for sea surface temperature (SST), chlorophyll *a* (chl *a*), sea surface salinity (SSS), bathymetry, sea level anomalies, and large-scale oceanic processes. Although these are common habitat modeling methods, it has been argued that these models can prove to be inappropriate if species/environmental relationships are unimodal and interactive (McCune 2011). Nonparametric multiplicative regression (NPMR) may be a more appropriate habitat modeling approach because it fits a local mean to the predictive points, allows the data to have any shape, and allows for environmental variable interaction, and complex non-linear responses (McCune 2006).

A recent study investigating the correlation of oceanographic conditions to Humboldt squid catch in the northern California Current system found that Humboldt squid presence has been closely associated with salinity, while abundance corresponded best with station depth, subsurface temperature, salinity, and density (Litz et al. 2011). Using GAMs, Litz et al. 2011 analyzed seasonal fishery-independent survey and oceanographic data from the National Oceanic and Atmospheric Adminis-

tration (NOAA) Fisheries Predator and Stock Assessment Improvement Plan (SAIP) from 2004–09 off Oregon and Washington. Litz et al. 2011 found Humboldt squid present in 60 of the 947 total trawls, and established that Humboldt squid abundance corresponded best with a station depth of 1000 m, 11°–13°C subsurface water temperature, 32.4–32.8 psu, and a density of 24.5–25.0 kg m⁻³ at 20 m. While their results provided significant baseline information for Humboldt squid monitoring in the Pacific Northwest, Litz et al. 2011 expressed need for broader scale distribution data analysis.

The goal of this study is to establish distribution data and explore the relationship between broad-scale temporal and spatial oceanographic conditions and Humboldt squid occurrence off Oregon and southern Washington so as to contribute to baseline information on Humboldt squid interannual variability. Due to the coarse-scale of our data, we did not seek to explain squid behavior or migratory patterns. This study analyzes aggregate Humboldt squid occurrence information from three fishery-independent surveys, fisheries-dependent data from one observer program, and sightings by fishermen with annual remote sensing and field oceanographic data from 2002–11.

METHODS

Study Area

The study area is in the northeast Pacific Ocean, United States. Our research is focused predominantly off the Oregon coast to 131.0000°W but includes some data points off southern Washington (42.0080°N, 131.0000°W to 46.7008°N, 131.0000°W). The range of the study area was chosen to enable the inclusion of nearshore and offshore Humboldt squid occurrences (fig. 1).

Positive Occurrences and Oceanographic Conditions

Positive occurrences, or sightings of one or more Humboldt squid, were compiled from fishermen, fisheries-dependent observer records, and fisheries-independent surveys between 2002–11 for a total of 339 positive occurrences (fig. 1, table 1). Temporal and spatial data on Humboldt squid occurrence was collected by interviewing 54 fishermen. Interviews were conducted by telephone, e-mail, and in-person from October 2011–May 2012. Of those 54 interviewed, 20 fishermen sighted Humboldt squid between 2002–11 for a total of 173 positive occurrences. Fishermen's data ranged from recollection to detailed logbook records. Although some fishermen provided a specific latitude and longitude, a majority of the fishermen provided sightings based on depth and topography. Fisheries-dependent catch

TABLE 1
 2002–11 Humboldt squid occurrence data from the Hake Acoustic, Predator,
 and SAIP Surveys, A-SHOP, and Fishermen sources.

Year	Number of Positive Occurrences from Hake Acoustic Survey	Number of Negative Occurrences from Hake Acoustic Survey	Number of Positive Occurrences from Predator Survey	Number of Negative Occurrences from Predator Survey	Number of Positive Occurrences from SAIP Survey	Number of Negative Occurrences from SAIP Survey	Number of Positive Occurrences from At-sea Hake Observer Program	Number of Negative Occurrences from At-sea Hake Observer Program	Number of Positive Occurrences from Fishermen
2002	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	9
2003	0	20	N/A	N/A	N/A	N/A	N/A	N/A	6
2004	N/A	N/A	0	106	12	41	N/A	N/A	9
2005	0	18	0	118	2	79	N/A	N/A	5
2006	N/A	N/A	1	94	9	40	11	497	9
2007	0	22	0	73	8	64	18	490	24
2008	N/A	N/A	0	59	1	67	30	482	26
2009	11	20	11	72	16	71	14	496	64
2010	N/A	N/A	0	11	0	54	22	507	15
2011	0	11	0	20	0	67	N/A	N/A	6
Total	11	91	12	553	48	483	95	2472	173

Positive occurrences (presence points) include one or more Humboldt squid. Negative occurrences (absence points) are equivalent to where sampling occurred but Humboldt squid were not encountered. The light gray box indicates data used in NPMR species distribution modeling. In 2009 there were the greatest number of Humboldt squid occurrences. No Humboldt squid were observed by the fishery-independent surveys in 2011.

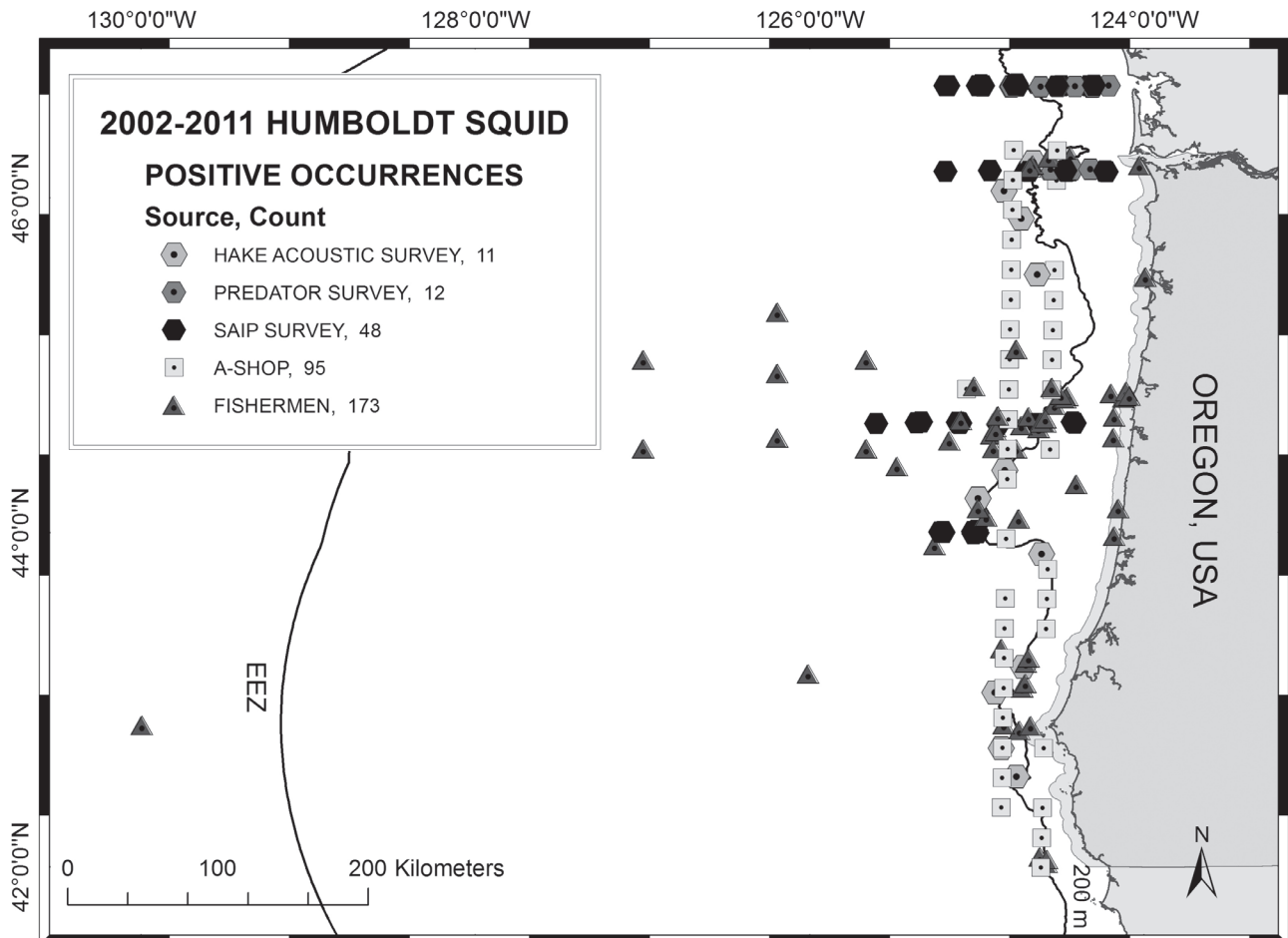


Figure 1. Study area extent with 2002–11 positive Humboldt squid occurrences from the Hake Acoustic Survey, Predator Survey, SAIP Survey, A-SHOP, and Fishermen. Negative occurrences are not illustrated. Positive occurrences shown include one or more Humboldt squid. For the NPMR modeling process, only survey and A-SHOP data were used.

TABLE 2
 Descriptions of remote sensing and in situ oceanographic variables (SST, Chl *a*, SSH, DO at 30 m depth, and SSS).

Ocean condition	Type	Satellite	Resolution	Description	Acquired using	Source
SST (°C)	Moderate Resolution Imaging Spectroradiometer (MODIS)	Aqua	4 km/pixel	11 μ Nighttime seasonal composite	Marine Geospatial Ecology Tools (MGET) in ArcGIS 10	oceancolor.gsfc.nasa.gov
Chl <i>a</i> (mg/m ³)	Moderate Resolution Imaging Spectroradiometer (MODIS)	Aqua	4 km/pixel	11 μ Nighttime seasonal composite	Marine Geospatial Ecology Tools (MGET) in ArcGIS 10	oceancolor.gsfc.nasa.gov
SSH anomalies (m)	Composite satellite altimetry from archiving, validation, and interpretation of satellite oceanographic data (AVISO)	Jason 1&2/ MERIS ENVISAT	1/3° x 1/3° (approx. 28 km/pixel)	SSALTO/DUACS DT; global DT-REF merged MLSA SSH (gridded monthly)	Marine Geospatial Ecology Tools (MGET) in ArcGIS 10	aviso.oceanobs.com
DO at 30 m (ml/L)	in situ	N/A	in situ	Interpolated using inverse distance weighting in ArcMap 10.0 (Esri 2012); gridded to 28 km	N/A	http://www.nodc.noaa.gov and Childress (2010)
SSS (psu)	in situ	N/A	in situ	Interpolated using inverse distance weighting in ArcMap 10.0 (Esri 2012); gridded to 28 km	N/A	http://www.nodc.noaa.gov

data was provided by the NOAA NWFSC At-sea Hake Observer Program (A-SHOP) where there was a minimum of three vessels fishing and were provided gridded by 20 x 20 km cells. The A-SHOP recorded 95 positive Humboldt squid occurrences and 2,472 negative occurrences between 2006–10. NOAA NWFSC Joint U.S./Canada Pacific Hake Acoustic Survey Database (Hake Acoustic), and NOAA NMFS NWFSC (SAIP and Predator studies) provided fisheries-independent Humboldt squid data. The Hake Acoustic surveyed biannually from 2003–11 and documented 11 positive occurrences and 91 negative occurrences. The Predator and SAIP studies provided data from 2004–11 and observed 12 positive Humboldt squid occurrences and 553 negative occurrences, and 48 positive occurrences and 483 negative occurrences, respectively. This study utilizes the same Predator and SAIP studies data for 2004–09 from Litz et al. 2011 and unpublished data for 2010–11. The data sources with monthly information recorded positive Humboldt squid occurrences from June–December. However, A-SHOP and most fishermen data were provided on an annual scale. Due to restricted temporal resolution of the data, presence and absence records from all sources were grouped annually. The data were then standardized to the environmental predictor variable with the lowest resolution, 28 square km cells, for modeling.

Consistent with previous model results (Valavanis et al. 2004; Lefkaditou et al. 2008; Sanchez et al. 2008; Chen et al. 2010; Litz et al. 2011), we selected physical and chemical oceanographic parameters associated with Humboldt squid distribution (Nigmatullin et al. 2001; Brodeur et al. 2006; Gilly et al. 2006; Bograd et al. 2008; Keyl et al. 2008; Mejía-Rebollo et al. 2008; Bazzino et al. 2010; Rosa and Seibel 2010; Litz et al. 2011; Stewart et al. 2012). Annual average SST (°C), chl *a* (mg m⁻³), mean sea level anomalies (MSLA) for sea surface height (SSH, m), 30 m dissolved oxygen (30 m DO, ml L⁻¹), and SSS (psu) were chosen as oceanographic predictor variables for 2002–11 (table 2). Temporal resolution of each environmental parameter was restricted by annual squid occurrence data. We assumed that any seasonal changes in the study area would be reflected in the overall mean annual response, because sample sizes restricted our ability to investigate relationships between squid occurrence and oceanographic variables on shorter time scales.

Satellite data for SST and ocean color and compiled satellite altimetry data for MSLA–SSH were acquired for analysis through Marine Geospatial Ecology Tools in ArcMap 10.0 (Esri 2012). To model the data across the study area, inverse distance weighting in ArcMap 10.0 (Esri 2012) was used to spatially interpolate continuous surfaces for annual mean values of 30 m DO and SSS based on annual point data obtained from NOAA's

National Ocean Data Center World Ocean Data Select database (www.nodc.noaa.gov) and Oregon Fishermen in Ocean Observing Research (Childress 2010). All analyses were performed using the interpolated surface for SSS and 30 m DO. The environmental predictor variables were averaged for all values within a 28 square km cell. Values for SST, chl *a*, SSH, 30 m DO, and SSS were extracted at each positive squid occurrence point. Kernel density plots were developed for exploratory analysis of the overall trend in spatio-temporal fluctuations of the density distribution of environmental conditions across the study area vs. the observed distribution of environmental conditions where Humboldt squid occurred from 2002–11. All density estimations were performed in R (R Development Core Team 2012) version 2.15.0.

Model Selection

To explore the relationship between Humboldt squid occurrence and the environment, oceanographic predictors of Humboldt squid likelihood of occurrence from the NOAA fisheries data were modeled using NPMR in HyperNiche (v2.11) software (McCune and Mefford 2004). NPMR was chosen because it enabled the consideration of multiple oceanographic predictor variables simultaneously and we assumed the response of Humboldt squid to the predictor variables would be complex, nonlinear, and would contain interactions between the predictor variables (McCune 2006). NPMR estimates probability of occurrence by modeling species response to environmental factors by multiplicatively combining all predictors (McCune 2006). Through a cross-validation process, the method uses a local model with a set of predictor variables (Yost 2008). The leave-one-out cross-validation applies local smoothing functions using kernel functions, estimating a target point by weighting nearby observations in the predictor space (McCune 2006).

We followed the binary modeling method from McCune 2011. For a mathematical interpretation of the NPMR model see McCune 2006, and for an additional detailed explanation of the modeling process see Yost 2008. Presence and absence information were only available from the fisheries-independent survey and fisheries-dependent observer program data; therefore, fishermen data could not be used in the model process. The data used in the model included 166 Humboldt squid positive occurrences (presence points) and 3,599 negative occurrences (absence points) from 2003–11 (table 1). Annual SST, chl *a*, SSH, 30 m DO, and SSS were used as environmental predictor variables for the model.

A local mean (LM) based on a Gaussian weighting function (LM-NPMR) was used as the local model to calculate probability of occurrence. Within the software, a model search was utilized to select a model with the most optimum combination of predictor variables,

to choose the standard deviations used in the Gaussian smoothers for each predictor variable (tolerances), and to evaluate model performance (Yost 2008). Within the software settings, a moderate neighborhood size was selected with a 5% range in order to protect against over-predicting or estimating a response in a region without data. The model neighborhood size is the amount of data bearing on the response estimate at any particular point (McCune 2011). We used three evaluation statistics. For a binary response, the statistic used to evaluate model fit is the log likelihood ratio (logB), which provides a measure of optimization for model selection. LogB is the ratio of cross-validated estimates from a fitted model to estimates over a “naïve” model, or the species average frequency of occurrence (i.e., prevalence) in the data set (Schroeder et al. 2010; McCune 2011). Second, we evaluated model performance using the area under the receiver operator characteristic curve (AUC) (Hanley and McNeil 1982). An AUC represents the proportion of correctly predicted presences and absences. An AUC value greater than 0.5 indicates that the model discriminates better than chance. Third, we used the improvement %, or the ratio of cases with species probability estimates improved over the observed species prevalence (Schroeder et al. 2010).

Fitted response surfaces were created to illustrate the effect of interacting environmental conditions on the probability of Humboldt squid occurrence as well as the response curves for the model. Maps of the model prediction output for the year with the greatest positive occurrences in the survey and observer data, 2009, and the least positive occurrences, 2011, were created in ArcMap 10.0 (Esri 2012). Prediction maps were utilized to visually compare the predicted likelihood of Humboldt squid occurrence with overlaid observed positive occurrences made by fishermen, which were not included in the model.

RESULTS

Positive Occurrences and Observed Ocean Conditions

Positive Humboldt squid occurrences varied greatly across years 2002–11 (table 1). In the study area, Humboldt squid occurrences were greatest in 2009 with 116 positive occurrences, and virtually absent in 2011 with 6 positive occurrences. The majority of positive squid occurrences took place 124.4000°W to 125.0000°W in proximity to the shelf-break at the 200-m isobath (fig. 1). Kernel density plots of annual mean SST, chl *a*, SSH, 30 m DO, and SSS in the study area (environment) and at positive squid occurrence sites (observed) suggest that Humboldt squid have some affinity for particular environmental conditions (fig. 2). From 2002–11, Hum-

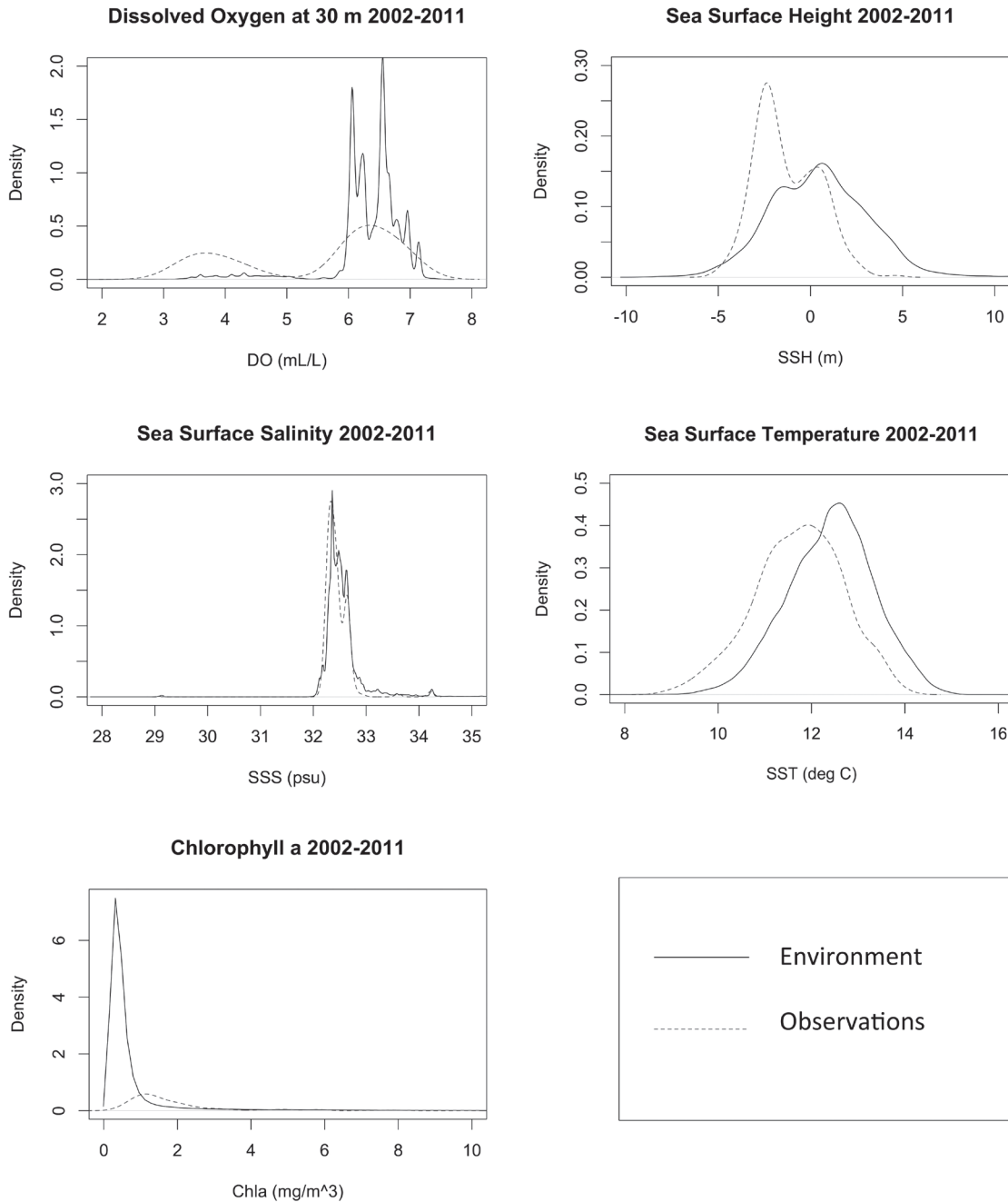


Figure 2. Kernel density plots for 30 m DO (ml L^{-1}), SSH (m) anomalies, SSS (psu), SST ($^{\circ}\text{C}$), and chl a (mg m^{-3}) distributed across the study area (environment; solid) and at positive squid occurrences (observed, dashed) from 2002–11. Humboldt squid were more frequently observed at $3.0\text{--}4.5 \text{ ml L}^{-1}$ and $6.0\text{--}7.0 \text{ ml L}^{-1}$, $-4\text{--}1 \text{ m}$, $32.2\text{--}32.8 \text{ psu}$, $10.5\text{--}13.0^{\circ}\text{C}$, and $0.26\text{--}3.00 \text{ mg m}^{-3}$.

boldt squid more frequently occurred over a SST range of $10.5\text{--}13.0^{\circ}\text{C}$; average 11.7°C and sea level anomalies for SSH from $-4.0\text{--}1.0 \text{ m}$; average -1.3 m . Positive squid occurrences were greatest at $0.26\text{--}3.00 \text{ mg m}^{-3}$; average 1.90 mg m^{-3} chl *a* concentrations. Squid response to DO at 30 m depth was variable with a bimodal response at $3.0\text{--}4.5 \text{ ml L}^{-1}$ and $6.0\text{--}7.0 \text{ ml L}^{-1}$; average 5.5 ml L^{-1} . Humboldt squid most frequently occurred at a SSS range of $32.2\text{--}32.8 \text{ psu}$; average 32.5 psu .

Model Evaluation and Output

Alternative models from the model search process in NPMR are titled by number. LM-NPMR binary Model 960 was chosen as the best model for predicting the probability of Humboldt squid occurrence yielding a logB of 35.91, a cross-validated AUC of 0.810, and an improvement % of 76.1 % for the fisheries-independent and dependent presence/absence data (table 3). Based on the model results, the best predictors for Humboldt

TABLE 3
 HyperNiche (V. 2.11) model evaluation for
 NPMR presence and absence model.

Binary LM-NPMR 960			
Average neighborhood size (N*)	Minimum neighborhood size		
178.7	1		
Input predictor	Min	Max	Range
chl <i>a</i> (mg/m ³)	0.24	19.79	19.55
SST (°C)	9.362	14.35	4.989
SSH (m)	-9.108	7.525	16.63
SSS (psu)	32	35.99	3.992
30 m DO (ml/L)	3.261	7.197	3.936
Model 960 predictor	Tolerance	Tolerance %	
chl <i>a</i> (mg/m ³)	0.977	5	
SST (°C)	0.748	15	
SSS (psu)	0.399	10	
30 m DO (ml/L)	0.394	10	
LogB	Cross-validated AUC	Improvement %	
35.91	0.81	76.1	

Hake Acoustic, Predator, SAIP surveys and the A-SHOP data from 2003–11 for 166 Humboldt squid presence points and 3,599 absence points were modeled using NPMR. LM-NPMR 960 was chosen as the most parsimonious model. Based on model results, annual average chl *a* (mg/m³), SST (°C), SSS (psu), and 30 m DO (ml/L) are the best predictor variables for Humboldt squid likelihood of occurrence with a logB of 35.91, AUC of 0.810, and an improvement % of 76.1%.

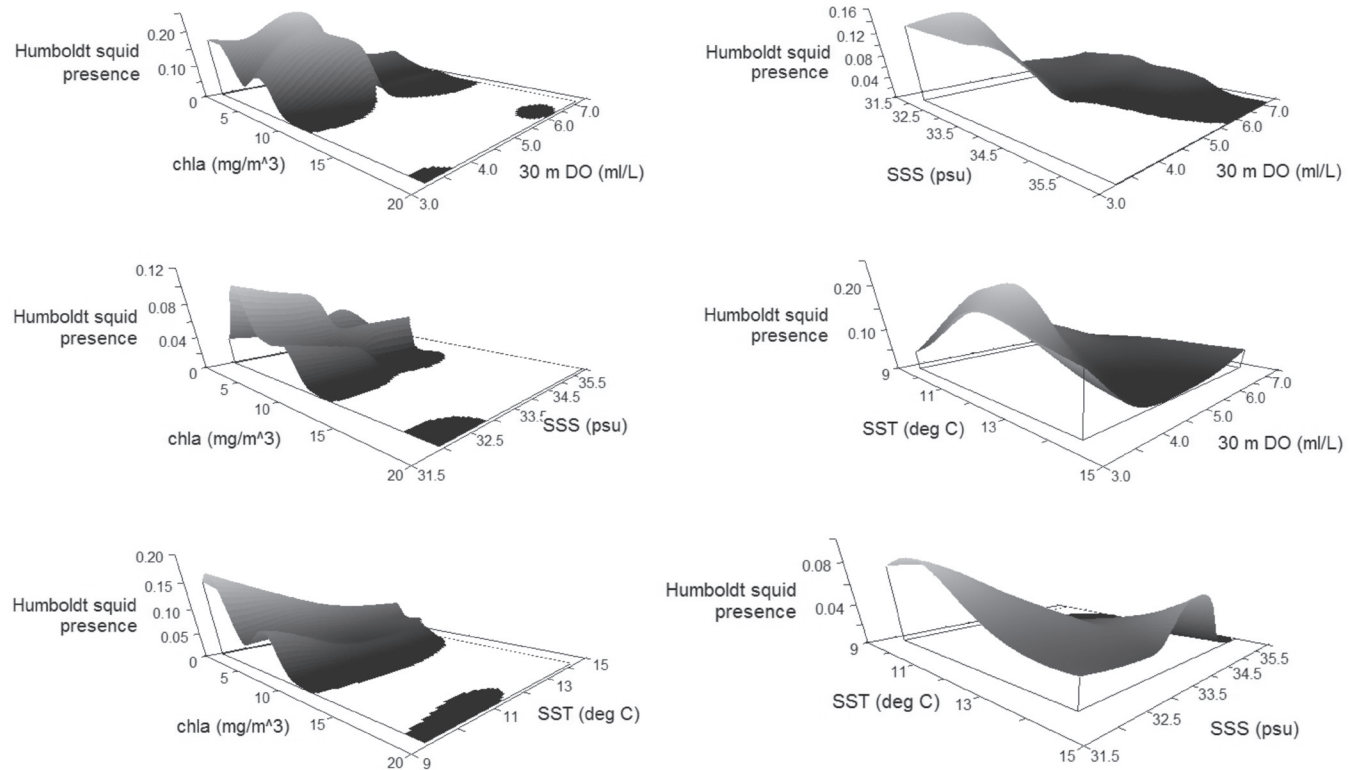


Figure 3. Three-dimensional projected response surfaces from LM-NPMR Model 960. Surfaces represent predictor variable interactions between chl *a* (mg m⁻³), 30 m DO (ml L⁻¹), SSS (psu), and SST (°C) and the impact on positive Humboldt squid occurrence.

squid likelihood of occurrence at 28 square km resolution were determined to be chl *a*, SST, SSS, and 30 m DO. Counter to previous research by Chen et al. 2010, our best fit model did not include SSH, suggesting that SSH anomalies are not a good indicator of squid presence. Fitted response surfaces are given in Figure 3 and the response curves in Figure 4. Geographic information system (GIS) probability maps of Humboldt squid likelihood of occurrence overlaid with observed fishermen sightings within the study area in the year 2009 and 2011 are given in Figure 5.

DISCUSSION

Response and Predictor Variables

Our results suggest that oceanographic conditions are linked to Humboldt squid occurrence in Oregon based on information compiled from fishermen, NOAA fisheries surveys, and observer program data. LM-NPMR model results indicate that 30 m DO is a viable explanatory variable for Humboldt squid likelihood of occurrence. Nutrient-rich bottom waters with low DO content are brought to the surface by upwelling events (Venegas et al. 2008). Humboldt squid are highly tolerant to low DO and unlike other squid, they are able to suppress metabolic activity in the OML and maintain

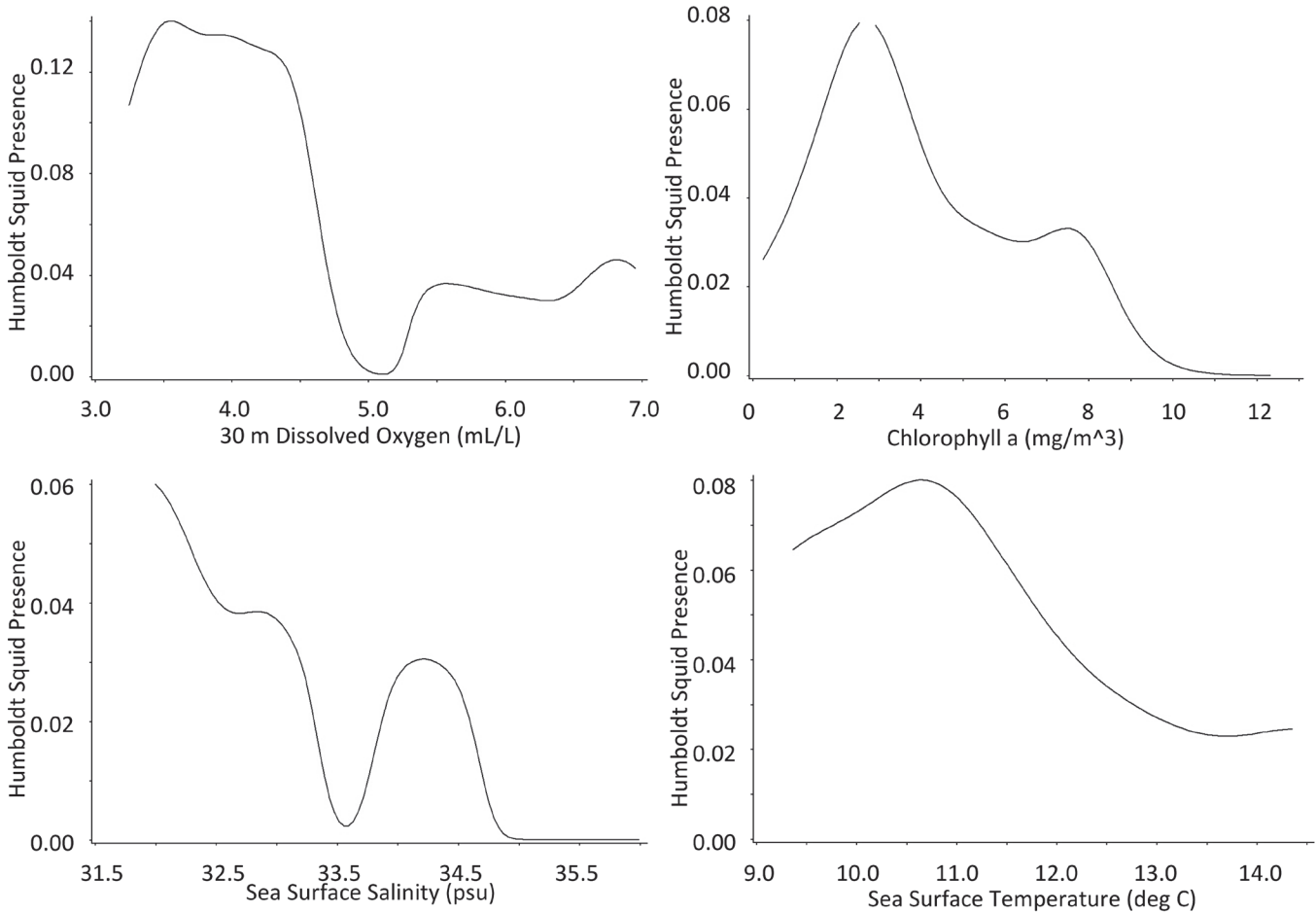


Figure 4. Predicted response to 30 m DO (ml L⁻¹), chl a (mg m⁻³), SSS (psu), and SST (°C) by Humboldt squid derived from NPMR.

activity levels (Gilly et al. 2006). Humboldt squid display diel fluctuations greater than 250 m in vertical movement, where they are found to exploit the OML and avoid high surface temperatures during the day (Gilly et al. 2006; Bazzino et al. 2010; Rosa and Seibel 2010).

Shelf water DO concentrations have been decreasing and the OML has shoaled up to 90 m in the California Current (Bograd et al. 2008) and up to 100 m in the eastern subarctic Pacific (Whitney et al. 2007). Hypoxia has been observed off Oregon since 2002 (Chan et al. 2008) with an unprecedented occurrence of anoxia in the inner-shelf (<50 m) and expansion of hypoxia from the shelf to the inner shelf in 2006 (Chan et al. 2008). Litz et al. 2011 found that in 2009 Humboldt squid density was greatest in the hypoxic waters off of the Columbia River. A greater number of DO measurements are needed to create a robust interpolated surface for DO and further analysis of the effect of DO concentrations on Humboldt squid occurrence should be a research priority.

Our results suggest that SST and chl *a* content are additional predictor variables for Humboldt squid like-

lihood of occurrence. SST has been used as a significant predictor of squid habitat using a GIS (Valavanis et al. 2004), Maxent, and GAMs modeling approaches (Lefkaditou et al. 2008; Litz et al. 2011). Humboldt squid can tolerate wide temperature ranges (Bazzino et al. 2010; Staaf et al. 2011). Humboldt squid thermal plasticity is a key factor to their episodic range expansion (Field et al. 2012). Adult Humboldt squid have been reported to have a temperature threshold of 25°C in the laboratory with an average metabolic rate range between 10°–20°C (Rosa and Seibel 2010) and a daytime preferred temperature range of 10°–14°C at seawater depths greater than 10 m (Bazzino et al. 2010). Our results are consistent with previous research by Litz et al. 2011 for 20 m depth seawater temperature data through 2009 indicating an increase in positive Humboldt squid occurrence at 10.5°–13.0°C from 2002–11. Since these temperatures are too cold for Humboldt squid spawning, squid must migrate to spawn (Staaf et al. 2011) resulting in fluctuations in positive occurrences in the study area.

Our results were similar to previous habitat modeling approaches performed for short-fin squid using GIS

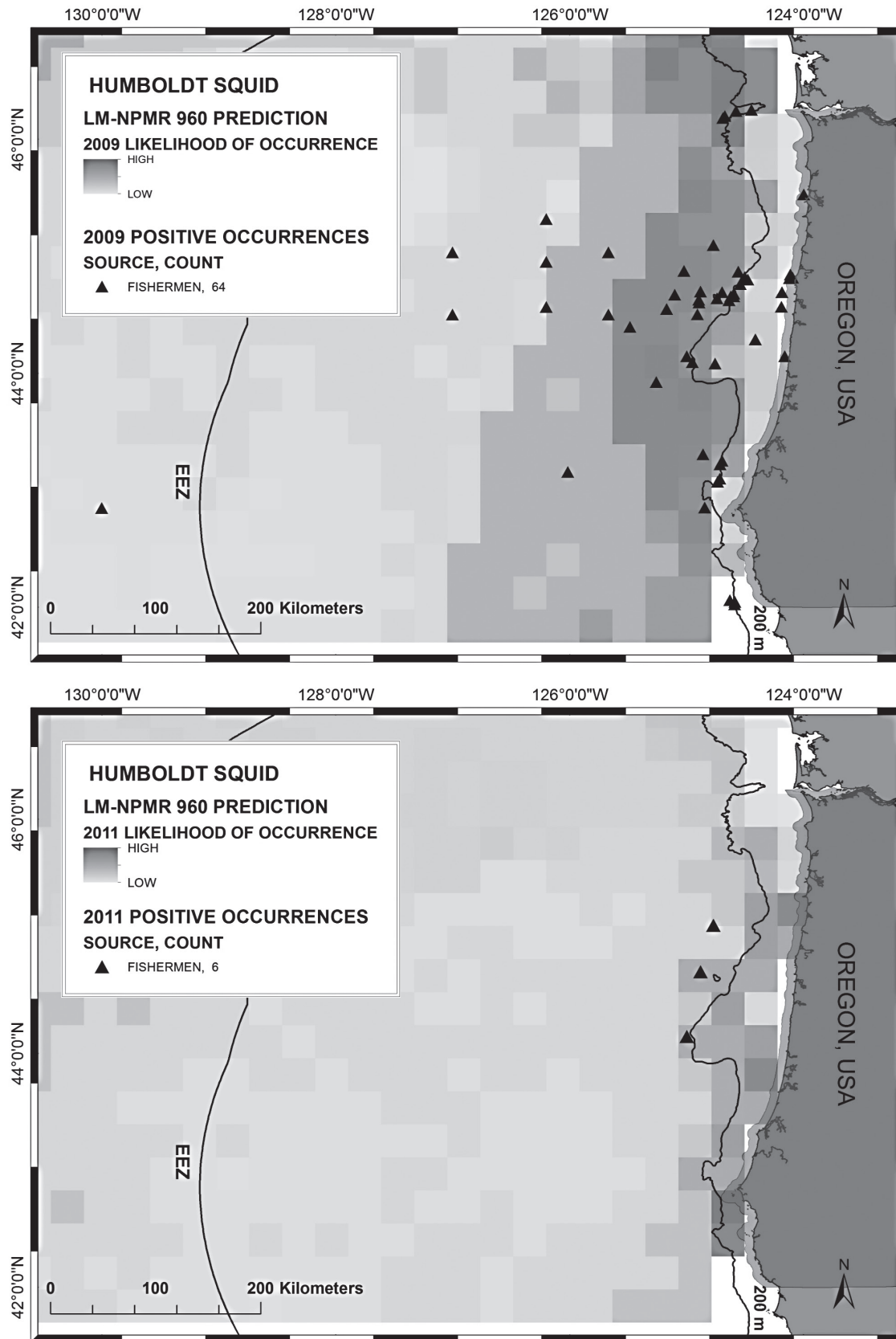


Figure 5. Maps of predicted likelihood of positive Humboldt squid occurrence in 2009 and 2011 overlaid with observed positive occurrences from fishermen not included in the NPMR model.

Essential Fish Habitat modeling (Valavanis et al. 2004), GAMs, and Maxent presence/absence survey data (Lefkaditou et al. 2008) in which chl *a* content was a main predictor of squid occurrence. Chl *a* content can be a proxy for productivity and DO content. We feel that the chl *a* signal could also be an indicator of their spatial distribution in relation to prey availability and fishing effort since most squid were observed around the shelf-break. Future analysis should include more detailed offshore sampling of Humboldt squid in order to evaluate the significance of chl *a* as a main-effect environmental predictor, taking seasonal fluctuations in this variable into account.

Higher SST (Schwing et al. 2002) and lower chl *a* (Chavez et al. 2002) can be found during El Niño events. Water temperature regime shifts caused by La Niña/El Niño events modify environmental conditions and food availability and therefore can potentially change Humboldt squid migration routes (Nigmatullin et al. 2001; Keyl et al. 2008; Mejía-Rebollo et al. 2008). Humboldt squid were first documented in Oregon during the strong El Niño in 1997–98 (Pearcy 2002). Although research has indicated that El Niño events may be one driver for Humboldt squid expansion, it is important to note that Humboldt squid were observed in both fishermen data and survey data during neutral ENSO years and La Niña years between 2002 and 2011. Zeidberg and Robison 2007 found that while El Niño driven expansions and a warm water affinity may have facilitated Humboldt squid presence in central California, these conditions do not dictate their distribution due to their physiological plasticity. Therefore, as a result of complex environmental interactions, considering the contribution of individual oceanographic variables in addition to long-term climatic processes may be more appropriate for establishing when Humboldt squid are most likely to occur off Oregon and southern Washington.

Model Limitations, Sources of Uncertainty, and Error

Numerous habitat modeling techniques are available and NPMR might not be the most suitable approach for a particular data set. NPMR is computationally expensive and is not optimal for extremely small datasets ($n < 10$ times the number of critical habitat factors) or presence only data. Furthermore, it is not suitable if the relationship between the response variable and predictor variables is linear, there is only one predictor variable, or the values of one predictor variable doesn't influence the response to other predictors (McCune 2011). Additionally, if the goal of the research is to predict the equilibrium range of a species, NPMR may underestimate the range of species undergoing expansion or overestimate a range of a species undergoing contraction by the inclusion of geographic variables (Reusser and Lee 2008).

In this study we overcame these limitations by having a sufficiently large data set in which our goal was to predict Humboldt squid occurrence within the proscribed study area extent. While this study was successful in mapping the distribution of Humboldt squid occurrence and the modeling matches expected outcomes, there were sources of uncertainty and error inherent in our data set. Potential sources of error include presence and absence records, interpolation of 30 m DO and SSS surfaces, and annual aggregation. False presence and absence records could have been present in the occurrence data from the observer program and fishermen. With the exception of sightings from two fishermen who targeted Humboldt squid in 2009, positive occurrence records were comprised of bycatch only information, making it difficult to distinguish false records. Although the fishermen data varied in degree of accuracy, the broad resolution that the occurrences were analyzed for did not affect the distribution mapping greatly and contributed to the analysis because it was less uniform and acted as test data for the HyperNiche LM-NPMR model.

Interpolation of SSS and 30 m DO surfaces from in situ measurements were established based on a varying number of measurement points per year. Less data for certain years resulted in spatial clustering, which decreases variability in areas with fewer measurements. This could have resulted in inaccuracies in the projected values. However, despite spatial clustering, relative changes in concentrations of DO at 30 m depth and SSS were captured in the interpolated surfaces because the in situ measurements spanned the study area extent.

Limitations in the temporal resolution of the A-SHOP and fishermen data resulted in the annual aggregation of all occurrences and oceanographic data. Humboldt squid are known to migrate seasonally along the California Current and make seasonal offshore-onshore movements (Field et al. 2012). Additionally, oceanographic conditions vary seasonally. Therefore, annual analysis could have reduced a potential signal of seasonal influences in Humboldt occurrence. However, positive squid occurrences varied highly across years and any seasonal changes in the environmental data, although smoothed, would still be reflected in the overall mean response.

CONCLUSION

This was the first use of NPMR to map Humboldt squid potential habitat in the study area, and based on our results, chl *a*, SST, SSS, and 30 m DO influence the likelihood of Humboldt squid occurrence. For our study purposes, HyperNiche LM-NPMR 960 appeared to be the most appropriate modeling approach to analyze the relationship between broad-scale oceanographic conditions and baseline Humboldt squid distribution. Visual

interpretation of the estimated likelihood of occurrence map outputs for 2009 and 2011 show that predicted Humboldt squid occurrence is consistent with observations from fishermen.

Although examination of annual SSH, SST, chl *a*, 30 m DO, and SSS provided insight into the relationship between the environment and Humboldt squid occurrence, it is critical to consider the influence of prey availability in Humboldt squid migration. Additionally, we feel that it is necessary to evaluate Humboldt squid response to seasonal variability in the oceanographic conditions. Collecting more off-shelf data would be beneficial and provide for a more robust analysis. We recommend that future research include regional occurrences and analysis of SST, SSS, SSH, chl *a*, and DO at varying depths as well as bathymetry. We hope that our results contribute to better understanding Humboldt squid behavior and the impact of Humboldt squid migration in order to help direct future management efforts.

ACKNOWLEDGMENTS

The authors would like to thank all of the collaborators that contributed data and valuable insight to this project including Oregon fishermen, NOAA NWFS FRAM Division, and NOAA NMFS NWFS Predator and SAIP Studies. Many thanks to Al Pazar, Port Orford Ocean Resource Team, Marlene Bellman, Patty Burke, Steve de Blois, Janell Majewski, Rebecca Thomas, Vanessa Tuttle, Ric Brodeur, Bob Emmett, Marisa Litz, Jason Phillips, Jeremy Childress, and Flaxen Conway. This research was sponsored by Oregon Sea Grant under award number NA10OAR4170059 (project number R/RCF-29) from the National Oceanic and Atmospheric Administration's National Sea Grant College Program, U.S. Department of Commerce, and by appropriations made by the Oregon State legislature. The statements, findings, conclusions and recommendations do not necessarily reflect the views of these funders.

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