Distribution patterns of Pacific halibut (*Hippoglossus stenolepis*) in relation to environmental variables along the continental shelf waters of the US West Coast and southern British Columbia

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ABSTRACT

Knowing how Pacific halibut (*Hippoglossus stenolepis*) distribute in relation to ocean conditions is of primary importance to halibut managers, as they are tasked with estimating stock size and designing effective monitoring programs amidst a changing climate. This research examined near-bottom environmental data alongside halibut survey catch data for the years 2006–2009 on the continental shelf of Oregon, Washington, and southern British Columbia. The objectives of the research were to: (1) characterize summer environmental conditions and halibut distribution; (2) explore ranges and possible tolerance thresholds for halibut in relation to temperature, dissolved oxygen (DO), salinity, and pH; and (3) identify the primary environmental factors affecting distribution of halibut and model the observed relationships. Seasonal hypoxia is an annual feature of the study area and results suggest halibut exhibited an apparent DO minimum threshold of 0.9 mL L^{-1}. Ordinary least squares multiple regression analysis indicated that depth, temperature, and DO were significant variables in predicting halibut distribution, whereas salinity and bottom type were not. Ambiguity in model results led to the use of two additional analytical methods, geographically weighted regression (GWR) and tree regression, to examine regional variation and the overarching structure of halibut distribution. The three models yielded similar results indicating the importance of DO and temperature as variables describing structure. The GWR model yielded the best fit of the three when using DO as a predictor variable, indicating that regional variation is a factor. These results suggest that low, but above-threshold, DO may be contributing to catchability differences in the survey.

INTRODUCTION

Pacific halibut (*Hippoglossus stenolepis*) have been commercially harvested along the US and British Columbia west coast since 1888 and fished by the many tribes of the region for hundreds of years. Today, the fishery spans the entire North American habitat range from northern California to the Bering Sea and remains an important commercial, tribal, subsistence, and recreational resource (IPHC, 1998). Since 1923, Pacific halibut have been managed by the International Pacific Halibut Commission (IPHC), which conducts stock assessments predominantly using catch statistics, age analyses, size, and sex data (Clark and Hare, 2006). In recent years, as ecosystem-based models have become more widely explored in fisheries and evidence of environmental variability due to climate change mounts, the need to better describe and understand halibut habitat and the effects of environmental variability on distribution, physiology, and behavior has arisen.

The waters off the coasts of Oregon, Washington, and southern British Columbia encompass a transition zone for large-scale upper ocean currents and gyre systems in the northeast Pacific Ocean (Fig. 1). Due to

Figure 1. Major ocean currents within the study area spanning from 42°N latitude to 52.10°N latitude off the US and southern British Columbia west coast. Due to frequent periods with north winds in spring and summer and a southward flowing upper ocean current, upwelling events dominate oceanographic processes along the shelf in the central and southern portions of the study area as indicated by the cross-shelf arrows. Likewise, intermittent downwelling is present to the north.
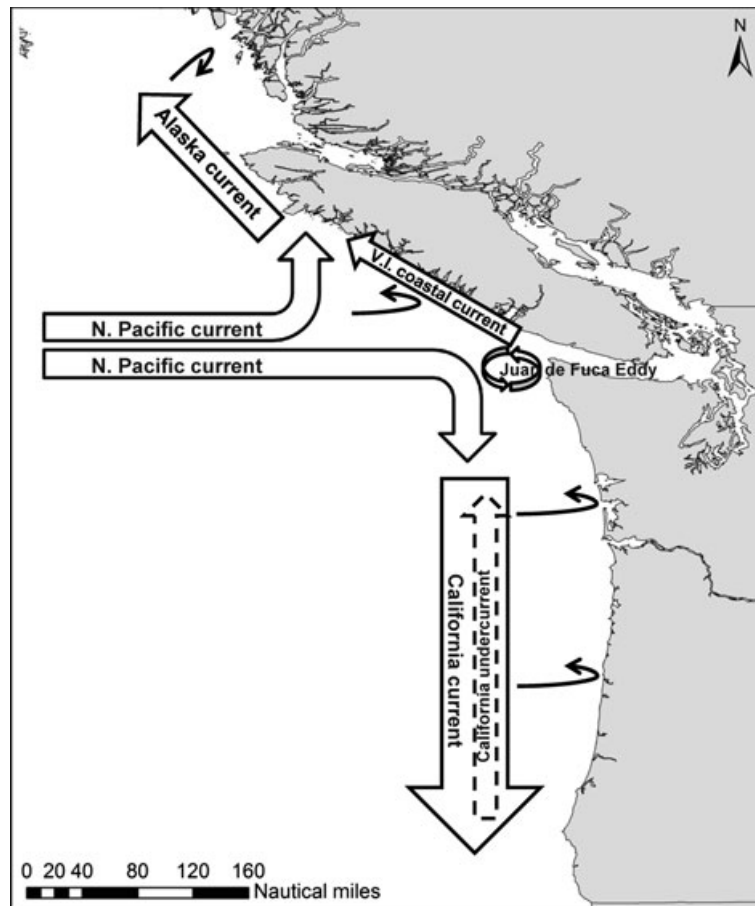
frequent periods with north winds in spring and summer and a southward flowing upper ocean current, upwelling events dominate oceanographic processes along the shelf in the mid and southern portions of the study area. This upwelling brings cool, nutrient-rich, and low dissolved oxygen (DO) water near to the surface which, coupled with high primary production, results in areas of particularly low oxygen. Other features such as the northward flowing California Undercurrent, submarine canyons, and riverine and estuarine outflow contribute to the intensity of upwelling effects (Hickey and Banas, 2003). In the northern part of the range is Queen Charlotte Sound, close to the origin of the Alaska Current, which also receives nutrient-rich fresh water via the Strait of Georgia on the east side of Vancouver Island (Crawford *et al.*, 2007). Studying these environmental variables at the extreme of the larger habitat may be particularly informative in identifying thresholds and tolerances.

Projected increases in global temperatures have inspired myriad studies looking into the effects of climate change on species distributions (e.g., Hollowed *et al.*, 2012; Stabeno *et al.*, 2012), especially where commercial fisheries exist. Two-decade-long studies noted significant geographic relocation of fish habitats with increasing temperatures (Perry *et al.*, 2005; Sabates *et al.*, 2006). Mueter and Litzow (2008) showed that fish communities in the Bering Sea altered their range in concert with changes in sea-ice cover and the extent of the cold pool.

Dissolved oxygen concentration in ocean waters has gained increasing global attention in recent years as the number and expanse of hypoxic zones (DO < 1.4 mL L^{-1}) have increased (Diaz and Rosenberg, 2008, 2013). Seasonal hypoxic conditions occur off the coast of Washington State on the mid- to outer shelf and occasionally the inner shelf, according to Connolly *et al.* (2010) who studied historical

observations from 1950 to 1986. They reported that historical levels were comparable to those observed in the 2000s, with the exception of 2006, when hypoxic conditions were of a greater magnitude and spanned a broader range than seen previously. Off Oregon, the authors noted rare prior incidences of low DO, but regularly occurring seasonal hypoxia is thought to be a relatively new development on the inner-shelf region, having been detected annually since 2002 (Chan *et al.*, 2008; Gewin, 2010).

The study of fish response to low DO is of increasing concern as hypoxic zones that were once primarily features of the deep ocean, are shoaling and expanding onto the continental shelf (Keeling *et al.*, 2010). Different fish species likely have different tolerance thresholds for DO, and demersal fishes, especially those found in deeper water (and naturally lower DO) of the continental shelf, e.g., Pacific halibut, may be more tolerant of low levels than their pelagic or shallow counterparts. Studies have noted the effects of hypoxia, including notable displacement of mobile organisms, and mortality or density reduction of sessile organisms (e.g., Wannamaker and Rice, 2000; Rabalais *et al.*, 2001a,b; Breitburg, 2002). Specific to the west coast region, during the particularly intense hypoxic event off Oregon and Washington in 2006, Chan *et al.* (2008) used a remote submersible and found massive kills of stationary and slow-moving organisms, and an absence of mobile fishes (both dead and alive), suggesting that mobile fish were able to move to locations with more tolerable DO levels. Keller *et al.* (2010) described differences in biomass of trawl-caught species based on DO concentration and found that eight fish species showed a significant decrease in biomass with lower DO, although another seven showed no significant difference. It is unclear whether the fish simply moved out of the hypoxic zone or actually suffered mortality as a result of DO stress.

Ocean acidification, i.e., decreasing pH in the global ocean due to seawater reacting with increasing atmospheric CO_2 concentrations, is now a widely accepted concept (Caldeira and Wickett, 2005). However, not all seawater has the same chemical properties. Deep water that is upwelled, for example, is typically of low pH and can be under-saturated with respect to aragonite. Recent research (Hofmann and Schellnhuber, 2009) has shown that ocean acidification does not exist independently of other environmental factors but is part of a complex system where acidification triggers or contributes to the expansion of marine hypoxic zones.

Studies on the effects of acidification on biological processes have shown a multitude of results. For fishes,

metabolic suppression to wait out temporary periods of acidified water like that found in upwelling zones (Feely *et al.*, 2008) is one identified coping mechanism (e.g., Guppy and Withers, 1999; Seibel and Walsh, 2001; Michaelidis *et al.*, 2007). Consequences of metabolic suppression over the long term are decreases in growth and reproduction which could impact the health of the population, although species routinely exposed to environmental fluctuations of pH, may possess a higher tolerance to periodic low pH compared with animals that are not exposed (Fabry *et al.*, 2008). There may also be compounded effects with other environmental factors such as DO and temperature (Pörtner, 2008; Vaquer-Sunyer and Duarte, 2011).

Adult halibut distribution, like that of its juvenile counterparts (Stoner and Titgen, 2003), may be influenced by bottom-type preferences. For example, structured bottom may act as refuge from predators, sandy or muddy bottom may allow for burrowing, and each bottom type likely hosts a unique set of prey species.

Research of environmental factors relating specifically to Pacific halibut, has focused primarily on temperature. The earliest effort (Thompson and Van Cleve, 1936) to describe distribution in relation to an environmental factor, was a detailing of temperature and catch data gathered from the commercial fishery for a similar species, Atlantic halibut (*Hippoglossus hippoglossus*). This analysis determined that 3–8°C was the most favorable to halibut, but also recognized considerable variability around that range. Subsequent studies on Pacific halibut broadly support that finding. In the Bering Sea and Aleutian Islands, juvenile halibut catch was highest in 4–5°C and they were rarely caught below 2°C (Best, 1977). Satellite tagging research in the Bering Sea and Gulf of Alaska found adult halibut occupied waters from 1.4 to 11.6°C but spent the majority of time in the middle of the range (Loher and Seitz, 2006; Seitz *et al.*, 2007, 2008). A separate study in the same area recorded temperatures ranging from 5 to 10°C, but found no significant catch differences within the observed range (Loher, 2008). Particularly applicable to the study region are results from a satellite tagging study conducted off the west coast that showed adult halibut occupying temperatures from 3.6 to 13.6°C, also with a tendency toward occupying the middle of the range the majority of the time (Loher and Blood, 2009).

Other recent studies involving halibut have looked at the effect of temperature and climate on stock size, growth, and recruitment. Hurst *et al.* (2005) noted increased growth with increasing temperature in juvenile halibut. In a study examining the effects of interannual and decadal environmental variability, Clark

and Hare (2002) concluded that Pacific halibut year-class recruitment was strongly influenced by climatic regime in the year of spawn. Stoner *et al.* (2006) conducted laboratory experiments focusing on activity level and feeding behavior, and found that temperature affected both. Stoner and Titgen (2003) found that bottom type affected distribution of juvenile halibut, but no such studies have been conducted on adults. The authors are not aware of any research involving Pacific halibut and other environmental variables such as DO, salinity, or pH.

This study focused on three objectives: (1) characterizing summer environmental conditions and halibut distribution observed at depth during the IPHC setline survey throughout the study area; (2) exploring ranges and possible tolerance thresholds for halibut in relation to temperature, DO, salinity, and pH; and (3) identifying the primary environmental factors affecting distribution of halibut and modeling the observed relationships.

METHODS

Data collection

The geographic location spanned southern Oregon's continental shelf (latitude 42°00′N) northward to Queen Charlotte Sound (latitude 52°10′N) in depths of 29–536 m. Data were collected at 168 stations during the IPHC setline survey where sampling stations were located on a 10 × 10 nautical mile grid (nmi, one nautical mile = 1.852 km) (Fig. 2). The spatial configuration of the survey sampling design was selected to minimize variance of mean catch per unit effort (Parma *et al.*, 1994), maximize density of stations (Randolph and Larsen, 1999), and provide a logistically feasible design that could be sampled efficiently (Soderlund *et al.*, 2012). Each survey station was sampled annually and each year's sample occurred during the months of June to August. Data were collected from 2006 to 2009 and all regions were fished in those years. However, environmental data were collected over the entire region only in 2008 and 2009, in the entire region except the Washington coast in 2007, and north of Washington state-only in 2006. Table 1 summarizes data collected for this analysis which totaled 527 station samples over the 4 yr. time frame. Note that pH sensors were only available for part of the study period.

The survey was standardized in terms of gear used and fishing practice. It included a longline consisting of skates (one skate = 1800 feet, or 549 m) equipped with 100, number three circle hooks (also known as 16/0), each spaced 18 feet (5.49 m) apart (IPHC, 2008). The number of skates fished at each station

varied by year, ranging from five to seven. The gear was set and allowed to soak for a minimum of 5 h before retrieval. Species catch counts were conducted as the gear was pulled from the water. Catch data were then converted to numbers per unit effort (NPUE, numbers per skate) at that geographic location.

Just prior to haul back of the fishing gear, a water column profiler manufactured by Sea-bird Electronics, Inc. (models SBE19, SBE19plus, and SBE19plus V2) was deployed to obtain coincident environmental data. The deployment assembly (Hare, 2001) consisted of floats attached to the top of the profiler along with a line connecting it to the deck of the vessel at all times, and a 40-pound anchor at the bottom. The float and anchor assembly allowed the profiler to drop through the water column at a rate of approximately $1–2$ m s^{-1} and descend to within 5–10 m of the sea floor. Once the anchor hit bottom, the floats provided positive buoyancy for the profiler, pulling it toward the surface so that it would not become damaged by impacting the ocean floor. In this study, the instrument's recorded readings at the profiler's maximum depth were used to represent the conditions experienced by the animals caught by the gear.

The environmental variables collected and evaluated in this study included pressure (comparable to depth in meters and referred to as such in this manuscript), temperature, salinity, pH, and DO (Table 2). Malfunction of the pH sensor during portions of the data collection resulted in a total of 222 useable pH observations. The result was that pH was used qualitatively in this study, but was not used as an explanatory variable in the regression models.

Bottom type was not collected during the survey but was added as a variable using data from U.S. Geological Survey (USGS[1]) and Fisheries and Oceans Canada (DFO[2]). Off Oregon and Washington, bottom type was based on data collected during multiple cruises and sources compiled by the USGS. Stations for this study were assigned a bottom type based on the closest sampled stations. For southern BC, three bottom type categories were presented as a surface map. Stations for this study were overlaid on the map and assigned the corresponding bottom type. There were more categories of defined bottom type off the West

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[1]Data retrieved from the United States Geological Survey (USGS) website. usSEABED: Pacific Coast Offshore Surficial-Sediment Data Release, version 1.0. 12 March 2012.http://pubs.usgs.gov/ds/2006/182/usseabed.html.
[2]Data retrieved from Fisheries and Oceans Canada (DFO) website. Mapster v3. 12 March 2012. http://www.pac.dfo-mpo.gc.ca/gis-sig/maps-cartes-eng.htm.

Figure 2. The study area extends from southern Oregon to Queen Charlotte Sound, B.C. Both catch and oceanographic data were collected on a 10 × 10 nmi grid depicted on this map (+) for each sampling station. The 200-m and 500-m depth contours are shown.
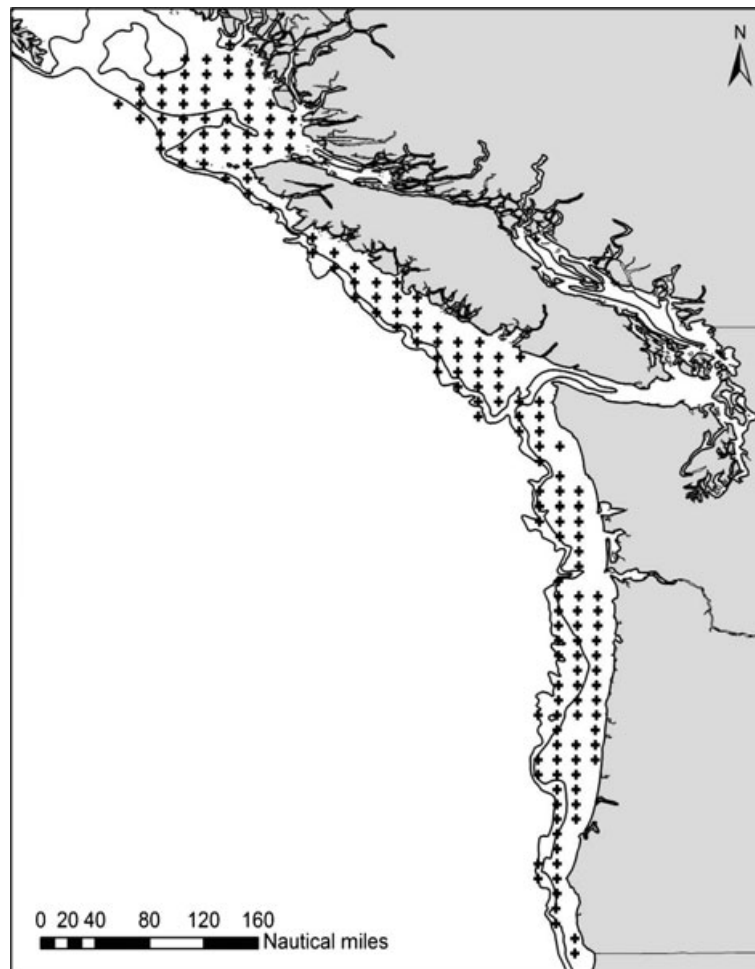
Coast than in British Columbia (BC), so the West Coast categories were collapsed into three. The final categories were: mud/silt, sand, and pebbles/hard bottom.

Analysis methods

Isosurface maps of near-bottom environmental conditions were generated using OCEAN DATA VIEW software (Schlitzer, 2010) and maps of NPUE were generated using ARCGIS software. Untransformed data for all years were combined for exploratory purposes to examine the relationships between NPUE and environmental factors, using scatterplots and loess smoothed least squares regression lines. These comparisons helped to identify both geographic and overall patterns in the data. Additionally, understanding how or whether explanatory variables are correlated is essential to interpretation of both the simple as well as the more complex models. To that end, a Kendall's tau correlation test was performed on each variable pairing.

Three different types of models were used to examine species NPUE in relation to environmental variables. First, a multiple regression model was used to characterize which factors were most influential on the distribution of halibut, the nature of the relationship between halibut and the significant factors, and to explore to what degree NPUEs can be predicted by a linear model with the suite of variables available. Secondly, spatial analysis was used to study clustering of model residuals and regional variability (also called non-stationarity), i.e., the validity of the linear regression model across the study area. Finally, tree regression analysis was used to identify which variables were most influential area-wide versus those more influential on a local level, and to explore non-linear relationships that may exist.

Table 1. Number of sampling sites and type of oceanographic data collected during the 4-yr study, organized by geographic region.

Year	Sampling sites	Region	Depth, temperature, salinity	Dissolved oxygen	pH
2006	0	Oregon	0	0	0
	0	Washington	0	0	0
	33	Vancouver Island	33	33	0
	42	Queen Charlotte Sound	42	42	0
2007	56	Oregon	56	56	56
	0	Washington	0	0	0
	32	Vancouver Island	32	32	0
	40	Queen Charlotte Sound	40	40	0
2008	55	Oregon	55	55	47
	24	Washington	24	24	21
	36	Vancouver Island	36	36	0
	42	Queen Charlotte Sound	42	42	0
2009	57	Oregon	57	57	57
	26	Washington	26	26	26
	38	Vancouver Island	38	38	11
	46	Queen Charlotte Sound	46	46	4
Total	527	4 regions	527	527	222

Table 2. Model names and manufacturer-published accuracy specifications of oceanographic instruments used in this study.

Instrument/Model	Initial accuracy	Resolution	Stability
SBE19plus V2 CTD			
Pressure (strain gauge db)	1	0.02	1/yr
Temperature (°C)	0.005	0.0001	0.0002/month
Conductivity (S/month)	0.0005	0.00005	0.0003/month
SBE19plus CTD			
Pressure (strain gauge db)	1	0.02	0.5/yr
Temperature (°C)	0.005	0.0001	0.0002/month
Conductivity (S/month)	0.0005	0.00005	0.0003/month
SBE19 CTD			
Pressure (strain gauge db)	2.5	0.15	None posted
Temperature (°C)	0.01	0.001	
Conductivity (S/month)	0.001	0.0001	
Dissolved oxygen – SBE 43	2% of saturation		0.5% per 1000 h
pH – SBE 18	0.1 pH		Variable

The NPUE data were highly skewed with large numbers of zero stations. A number of transformations were examined to normalize the data and they were ultimately transformed using a Box–Cox power transformation (Box and Cox, 1964), which can be more effective in dealing with zero value data than traditional methods (Osborne, 2010). Power transformations are selected based on the value that provides the lowest standard deviation and as close to a normal distribution as possible. After consultation with a biometrician at IPHC (R. Webster, pers. comm., 2320 W Commodore Way, Seattle, WA 98199, U.S.A.), a power transformation of 0.4 was ultimately selected (Eqn 1).

$$\text{Boxcox}(y) = (y^{0.4} - 1)(0.4) \qquad (1)$$

Ordinary least squares (OLS) regression (Eqn 2) was conducted on the two full years of data combined (2008 and 2009) using a backward elimination process

to select explanatory variables, where significance was determined by a *P*-value of ≤0.05. The regression equation is:

$$Y = \beta_0 + \beta_1 x_1 + \ldots \beta_n x_n + \varepsilon_s \qquad (2)$$

where Y = NPUE, β_n = regression coefficients, n is an index for each predictor used, and x is the predictor variables. A k-fold cross validation method (Kohavi, 1995) was used to test the robustness of the model and the validity of the explanatory variables. In this case, the data were divided into three subsets, two being used as the training set and one as the validation set.

Spatial analysis was conducted on the 2009 data using ArcGIS software v.9.3.1. This software allowed the examination of model results geographically, which can provide information on the spatial structure of the data that may be missed with other methods. As a first step, OLS linear regression was used to confirm that the significant variables found in the combined multiple regression analysis were valid for the single-year model used here. Residuals were mapped geographically and examined with Moran's I (Moran, 1950), QQ plots, and histograms.

Using only environmental data, residuals were not normally distributed and Moran's I confirmed a high level of residual clustering. The data were examined by geographically mapping NPUE as well as the residuals from the base model. A new variable was added to account for the clustering, termed *A* or the *aggregating variable* (Eqn 3). This new weighting variable was developed by accounting for relative numbers of halibut (NPUE) at survey stations directly adjacent to and, in most cases, within 10 nmi (Fig. 2) of the data point being evaluated. The only exception was a station off of north Vancouver Island where the nearest station was approximately 14 nmi away and so that station was used. The following formula was used to calculate A for each data point:

$$A_a = \text{Mean}(\text{NPUE}_{\text{adjacent stations}}) / \sum \text{NPUE}_{\text{all stations}} \qquad (3)$$

where a = the station being evaluated. Therefore, A was always less than one, larger for stations with higher adjacent NPUEs, and smaller for lower adjacent NPUEs.

The addition of the aggregating variable stabilized the multiple regression model. Ruppert *et al.* (2009) applied a similar solution when looking at Atlantic cod (*Gadus morhua*) distributions in relation to environment. The variables ultimately available for the regression models included depth, temperature, salinity, DO, substrate (bottom) type, and aggregation.

Model diagnostics such as Joint Wald, Joint F, and the Koenker statistic were used to ensure the model was valid. The best model fit was selected using R^2_{adj} and Akaike's information criterion (AIC) values.

Even given the addition of the aggregating variable, an examination of standardized residuals continued to indicate non-significant but mild clustering (regional variation). Geographically weighted regression (GWR), developed by Fotheringham *et al.* (1997, 1998) and available as an application in ArcGIS software, was used to address this. Specifically, GWR develops regression coefficients and intercepts for each data point, working from the base assumption that these may not be the same throughout the study area (Brunsdon *et al.*, 1998). Exploration of the kernel bandwidth parameter led to the ultimate use of a fixed kernel (i.e., allowing the program to choose the optimal distance) as opposed to an adaptive kernel where the number of neighbors (i.e., stations) is defined. GWR was an improvement over OLS but the number of variables used was reduced to avoid collinearity problems that arose, due to fewer stations being involved in each calculation. As with OLS, standardized residuals were examined using histograms, normal QQ plots, and Moran's I.

Questionable model performance, i.e., clustering of residuals in this case, can also be caused by spatially correlated variables. A univariate-response tree regression (Breiman *et al.*, 1984) was undertaken with halibut NPUE plotted against the environmental variables: latitude, depth, temperature, DO, and bottom type. Salinity was removed because of its high correlation with other variables and because it was within the range where there was no expectation of fish preference or avoidance behavior. There were also a large number of missing values for pH which, when using this statistical package, resulted in station/rows being dropped from the analysis, so it was not used for the 2009 model. Finally, the aggregating variable was not used since it had been constructed to stabilize the residuals in the linear models and was not needed for that purpose here.

The tree model, a form of clustering, builds a tree structure that splits into branches where the dissimilarity of sites within clusters is minimized (i.e., each split minimizes the total sums of squares within the two nodes and maximizes between nodes) (De'ath, 2002). The structure is such that splits at the top of the tree reflect variables that operate at larger, area-wide, spatial scales, and subsequent splits reflect finer scale (local) variability (Moore *et al.*, 1991; Ruppert *et al.*, 2009). This model type yields interpretable results even when variables are collinear (Loh, 2006), and in

the face of non-linear and interactive relationships between variables (De'ath and Fabricius, 2000). Franklin (1998) and Vayssieres et al. (2000) compared tree regression analysis with generalized linear models and generalized additive models and found that tree models yielded better predictions. In this study, the tree regression was used as a complement to the other models in identifying structure of the distribution as well as to help identify underlying issues. A pseudo-R^2 (Eqn 4) was calculated using deviance so that model performance could be compared with the OLS and GWR methods.

$$\text{pseudo} - R^2 = 1 - (\text{model deviance/null deviance})$$
$$(4)$$

where the model deviance is the measure of model fit with explanatory variables and the null deviance is the model fit without explanatory variables, i.e., uses only the grand mean and reflects natural variability. The lower the deviance, the better the model fit.

The tree was examined to see whether 'pruning' was needed using the cross-validation method where deviance was examined for each split to detect where the tree had the smallest predicted mean square error (described in Breiman et al., 1984). Ultimately, it was determined that the package default of a 1% threshold for terminal nodes was sufficient (i.e., where the mean square error was 1% or below and no splits were made beyond that level).

The R statistical package was used for all tree analyses described here (http://www.r-project.org). Major supplemental libraries included: vegan (Oksanen et al., 2012), MASS (Ripley et al., 2012), and tree (Ripley, 2012).

RESULTS

Halibut were found at all latitudes within the study area but were clearly in higher numbers with increasing latitude. Figure 3 illustrates the catch results for each study year along with iso-surface renditions of concurrent near-bottom DO and temperature. DO ranged from 0.49 to 6.09 mL L^{-1} for all years combined with the lowest concentration observed in 2007 off Oregon. Temperature ranged from 5.15 to 10.54°C with the general pattern of lower temperatures to the north and within the upwelling zone off the west coast. The highest temperatures were observed at shallow, nearshore stations and at a group of shallow stations in Queen Charlotte Sound, called Goose Island Bank. Both the lowest and highest temperatures observed during the study were observed in 2009.

The survey spans the known summer depth distribution of halibut (IPHC, 1998) and halibut were found to depths of 389 m during the study. All of the stations with depth >389 m were located off Oregon where DO was very low. Figure 4 illustrates the untransformed relationship between halibut NPUE and each of four variables: depth, DO, pH, and temperature for all years combined. This relationship was statistically significant for depth (P-value 3.8e-08) and DO (P-value <2.2e-16), but not temperature (P-value 0.7613) or pH (P-value 0.0947). The data suggest that halibut are able to tolerate DO concentrations to about 0.9 mL L^{-1}, but not below this level (i.e., halibut were readily observed in DO concentrations above this level, but not below it). A closer examination of the relationship reveals that there was also a tendency for increasing NPUE between 0.9 mL L^{-1} up to approximately 3 mL L^{-1}, where it then leveled off. Near-bottom pH in the area ranged from 7.5 to 8.0. Halibut were found in highest concentrations between 7.6 and 7.8, but were also found throughout the range of values seen in the study, so no apparent threshold was identified. Temperatures above approximately 8.5°C yielded no zero halibut stations, whereas temperatures below 8.5°C yielded both zero and non-zero halibut stations. Temperature thresholds for halibut did not appear to be reached during the survey.

Multiple regression modeling showed that several variables play a role in halibut NPUE, yielding significant values for all variables except salinity and bottom type. Coefficients indicated a positive correlation between NPUE and DO, and a negative correlation with depth and temperature. Aggregation was also significant, but was considered an explanatory variable only in its use as a stabilizer. The R^2_{adj} for the 2-yr regression model was 0.57, and 0.64 for the 2009-only model (Table 3). The inclusion of the aggregation variable reduced the clustering of residuals in the model, but the Moran's I test continued to indicate statistically non-significant but mild clustering. To specify the GWR model, different combinations of statistically significant (as determined using the OLS model) explanatory variables were tested and the combination of DO and aggregation was ultimately chosen, improving the fit considerably over OLS with an R^2_{adj} of 0.72. When mapped geographically, the residuals for both the OLS and GWR models (Fig. 5) showed more clustering in the south (i.e., groupings of like-colored points) compared with the more random pattern in the north. Additionally, the GWR model showed less clustering overall than the OLS model, especially in the mid-latitudes of the study area, and was thus determined to be a better fit. The OLS model

Figure 3. Observed Pacific halibut NPUE (left column) and concurrent near-bottom environmental conditions shown as iso-surface maps (second and third columns) for each year 2006–2009 along the northern US and southern British Columbia coast. Iso-surface maps generated using OCEAN DATA VIEW (Schlitzer, 2010).
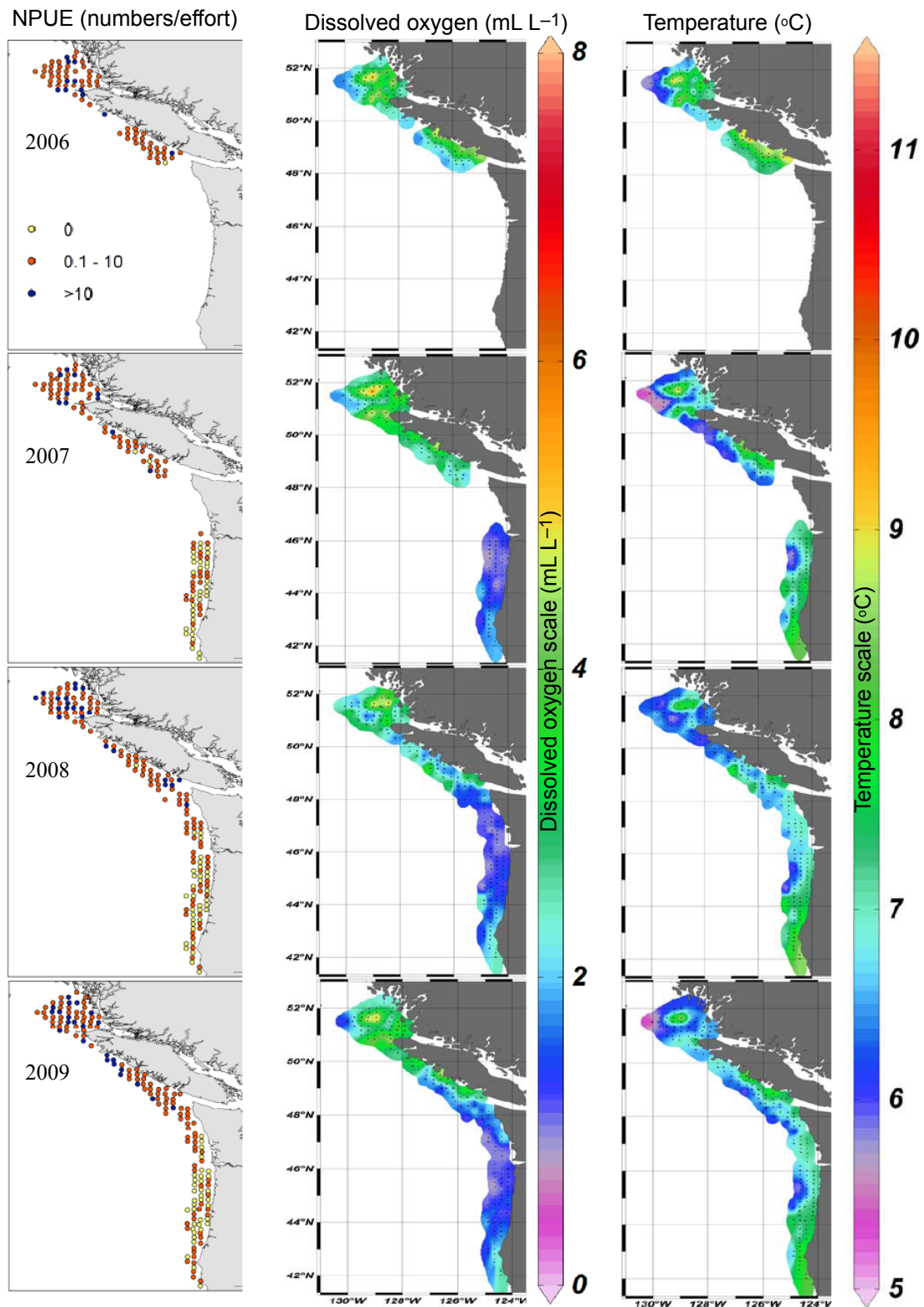
Figure 4. Scatterplots of halibut NPUE for all study years combined (*y*-axis) plotted against depth, dissolved oxygen concentration, pH, and temperature. A loess smoothed regression line is included.
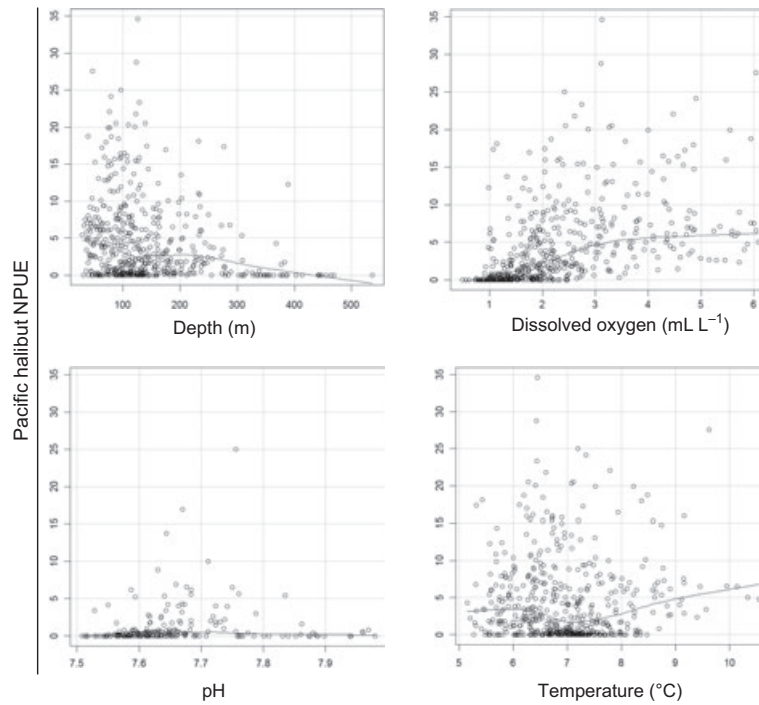

Table 3. Final multiple regression model results for Pacific halibut.

	2008–2009 combined OLS			
Variable	Coefficient	SE	*P*-value	K-fold *P*-value
Intercept	9.056	1.368	1.50e-10	–
Pressure	−0.006	0.001	4.70e-06	3.60e-13
Temperature	−1.547	0.193	2.30e-14	<2e-16
Oxygen	1.274	0.132	<2.0e-16	<2e-16
Aggregation	99.773	21.381	4.50e-06	4.5e-06
R^2	0.59			
R^2_{adj}	0.57			

	2009 only					
	OLS			GWR		
Variable	Coefficient	SE	*P*-value	Variable		
Intercept	7.467	1.865	0.0001	–	Bandwidth	146 732
Depth	−0.003	0.002	0.0454	–	Res. Squares	261.05
Temperature	−1.414	0.259	0	–	Eff. Number	24.69
Oxygen	1.342	0.171	0	X	Sigma	1.35
Aggregation	100.640	28.414	0.0005	X		
AIC	625			595		
R^2	0.65			0.76		
R^2_{adj}	0.64			0.72		

OLS refers to ordinary least squares regression and GWR refers to geographically weighted regression.

also failed to distinguish between zero and low NPUE stations in the south. The GWR model prediction showed less variability in NPUE among stations north of Washington than the observed, but the general distribution pattern was captured. Figure 6 illustrates the observed NPUE and predicted NPUE of the three model types.

The Kendall's tau correlation test revealed that nearly all variable combinations were correlated with one another (Table 4). The two exceptions both involved pH as one of the variables (i.e., depth/pH and salinity/pH combinations). Because there was a high rate of correlation, using a model that tolerated correlated variables (the tree regression model) was a logical next step to examining structure. This model identified the same explanatory variables found with the OLS and GWR models, i.e., location (latitude), DO, depth, and temperature. It was also useful in identifying non-linear relationships within the data such as the fact that the relative importance of DO and temperature to determining NPUE varied in relation to depth, i.e., in areas above threshold, DO appeared to be a stronger determinate in shallow water and temperature was a stronger determinate in deeper depths.

Placement of a variable on the tree and the relative length of the vertical arms both reflect structure (Fig. 7). Latitude was the primary splitting factor followed by DO, meaning that those two variables were the most important in explaining the area-wide distribution pattern. They also exhibited the longest vertical branches, meaning that a large amount of variability was explained with those two splits alone. Depth, temperature, and DO were splitting factors further down on the tree, which can be interpreted as those being the most important factors on smaller geographic scales. The lowest mean NPUE of 0.34 was found at lower latitudes with no other significant variables, which included southern Washington and Oregon. The highest mean NPUE of 17.0 was at latitudes north of southern Washington, where DO was >2.3 mL L^{-1}, temperature was between 6.5 and 7.2°C and depth was >92 m.

When compared with the other two model types, the tree regression model yielded a pseudo-R^2 of 0.65, which was a slight improvement over the OLS model but lower than the GWR model. It also failed to predict zero versus low NPUE stations in the south, leaving the GWR model as the only one of the three types that did so. Note that the R^2 values were a useful tool to compare among model fits, but caution should be taken in using the R^2 values as true model fit. The aggregation variable was used only for stabilization and likely inflated results.

DISCUSSION

Each modeling method had its strengths and, ultimately, each one provided a unique clarity on the importance of the explanatory variables. Common to all three methods was the significance of DO as a describing variable for halibut distribution. Temperature was significant in two of the three models and was excluded from the GWR spatial model primarily because of collinearity problems not related to significance. Based on these results, both DO and temperature appear to be important environmental factors in halibut distribution. When attempting to build predictive models of distribution, assessing the variables for spatial correlation and regional variation can help provide clarity to additional underlying processes or conditions affecting the populations and/or the results of stock monitoring methods. The Pacific halibut stock assessment relies heavily on the IPHC longline survey, and knowing how environmental factors affect the animals in relation to distribution and catchability is imperative to using these data accurately.

Moran's I spatial analysis revealed that minor clustering (although non-significant) persisted in the OLS model, suggesting that there was a condition of collinearity of variables, regional variation, or both. Kendall's tau test revealed that collinearity was certainly present, and the tree model, able to handle collinear variables, was especially informative in examining the structure of distribution both on an area-wide as well as a local level. However, the fact that the model with the geographic smoother (GWR), designed to deal with regional variation, resulted in a good model fit (i.e., high R^2), suggests that geographically varying catchability where DO is involved, could be a factor.

When analyzing rapidly changing environmental variables such as DO, it is necessary to consider the ability of an animal to respond appropriately when faced with conditions that may be outside of the normal range (Rosenberg et al., 1992). Many studies have illustrated the ability of mobile macro-fauna to detect decreasing oxygen and emigrate to more oxygenated waters adjacent to the hypoxic zone or to layers nearer to the surface (e.g., Howell and Simpson, 1994; Wannamaker and Rice, 2000; Breitburg, 2002; Gray et al., 2002). Pacific halibut are highly migratory (Webster et al., 2013) and undoubtedly experience a wide range of environmental conditions naturally. The absence of animals caught in this study from stations with DO < 0.9 mL L^{-1}, could indicate either that halibut were present but were not feeding on the gear, or that they were truly absent. The multitudes of studies showing the ability of fishes to detect and migrate from an

Figure 5. Standardized residuals for both the final OLS model for halibut (left) and the final GWR model (right) are mapped geographically. The residuals appear more randomly distributed in the GWR model, especially in the northern portion of the study area, signifying a better fit than the OLS model.
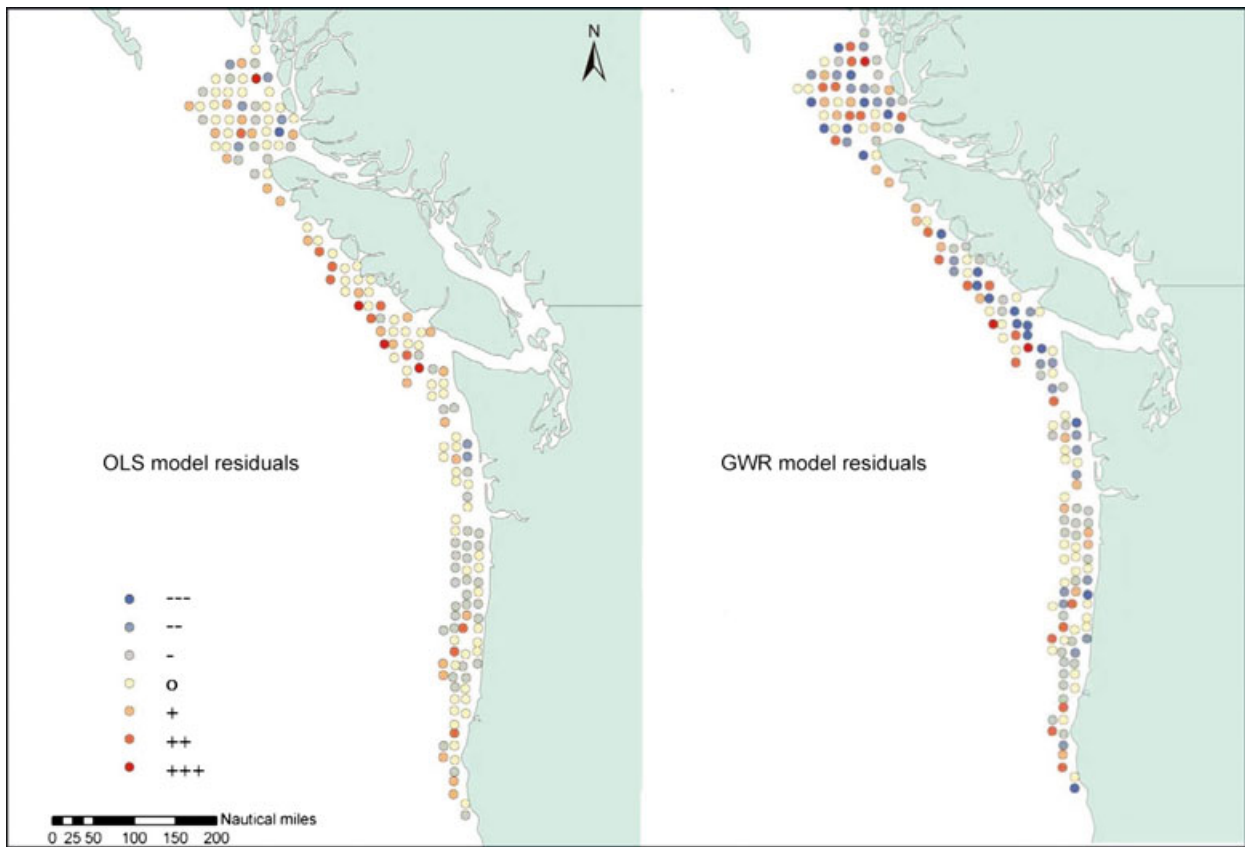

Figure 6. Pacific halibut observed NPUE (left panel) and NPUE predictions from each of the three model types. The GWR model had the highest R^2_{adj} (0.72) of the three and captured the variability in the southern half of the range, whereas the other two model types did not.
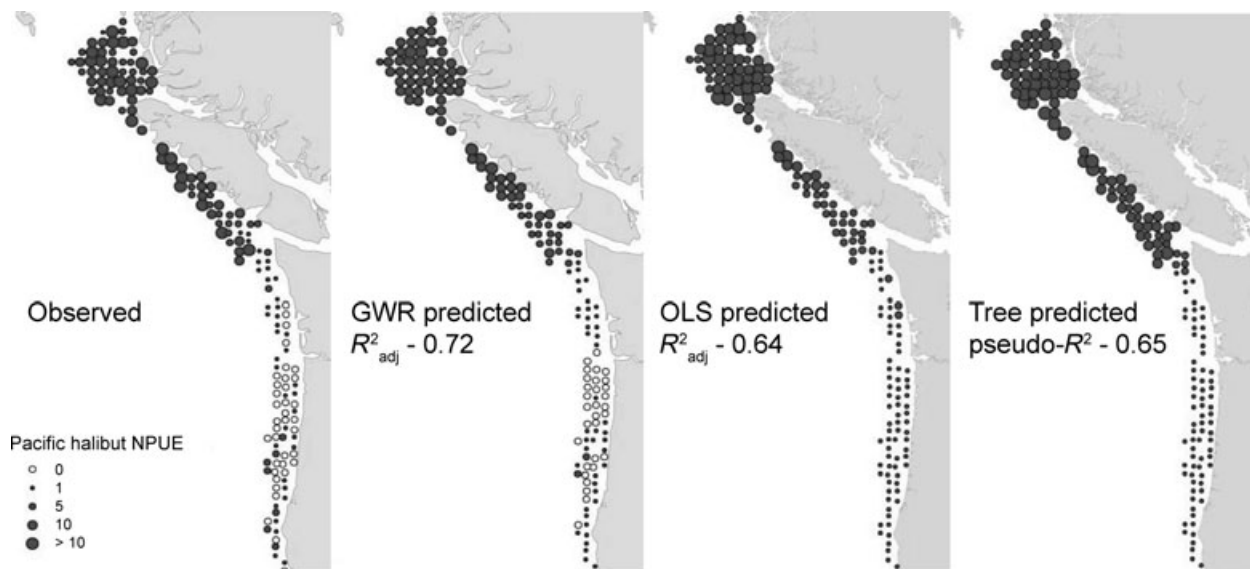
Table 4. Results of a Kendall's tau (τ) correlation test on the environmental variables collected for this study.

Variables	Z-score	P-value	τ	Correlation
Depth : temperature	**−18.07**	**<2.2e-16**	**−0.527**	**−**
Depth : oxygen	**−13.67**	**<2.2e-16**	**−0.398**	**−**
Depth : salinity	18.97	<2.2e-16	0.553	+
Depth : pH	1.90	0.05739	0.086	0
Depth : latitude	−2.24	0.02515	−0.069	−
Temperature : oxygen	**8.96**	**<2.2e-16**	**0.261**	**+**
Temperature : salinity	−11.90	<2.2e-16	−0.347	−
Temperature : pH	3.67	0.00024	0.166	+
Temperature : latitude	−7.60	2.75e-14	−0.236	−
Oxygen : salinity	−24.28	<2.2e-16	−0.708	−
Oxygen : pH	11.51	<2.2e-16	0.521	+
Oxygen : latitude	**13.52**	**<2.2e-16**	**0.419**	**+**
Salinity : pH	−1.67	0.09526	−0.076	0
Salinity : latitude	−13.078	<2.2e-16	−0.405	−
pH : latitude	−3.14	0.00169	−0.152	−

The highlighted relationships indicate those that were prominent in the tree regression model.

Figure 7. Tree regression model result for Pacific halibut using 2009 data. The length of vertical branches indicates the relative amount of variability explained for that split. Terminal nodes show mean NPUE for each cluster, and mean minimum and maximum NPUEs are circled. Values in parentheses indicate the number of stations within each cluster.
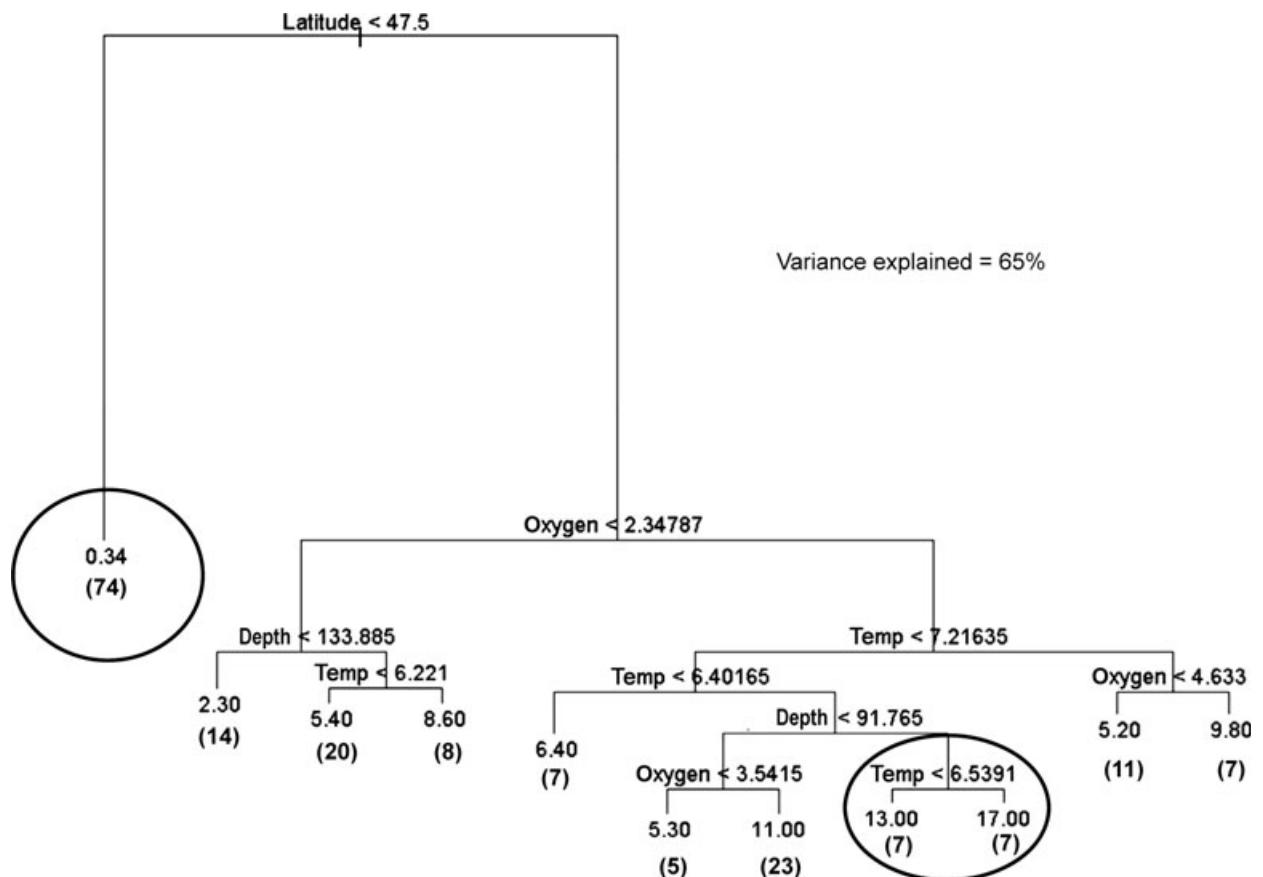
hypoxic area, along with findings from Chan et al. (2008), who noted that no fishes were present during a severe hypoxic event off Oregon, support absence. However, there remains the question of how animals may redistribute when forced from an area of low DO. In the case of halibut, a fish without a swim bladder and which must exert considerable energy to swim vertically up into the water column, likely chooses to make a lateral migration to more oxygenated waters adjacent to the hypoxic zone. It is then possible that uncharacteristically high densities of halibut may be found immediately outside of a hypoxic zone, as has been demonstrated for other animals (Rabalais et al., 2001a). This behavior may make them more vulnerable to predation or fishing pressure, and also make it more difficult for managers to assess their distributions and abundance through periods of varying DO concentrations, and where the 10 × 10 nmi resolution of the sampling grid may not be fine enough to capture the redistribution. Alternatively, if prey species (smaller fishes for example; IPHC, 1998) are exhibiting a similar response to low DO, then feeding may be temporarily enhanced. Future tagging studies using pop-up archival tags, for example, where animal movements can be tracked on short time scales, in conjunction with concentrated oceanographic monitoring could help to answer the question of fish proximity to threshold environmental conditions.

At the lowest levels of DO (below 0.9 mL L^{-1}), halibut appeared to be excluded, but model results suggest that intermediate levels of DO also play a part in NPUE variation. The tree model illustrates that DO affects NPUE at levels as high as 4.6 mL L^{-1}, and NPUE appears more sensitive to DO in shallower water. In the deeper depths, temperature appears to play a more prominent role, with higher NPUEs at greater temperatures. Stoner et al. (2006), Stoner and Sturm (2004), and Pollock et al. (2007) found that changes in temperature and DO affected predatory (feeding) behavior in fishes. For a passive gear such as the longline gear used in this study (i.e., where animals are required to interact with the gear), conditions that cause changes in feeding behavior will cause changes in catchability. It may be that catchability is not greatly affected within 'normal' ranges of environmental variables, but is affected in 'threshold' or near-threshold conditions, such as the low levels of DO experienced during this study. Current tolerance thresholds may also not be static for a given species as conditions change. Vaquer-Sunyer and Duarte (2011) predicted that benthic macrofauna minimum thresholds for DO will increase more than 25% if bottom water increases by

4°C as predicted by climate change models over the next century. For Pacific halibut, this would translate to a new minimum threshold of 1.125 mL L^{-1} at the same time that ocean-wide DO is expected to continue its decline (Deutsch et al., 2011).

The specific effects of ocean acidification on fishes is currently a subject of intense interest to researchers and fishery managers. Thus far, there is no evidence indicating that fishes can detect and avoid acidified water as has been demonstrated for low DO or variable temperatures. Halibut in this study were caught over a 0.5 pH range, indicating that they can tolerate this variability. Recent research suggests that a direct effect of acidification on marine fish may be sensory impairment (Munday et al., 2009; Dixson et al., 2010; Simpson et al., 2011). Cripps et al. (2011) studied a coral reef predator in a laboratory setting and found that elevated CO_2 and the resulting drop in pH caused a shift from preference to avoidance of prey, concluding that the olfactory senses were negatively impacted. The researchers further noted that an observed coincident increase in activity may facilitate a switch to visual detection of prey, which would be an advantage in a shallow habitat where ample light penetrates. Visual detection without the olfactory complement could be a challenge for a fish such as halibut, which lives in a low-light, demersal environment (Stoner, 2003).

Long-term changes in temperature have been demonstrated to result in altered species' ranges (e.g., Perry et al., 2005; Sabates et al., 2006). In this study, no apparent temperature threshold was reached for halibut, but it is necessary to consider the compounding effects of environmental factors to fully understand future impacts. Recent research has shown that increasing global temperatures are expected to increase the severity and duration of hypoxic zones (Rabalais et al., 2010) through strengthened stratification of ocean layers and decreased capacity of heated waters to hold DO. The increasing of minimum DO thresholds related to increasing water temperature (Vaquer-Sunyer and Duarte, 2011), along with other findings such as narrowing of temperature tolerances related to acidification, illustrates the complexity of possible outcomes with changing environmental factors. This study took place at the southernmost geographic range for this species where some of the highest temperatures within the halibut range are experienced. As long-term changes in climate persist, the temperature profile for the area is likely to change, with possible temperature-related outcomes for the halibut population being northerly movement of the

southernmost geographic range as seen in other species (Perry *et al.*, 2005; Sabates *et al.*, 2006) or intensification and/or expansion of the annual hypoxic zone (Deutsch *et al.*, 2011), resulting in exclusion from that area, or both.

Modeling halibut distribution was not a straightforward process, as evidenced by the requirement for multiple methods and the introduction of the aggregation variable to improve model performance. This variable helped account for the spatial structure of the animals that was not adequately explained by the included environmental variables alone. However, it is important to point out that this variable likely accounts for not only aggregation of the species as the name suggests but a combination of factors, as yet unidentified, influencing distribution. Examples of these may be primary production (Cooke *et al.*, 2006), sea surface temperature (Castillo *et al.*, 1996), predator/prey interactions (Anderson, 2001) or multi-species assemblage structures of the animals (Palsson *et al.*, 2009).

When examining environmental factors and attempting to build predictive models of distribution, it is important to assess the variables for spatial correlation as well as regional variation. This may help provide an understanding of additional underlying processes or conditions affecting the populations and/or the results of stock monitoring methods. The Pacific halibut stock assessment relies heavily on the IPHC longline survey. Knowing how environmental factors affect the animals in relation to distribution and catchability is imperative to use these data accurately. Further insight may be achieved by continued examination of this study region, the southern boundary of halibut habitat, as well as expanding the analysis over additional years and to other surveyed areas to the north and west.

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