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# Species-specific responses of demersal fishes to near-bottom oxygen levels within the California Current large marine ecosystem

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ABSTRACT: Long-term environmental sampling provided information on catch and near-bottom oxygen levels across a range of depths and conditions from the upper to the lower limit of the oxygen minimum zone and shoreward across the continental shelf of the US west coast (US–Canada to US–Mexico). During 2008 to 2014, near-bottom dissolved oxygen (DO) concentrations ranged from 0.02 to 5.5 ml $l^{-1}$ with 63.2% of sites experiencing hypoxia (DO < 1.43 ml $l^{-1}$). The relationship between catch per unit effort (CPUE) and DO was estimated for 34 demersal fish species in 5 subgroups by life history category (roundfishes, flatfishes, shelf rockfishes, slope rockfishes and thornyheads) using generalized additive models (GAMs). Models included terms for position, time, near-bottom environmental measurements (salinity, temperature, oxygen) and bottom depth. Significant positive relationships between CPUE and DO occurred for 19 of 34 groundfish species within hypoxic bottom waters. Community effects (total CPUE and species richness for demersal fishes) also exhibited significant and positive relationships with low near-bottom oxygen levels. GAM analysis revealed an apparent threshold effect at lower oxygen levels, where small changes in oxygen produced large changes in catch for several species, as well as total catch and species richness. An additional 7 species displayed negative trends. Based on Akaike's information criterion values, near-bottom oxygen played a major role in the distribution of flatfishes, roundfishes and thornyheads. By examining similarities and differences in the response of various subgroups of commercially important groundfish species to low DO levels, we uncovered ecological inferences of potential value to future ecosystem-based management.

KEY WORDS: Hypoxia · Groundfish · Environmental effects · US west coast · Ecological inferences

## INTRODUCTION

Dissolved oxygen (DO) concentrations play a pivotal role in the distribution of marine organisms, with ongoing and predicted worldwide declines amplifying the need to understand impacts on higher trophic levels (Gilly et al. 2013). Naturally occurring large pools of hypoxic bottom water, called oxygen minimum zones (OMZ; DO < 0.5 ml $l^{-1}$), are often associated with highly productive, eastern boundary current upwelling systems (Levin 2003, Gilly et al. 2013). Recent findings indicate OMZ boundaries, such as

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*Corresponding author: aimee.keller@noaa.gov those associated with the Benguela and Canary Current systems in the Atlantic and the Peru and California Current systems in the Pacific, are broadening (Chan et al. 2008, Stramma et al. 2008, 2010). Expansion and shoaling of OMZs, as well as declining minimum DO levels within these zones are a cause of concern and appear to be related to large-scale climate changes (Whitney et al. 2007, Keeling et al. 2010, Gallo & Levin 2016). Warming temperatures are predicted to cause further DO declines in the future via decreased DO solubility in surface waters and increased stratification leading to reduced subsurface ventilation (Stramma et al. 2012, Gilly et al. 2013). Here, we focused on near-bottom oxygen levels within the California Current large marine ecosystem (CCLME) along the US west coast to understand the potential impacts of DO and other environmental variables on the structure of demersal fish communities.

Increases in the spatial and temporal extent of hypoxic conditions are predicted to cause complex changes within marine ecosystems including the CCLME (Bograd et al. 2008, Pierce et al. 2012, Peterson et al. 2013). Onshore movement of the upper layer of the OMZ could lead to habitat compression for fish species with higher oxygen requirements while allowing expansion of species tolerant of low near-bottom DO. OMZs vary in extent based on ocean basin features, with the OMZ associated with the CCLME being the largest and most extensive worldwide (Pierce et al. 2012). Within the southern portion of the CCLME, oxygen levels have notably decreased (~0.016 ml $l^{-1}$ $yr^{-1}$) and shoaled (70 m) over the past 30 yr (Bograd et al. 2008). Underlying causes of decline in near-bottom DO in the southern CCLME appear to be linked to basin-scale or perhaps global climate processes (Koslow et al. 2011), including decreased DO in source waters of the north Pacific Ocean, changes in inorganic nutrient ratios in upwelling source waters of the Southern California Bight and changes in stratification related to climate variability combined with locally elevated primary productivity (Whitney et al. 2007, Stramma et al. 2008, Booth et al. 2014, Bograd et al. 2015). Within the northern CCLME, seasonal hypoxia has been reported annually since 2002 as a result of shoreward movement of low DO water onto the continental shelf and into coastal areas off Washington and central Oregon (Grantham et al. 2004, Chan et al. 2008). In these areas, the lowest oxygen conditions occur during the summer months when upwelled water, already low in DO, is further reduced by physical and biological processes (e.g. circulation, temperature and decomposition of organic matter) (Pierce et al. 2012). Shoaling of the OMZ results from a combination of climate-influenced changes in upwelling and currents, as well as advective processes carrying low DO into shallower regions (Grantham et al. 2004, Chan et al. 2008, Pierce et al. 2012) and longer term changes in DO of upwelling source waters (Peterson et al. 2013). Low DO in source waters is a function of the temperatures under which they form, with less DO present, in general, due to decreased solubility following warming at source locations, and small changes in oceanographic processes over long periods of transport to the CCLME (Pierce et al. 2012). Chan et al. (2008) noted increasing frequency of hypoxia off Oregon relative to historical data and Connolly et al. (2010) described exceptionally low DO off Washington in 2006, lower than values recorded at similar sites from 1950 to 1986. Within the CCLME, the concern is not only for increasing near-shore hypoxia but also the potential for expansion of the OMZ in response to warming of surface waters (Bond et al. 2015, Praetorius et al. 2015) and interactions with other stressors such as ocean acidification (Somero et al. 2016).

Declining oxygen concentration could potentially impact mobile organisms such as commercially important groundfishes, which could damage fisheries and alter energy flows, particularly if combined with other stressors (Diaz & Rosenberg 2008, Gao et al. 2012, Gallo & Levin 2016). Direct effects of severe hypoxia (DO < 0.5 ml $l^{-1}$) on demersal fish range from increased mortality to physiological impairment, movement/displacement out of hypoxic waters (Ono et al. 2010), habitat compression, alterations in predator–prey relationships and changes in foraging dynamics (Chan et al. 2008, Keller et al. 2010, 2015, Koslow et al. 2011, Seibel 2011). Encroachment of hypoxia onto the continental shelf may have even more pronounced effects on the organisms that live there compared to those that inhabit the OMZ, since organisms at these shallower depths are not adapted to low DO. The unprecedented and widespread severe hypoxia (DO < 0.5 ml $l^{-1}$) off the Oregon shelf in 2006 caused high mortality in demersal and benthic fauna, including commercially harvested species (Chan et al. 2008, Keller et al. 2010).

The Northwest Fisheries Science Center conducts an annual groundfish survey along the US west coast from the Canadian to the Mexican border at depths of 55 to 1280 m. The primary purpose of the West Coast Groundfish Bottom Trawl Survey (WCGBTS) is to provide data for stock assessments to evaluate the status and trends for a large number of commercially important west coast fish species. In 2006, the survey encountered several tows with dead and moribund fishes offshore of Oregon within the region typically sampled by the survey. As a result, the survey initiated studies in 2007 to examine the relationship between demersal catch and near-bottom DO (Keller et al. 2010). Over time, the WCGBTS added an expanding array of sensors deployed on trawl nets to provide measurements of catch and environmental variables for each tow. Since 2009, fishery and environmental sampling has occurred coast-wide, throughout the survey period from May to October.

Survey estimates of population biomass are highly variable, with much of the variability in the Northwest Fisheries Science Center's groundfish survey due to unaccounted processes driven by oceanographic features (environmental and/or habitat) (Thorson et al. 2011, Shelton et al. 2014). Prior studies have characterized Pacific coast groundfishes in relation to oceanographic variables (Allen & Smith 1988, Vetter et al. 1994, Weinberg 1994, Williams & Ralston 2002, Allen et al. 2006, Tolimieri & Levin 2006, Juan Jordá et al. 2009). For fish stock assessment and management purposes, our goal was to build on these past studies by describing relationships that affect the distribution and condition of specific groundfish species, particularly in the face of climate change (Vestfals 2009, Sagarese et al. 2014, Thorson 2015).

Results from a prior study along a hypoxic gradient off Oregon suggest an extremely dynamic situation where near-bottom DO explained up to 84% of the variation in biomass for individual species and 31 to 69% of the depth-specific variation in biomass (Keller et al. 2010). Significant and positive relationships between near-bottom DO and both catch per unit effort (CPUE; kg $ha^{-1}$) and species richness were found based on coast-wide studies from 2008 to 2010 (Keller et al. 2015). Rather than solely examining the known hypoxic area off Oregon, the latter study focused on the range of environmental conditions from the upper to the lower limit of the OMZ and shoreward across the continental shelf of the US west coast (Keller et al. 2015). Variable sensitivity to near-bottom DO occurred for 4 widespread and abundant groundfish species (Dover sole, petrale sole, spotted ratfish and greenstriped rockfish) based on probability of occurrence models that included terms for position, day of the year, near-bottom salinity, temperature, DO and bottom depth.

The primary objective of the present study was to examine the relationships between CPUE and environmental variables, with emphasis on DO, for 34 demersal fish species in 5 subgroups collected from 2008 to 2014. Similar studies within the CCLME, Bering Sea and Gulf of Alaska have successfully disentangled the impacts of environmental and demographic variables on the distribution of canary rockfish (Vestfals 2009), yellowfin sole (Bartolino et al. 2011), arrowtooth flounder (Ciannelli et al. 2012) and darkblotched rockfish (Shelton et al. 2014). Here, the goal was to identify explanatory environmental covariates related to species-specific CPUE for multiple groundfish species, based on the application of log-normal generalized additive models (GAMs). GAMs are increasingly being used to quantify relationships between environmental conditions and distributions of commercially important fish species including rockfishes in the CCLME (Thorson et al. 2015a,b), herring and spiny dogfish in the Northeastern Atlantic (Bailey et al. 1998, Maravelias et al. 2000, Sagarese et al. 2014), walleye pollock in the Bering Sea (Swartzman et al. 1994, 1995, Winter et al. 2007), Baltic cod in the Baltic Sea (Cardinale & Arrhenius 2000), Atlantic cod in the Barents Sea (Ciannelli et al. 2007) and European hake in the Mediterranean Sea (Bartolino et al. 2008). GAMs have also been used to model the distribution of pelagic fish, krill and loliginid squid as a function of geographical and environmental variables (Bellido et al. 2001, Denis et al. 2002, Murase et al. 2009). By providing insights into the relationships between environmental covariates and commercially important groundfish species, we hoped to uncover ecological inferences of value to the stock assessment process and move closer to reaching the goals set by ecosystem-based management in the USA federal waters.

## MATERIALS AND METHODS

### Survey design

The Northwest Fisheries Science Center conducted standardized trawl surveys of groundfishes off the US west coast (Bradburn et al. 2011), in conjunction with measurement of environmental variables including near-bottom DO, from 2008 to 2014. Annual surveys occurred from May through October from off Cape Flattery, Washington (48° 10′ N), to the US–Mexico border (32° 30′ N) at depths of 55 to 1280 m (see Fig. 1). Sampling typically took place onboard 4 chartered west coast fishing vessels (20 to 28 m length) using a stratified random sampling design. Stations (on average 700 annually) fell within 1.5 × 2 nautical mile grids (Albers Equal Area projection) that span the US west coast. A north–south division at 34° 30′ N (Point Conception, California) resulted in 2 geographic strata. The survey design further included 3 depth strata (shallow: 55 to 183 m, mid: 184 to 549 m and deep: 550 to 1280 m). Each vessel was equipped with a standard 4-panel, single-bridle, Aberdeen-type trawl with a 3.8 cm mesh liner (stretch measure), extending from the middle of the intermediate through the codend, to retain smaller fishes and invertebrates. All fishing operations complied with strict national and regional protocols detailed in Stauffer (2004).

### Environmental and biological sampling

A Simrad Integrated Trawl Instrumentation system (ITI Kongsberg Simrad Mesotech) was used to monitor and record net performance and geographic position for each haul. A differential global positioning system (DGPS) navigation unit (Garmin 152, Garmin International) was used to monitor towing speed during each haul. Standard survey haul positions (latitude, °N and longitude, °W) were estimated from DGPS data—generally the mid-point between net touchdown on the bottom and net liftoff positions. Mean net speed over ground and distance fished were calculated from the position data for the trawl and actual bottom time (Keller et al. 2008).

Near-bottom DO (ml $l^{-1}$), salinity (ppt), temperature (°C) and depth (m) were measured during each trawl using both a Sea-Bird SBE 39 and a Sea-Bird SBE 19plus conductivity, temperature, depth profiler (Sea-Bird Electronics), equipped with a calibrated SBE 43 polarographic membrane-type oxygen sensor. Sensors were factory calibrated before and after deployment on an annual basis. These units attached to the net about 2.8 m behind the headrope where the top wing panel meets the body of the net. Mean depth, temperature, salinity, and DO concentrations per tow were calculated from values measured during the center 80% of the on-bottom tow duration for comparison with CPUE. The current data analyses incorporated only those trawls with near-bottom DO measurements judged acceptable based on net performance standards (~95% of all tows) (Stauffer 2004).

For displaying results on an unequal sampling platform, contour plots of near-bottom DO concentrations were initially gridded using bottom depth as a coordinate, then remapped to geographic coordinates, and plotted using thin plate smoothing splines (Wahba 1990). The degree of smoothness was determined automatically by minimizing differences between data and fitted surface values at the data locations (generalized cross validation, GCV) with the final differences between the data and the surface values being small (0.003 to 0.018 ml $l^{-1}$ for 2009 through 2014, respectively).

Trawling occurred within randomly selected cells at a target tow speed of 1.13 m $s^{-1}$ (2.2 knots) for a target fishing time of 15 min. All fishes were sorted to species (or to the lowest possible taxon), and then weighed using an electronic, motion-compensated scale (Marel). We calculated estimates of species richness as the total number of demersal fish species taken per trawl sample. Total and species-specific (34 demersal fish species) CPUE were calculated based on area swept. Area swept was computed from the mean net width for each haul multiplied by the distance fished.

### Data analysis

Using data from 2008 to 2014, we calculated species-specific CPUE for 34 demersal fish species based on area swept. CPUE values were log transformed (ln CPUE + 0.1) before analysis to stabilize the variance (Gunderson 1993). To examine variation in latitude, longitude, DO, temperature, salinity and depth distributions among the 34 species selected for individual analyses, we calculated mean CPUE-weighted values for each species as:

$$X_j = \sum_{i=1}^{n}(\mathrm{CPUE}_i \times X_{ij}) \Big/ \sum_{i=1}^{n}\mathrm{CPUE}_i \qquad (1)$$

where $X$ is the parameter of interest (latitude, longitude, DO, temperature, salinity or depth), $j$ represents an individual species, and CPUE is catch per unit effort for each station $i$.

We used a lognormal GAM (Wood 2006) to correlate species-specific CPUE (ln CPUE + 0.1) of each selected groundfish species with co-located environmental and geographic variables during 2 periods (May to July and August to October). Given the high incidence of zeros in the bottom trawl catches, we constrained the GAM models for each targeted species to the geographic areas (latitude, °N) and depth (m) ranges that included 90% of the cumulative CPUE. Namely, the latitudinal range defined by $L_{0.05}$ and $L_{0.95}$ satisfies the following equations:

$$\begin{aligned} L_{0.05} &= \sum_{L_{\min}}^{L_{0.05}}\mathrm{CPUE}_L \Big/ \sum_{L_{\min}}^{L_{\max}}\mathrm{CPUE}_L \\ L_{0.95} &= \sum_{L_{0.05}}^{L_{\max}}\mathrm{CPUE}_L \Big/ \sum_{L_{\min}}^{L_{\max}}\mathrm{CPUE}_L \end{aligned} \qquad (2)$$

where $L_{\min}$ and $L_{\max}$ are the lowest and highest sampled latitudes, respectively. The depth range was similarly constrained.

By applying a species-specific constraint on the sampled region, we limited the analyses to only the area that represented the primary habitat for the species in consideration, and excluded locations where the species rarely or never occurs. Stations with zero catch per species still occur within the retained habitats, but at a consistently lower proportion than in the entire survey area, making the dataset more amenable to analyses with standard statistical packages (Welsh et al. 1996). Because of our focus on the impact of hypoxic bottom conditions on catch, we retained tows with zero catch within the core habitat since a species' absence within an area could be related to low oxygen conditions. Additionally, although it is possible that a species' absence outside the core habitat is related to low oxygen conditions, the approach adopted here should reduce such occurrences.

The habitat-constrained data were then analyzed using lognormal GAMs fitted to indices of abundance (ln CPUE + 0.1) for each of 34 demersal fish species (Wood 2006). An advantage of GAM over traditional regression analysis is the ability to model nonlinear relationships using non-parametric smoothers (Hastie & Tibshirani 1990). Near-bottom measurements, including salinity (S), temperature ($T$), and DO, as well as bottom depth ($Z$) were included as explanatory environmental variables in the model. We also included temporal (year and day of the year, DOY) and spatial (latitude and longitude) elements in the model. DOY was selected to capture the seasonal component of the survey, which annually runs from northerly to southerly latitudes during both periods (May to July and August to October). The same model structure was applied to each species and included the following terms:

$$\ln(\text{CPUE}_j + 0.1) = a_y + s_1(\text{long, lat}) + s_2(\text{DO}) + s_3(\text{S}) + s_4(\text{DOY}) + s_5(T) + s_6(Z) \quad (3)$$

where for each species $j$, a lognormal GAM was used to model CPUE (ln CPUE + 0.1) as related to $a_y$ (a year-specific intercept term), longitude (long, °W) and latitude (lat, °N), DOY, near-bottom DO, near-bottom salinity (S), near-bottom temperature ($T$), and bottom depth ($Z$); and $s_1$ and $s_{2\text{–}6}$ are 2-dimensional and 1-dimensional smooth functions, respectively, in this case thin plate regression splines (Wood 2006). The degrees of freedom for each smooth term in the GAM was constrained to 4 ($k = 4$), based on sensitivity analyses. GAM analyses were done using the 'mgcv' package (version 1.27-26) of the R program (version 3.0.3) (R Development Core Team 2012). Similar lognormal GAM models were developed for total CPUE (ln kg ha$^{-1}$) and species richness (ln n) for all demersal fishes. Neither of these community measures were habitat-constrained or transformed by adding 0.1, since values were always positive.

Akaike's information criterion (AIC) was used to evaluate support for a suite of models with different combinations of DOY, near-bottom DO, salinity, temperature and bottom depth (Sakamoto et al. 1986). To choose the most parsimonious model for each species, we removed competing variables from the model if they exhibited insignificant ($p > 0.05$) approximate p-values until the AIC value no longer decreased when a term was dropped. For each species, the model with the best fit was selected by the smallest AIC value (AIC$_{\min}$). To compare among models, the difference in AIC values for each model was calculated as:

$$\Delta_i = \text{AIC}_i - \text{AIC}_{\min} \quad (4)$$

The best model as defined above will have $\Delta_i = 0$, while models with $\Delta_i < 2$ have substantial support relative to the best model (AIC$_{\min}$) (Burnham & Anderson 2002). Model fit and parsimony were also evaluated through percent deviance explained and GCV (Green & Silverman 1994).

To explore generalities in the relationships between subgroups and their response to DO, the 34 groundfish species were partitioned into 5 subgroups based on taxonomy and/or life-history (as flatfishes, roundfishes, shelf rockfishes, slope rockfishes and thornyheads). We acknowledge that the species included in the roundfishes subgroup are linked primarily by body shape rather than life history features and are less tightly associated than those in other subgroups. We also examined the overall relationships between total species richness (demersal fish, n), total CPUE (sum of CPUE for all demersal fish per tow) and near-bottom DO using regression analysis in SAS for Windows (SAS Institute 1999) for all data over the study period (2008 to 2014). We incorporated DO in the analysis as a quadratic term, and to stabilize the variance, we used the natural logarithms of richness, CPUE and DO in the analyses.

## RESULTS

### Near-bottom oxygen

We collected information on near-bottom oxygen conditions at 3288 stations from 2008 through 2014 for comparison with demersal fish catch distributed throughout the survey area. During this period, we encountered hypoxia (DO < 1.43 ml $l^{-1}$) at 63.2% of sampling sites (n = 2077) and severe hypoxia (DO < 0.5 ml $l^{-1}$) at 29.0% of the sites (n = 954) with no indication of worsening conditions over time (Table 1).

Contour plots of coast-wide, near-bottom DO concentrations for both survey periods (May to July and August to October) indicated the persistent presence of low DO in deep water within the OMZ from 2009 to 2014 (Fig. 1). In general, low DO appeared to move shoreward as the summer progressed, and occurred later in the season (August to October) in shelf water offshore of both Washington and Oregon (Fig. 1). The distribution of low DO varied by year, with hypoxic conditions well developed off Washington during 2009, 2011 and 2012 and along the shelf of Oregon in 2011, 2012 and 2014 relative to other years (Fig. 1). In the southern portion of the study area, south of Cape Mendocino, California (44° 26′ N), low DO appeared more widespread in all years during the May to July period compared to later in the season.

### Environmental variables

We collected an average of 265 individual fish taxa each year (range: 252 to 310) throughout the survey from 2008 to 2014, with the 34 demersal fish species included in this analysis comprising >90% of the total catch. Histograms for the temporal, geographic and environmental variables included in the GAM analysis for all species indicate the range of values included in the analyses and emphasize the seasonal nature of the survey as well as the high number of sites with relatively low DO (Fig. 2). The average, catch-weighted environmental variables, shown by individual species over the study period, indicate that species at greater depths are characterized by higher salinity, lower temperature and lower DO, particularly those species known to inhabit the OMZ such as Dover sole and thornyheads (Table 2). Mean catch-weighted latitudes indicated that species with the northernmost distributions included arrowtooth flounder, flathead sole, spiny dogfish, canary rockfish, yellowtail rockfish and Pacific ocean perch. Curlfin sole, bocaccio, chilipepper, greenspotted, shortbelly, aurora and blackgill rockfishes were concentrated in the more southerly portion of the survey area. Shelf rockfishes occurred at mean-weighted depths ranging from 146 to 211 m, while slope rockfishes were somewhat deeper (245 to 462 m), confirming the depth-based designations defining shelf and slope rockfishes in general. On average, shelf rockfishes occupied waters with higher near-bottom DO levels, while slope rockfishes and thornyheads occurred at lower DO concentrations than other subgroups, again confirming expectations since DO decreases with depth within the depth ranges occupied by these subgroups. However, with the exception of thornyheads, considerable variation existed in the range of catch-weighted near-bottom DO by subgroup.

### Habitat restriction

Constraining the data to geographic areas (latitude, °N and depth) that contained 90% of the CPUE for each species reduced the average number of tows with zero catch from 73 to 33% (Table 2). Stations with zero catch originally ranged from a minimum of 16.3% for Dover sole to a maximum of 96.3% for rougheye rockfish (Table 2); however, after imposing restrictions the range was 3.2 to 80%.

Table 1. Total number of tows (n) with near-bottom dissolved oxygen (DO) measurements, average DO, standard deviation (SD), and range of DO, number and percent hypoxic (DO < 1.43 ml $l^{-1}$) and severely hypoxic (DO < 0.5 ml $l^{-1}$) stations from 2008 to 2014

| Year | Tows (n) | Average (±SD) DO (ml $l^{-1}$) | DO range (ml $l^{-1}$) | Hypoxic tows (n) | Hypoxic tows (%) | Severe hypoxia (n) | Severe hypoxia (%) |
|---|---|---|---|---|---|---|---|
| 2008 | 31 | 1.46 (1.46) | 0.04–4.21 | 20 | 64.5 | 9 | 29.0 |
| 2009 | 332 | 1.21 (0.87) | 0.07–4.25 | 217 | 65.4 | 91 | 27.4 |
| 2010 | 623 | 1.16 (0.79) | 0.02–3.97 | 388 | 62.3 | 176 | 28.3 |
| 2011 | 593 | 1.13 (0.81) | 0.05–4.69 | 393 | 66.3 | 178 | 30.0 |
| 2012 | 663 | 1.25 (0.95) | 0.04–4.60 | 412 | 62.1 | 203 | 30.6 |
| 2013 | 424 | 1.17 (0.78) | 0.06–3.72 | 268 | 63.2 | 117 | 27.6 |
| 2014 | 622 | 1.28 (0.97) | 0.03–5.51 | 379 | 60.9 | 180 | 28.9 |
| Total | 3288 | | | 2077 | | 954 | |

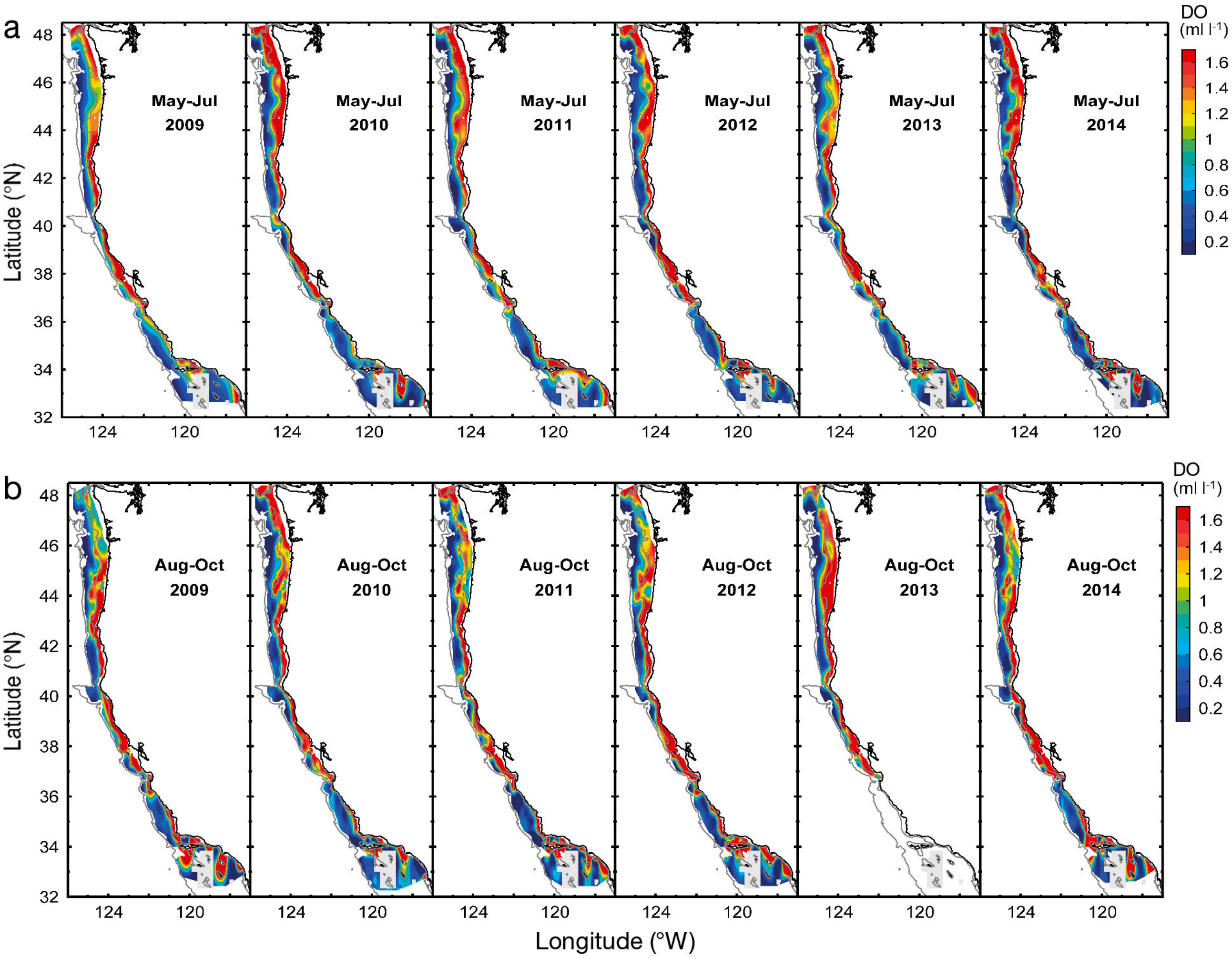

Fig. 1. Coast-wide contour plots of near-bottom dissolved oxygen DO) concentrations (ml $l^{-1}$) along the US west coast at depths of 55 to 1280 m from 2009 to 2014: (a) May to July and (b) August to October. Missing data during the August to October period in 2013 resulted from the disruption of the 2013 survey caused by the government furlough

### GAM models

Optimal models were selected for each species based on AIC values ($\Delta_i = 0$) by iteratively removing covariates with approximate p-values >0.05 until no further reduction in AIC occurred. On occasion, even if the p-value for a covariate was not significant, the covariate was retained if $\Delta_i = 0$ indicated inclusion in an optimal model. Because of our interest in hypoxia, the suite of final models (n = 11) that incorporated near-bottom DO are defined and shown in Table 3 while optimal models without DO are excluded here and in Table 4. Although $\Delta_i$ values for each step in the removal of covariates are not shown, covariates removed from all optimal models are shown by species (Table 4). Note that if an optimal model did not include DO, a $\Delta_i$ value = 0 is not seen in Table 4.

Latitude and longitude were retained in the final models for all species. For 4 species (curlfin sole, Dover sole, Pacific sanddab and sablefish), the best model ($\Delta_i = 0$) included all covariates. Among covariates, depth was retained in the optimal models most frequently (30 of 34 species). Depth was excluded from optimal models for 3 species within the shelf rockfish subgroup (bocaccio, chilipepper and sharpchin rockfish) and a single species (flathead sole) within the flatfishes subgroup (Table 4). DO was excluded from the optimal models for 8 species, all either shelf (canary, greenspotted, sharpchin and shortbelly) or slope (blackgill, Pacific ocean perch, redbanded and rougheye) rockfishes (Table 4). Temperature, DOY and salinity were retained in decreasing frequency in optimal models, with temperature removed from optimal models for 10 species, DOY removed for 16 species and salinity removed from 17

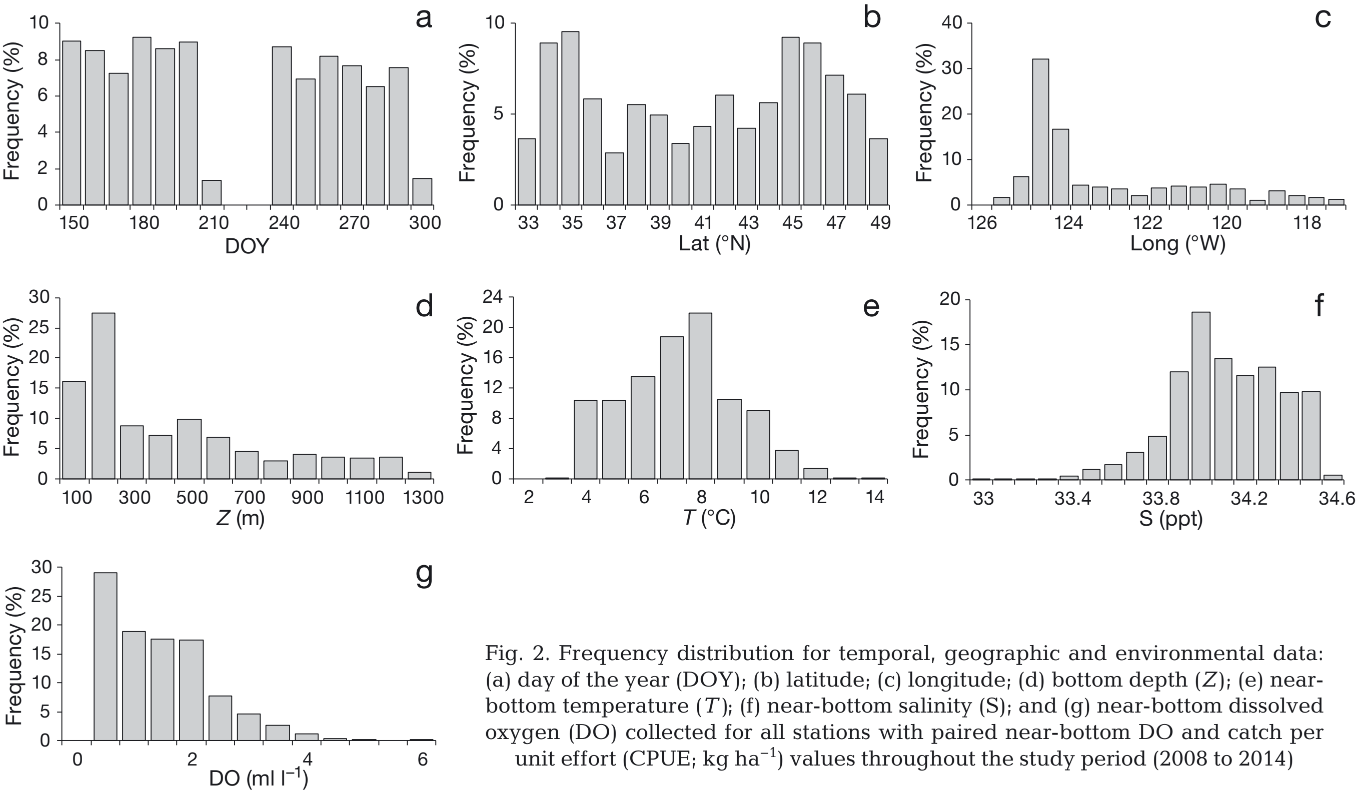

Fig. 2. Frequency distribution for temporal, geographic and environmental data: (a) day of the year (DOY); (b) latitude; (c) longitude; (d) bottom depth (*Z*); (e) near-bottom temperature (*T*); (f) near-bottom salinity (S); and (g) near-bottom dissolved oxygen (DO) collected for all stations with paired near-bottom DO and catch per unit effort (CPUE; kg ha$^{-1}$) values throughout the study period (2008 to 2014)

of 34 species-specific models (Table 4). Temperature was rarely removed from optimal models for flatfishes and thornyheads but commonly removed from the best fit models for roundfishes and rockfishes. In contrast, salinity appeared to be more important for shelf rockfishes relative to other subgroups and DOY more important for flatfishes and roundfishes relative to other subgroups. Most species had at least 1 and up to 4 models with $\Delta_i < 2$, usually on removal or addition of 1 or 2 covariates from the final model (Table 4). DO was retained in well-fit ($\Delta_i < 2$) models for 7 of the 8 rockfish species without DO in their optimal models (Table 4).

For both community measures (demersal fish total CPUE and demersal fish species richness) the best model ($\Delta_i = 0$) included all covariates with no additional models substantially supported (Table 4). Once optimal models were chosen based on $\Delta_i = 0$ for both individual species and community metrics, we saw no additional improvement in terms of GCV scores and percent deviance explained (Table 5). In general, the lowest AIC values and GCV scores tended to converge for species-specific models, total CPUE and species richness, and agreed with the highest percent deviance explained.

The percent deviance explained by the GAM analysis ranged from 17.5% for lingcod to 77.7% for Pacific ocean perch (Table 5). The average percent deviance explained declined from 61.5% for thornyheads (range: 47.4 to 75.5%) to 31.1% for roundfishes (range: 17.5 to 42.9%). The percent deviance explained for total CPUE (39.5%) was close to the average deviance explained (41.6%) for the 34 groundfish species examined and similar to the percent deviance explained for species richness (38.4%) (Table 5). GCV values varied for individual species based on changes in scale (range 0.612 for longspine thornyheads to 5.530 for chilipepper rockfishes) and indicate that overfitting did not occur (Table 5). Within individual species, AIC and GCV values were highly correlated ($r > 0.9$, $n = 11$) when the various combinations of predictor variables (Table 3) were tested.

Because of the focus on near-bottom DO levels and hypoxia, we additionally included the approximate p-values for DO, the directional relationship between predicted CPUE and DO within hypoxic (DO < 1.43 ml l$^{-1}$) bottom waters, the significance of DO based on $\Delta_i$ values (i.e. retention in the optimal models) and a summary of the covariates included in the final models for each species in Table 5. In most cases, significance based on approximate p-values ($p < 0.05$) and AIC values agreed when examining the interaction between CPUE and DO, although not always.

Table 2. Common and scientific names of 34 dominant demersal fish species collected during the 2008 to 2014 West Coast Groundfish Bottom Trawl Survey. Catch-weighted mean latitude (Lat), longitude (Long), near-bottom dissolved oxygen (DO), salinity (S), temperature ($T$), and depth ($Z$) of each species are shown. The percent of hauls with zero catch per species (All) decreased when compared to areas constrained (C) to 90% of the cumulative catch per unit effort (CPUE). Mean values are weighted by CPUE to accurately reflect species-specific location and environmental data

| Common name | Scientific name | Lat (°N) | Long (°W) | DO (ml $l^{-1}$) | S (ppt) | $T$ (°C) | $Z$ (m) | All (%) | C (%) |
|---|---|---|---|---|---|---|---|---|---|
| **Flatfishes** | | | | | | | | | |
| Arrowtooth flounder | *Atheresthes stomias* | 45.58 | 124.75 | 1.44 | 33.96 | 6.76 | 234.6 | 61.9 | 5.1 |
| Curlfin sole | *Pleuronichthys decurrens* | 38.17 | 122.64 | 2.34 | 33.80 | 9.41 | 91.7 | 86.9 | 61.2 |
| Deepsea sole | *Embassichthys bathybius* | 41.17 | 124.24 | 0.34 | 34.37 | 3.99 | 933.1 | 79.5 | 7.1 |
| Dover sole | *Microstomus pacificus* | 41.85 | 123.94 | 0.88 | 34.12 | 6.07 | 440.5 | 16.3 | 3.2 |
| English sole | *Parophrys vetulus* | 42.02 | 123.59 | 1.89 | 33.85 | 8.07 | 130.8 | 57.7 | 21.1 |
| Flathead sole | *Hippoglossoides elassodon* | 46.56 | 124.70 | 1.41 | 33.89 | 6.98 | 156.0 | 91.9 | 58.0 |
| Pacific sanddab | *Citharichthys sordidus* | 39.88 | 122.76 | 2.06 | 33.82 | 8.73 | 106.8 | 65.7 | 18.2 |
| Petrale sole | *Eopsetta jordani* | 41.86 | 123.96 | 1.86 | 33.91 | 7.98 | 155.2 | 54.6 | 7.5 |
| Rex sole | *Glyptocephalus zachirus* | 43.11 | 124.15 | 1.28 | 33.99 | 6.86 | 261.2 | 36.9 | 5.5 |
| Slender sole | *Lyopsetta exilis* | 42.71 | 123.62 | 1.38 | 33.97 | 7.33 | 201.9 | 49.1 | 9.2 |
| **Roundfishes** | | | | | | | | | |
| Lingcod | *Ophiodon elongatus* | 43.76 | 124.14 | 1.76 | 33.89 | 7.66 | 159.8 | 63.5 | 24.8 |
| Pacific hake | *Merluccius productus* | 40.80 | 123.43 | 1.24 | 34.02 | 7.38 | 243.8 | 54.3 | 29.4 |
| Sablefish | *Anoplopoma fimbria* | 41.33 | 123.88 | 0.89 | 34.16 | 5.97 | 506.8 | 36.5 | 11.8 |
| Spiny dogfish | *Squalus suckleyi* | 46.00 | 124.85 | 1.74 | 33.86 | 7.34 | 169.2 | 73.4 | 42.7 |
| Spotted ratfish | *Hydrolagus colliei* | 42.32 | 123.66 | 1.90 | 33.91 | 7.80 | 182.8 | 49.8 | 16.4 |
| **Shelf rockfishes** | | | | | | | | | |
| Bocaccio | *Sebastes paucispinis* | 36.71 | 122.12 | 2.06 | 33.98 | 8.92 | 211.1 | 92.8 | 60.6 |
| Canary rockfish | *Sebastes pinniger* | 46.41 | 124.86 | 1.84 | 33.84 | 7.23 | 146.5 | 92.1 | 73.6 |
| Chilipepper | *Sebastes goodei* | 38.65 | 123.55 | 1.93 | 33.99 | 8.29 | 208.9 | 84.3 | 18.0 |
| Greenspotted rockfish | *Sebastes chlorostictus* | 37.75 | 122.36 | 1.92 | 33.93 | 8.84 | 138.9 | 94.4 | 80.0 |
| Greenstriped rockfish | *Sebastes elongatus* | 44.75 | 124.58 | 1.68 | 33.91 | 7.31 | 162.1 | 73.1 | 14.3 |
| Rosethorn rockfish | *Sebastes helvomaculatus* | 43.86 | 124.32 | 1.63 | 33.95 | 7.11 | 182.7 | 91.8 | 79.7 |
| Sharpchin rockfish | *Sebastes zacentrus* | 44.63 | 124.78 | 1.51 | 33.99 | 6.81 | 210.9 | 93.1 | 59.3 |
| Shortbelly rockfish | *Sebastes jordani* | 36.03 | 121.51 | 1.51 | 34.06 | 8.79 | 188.4 | 89.0 | 51.5 |
| Stripetail rockfish | *Sebastes saxicola* | 39.55 | 123.50 | 1.63 | 34.02 | 8.08 | 209.8 | 77.7 | 12.1 |
| Yellowtail rockfish | *Sebastes flavidus* | 46.47 | 124.79 | 1.71 | 33.85 | 7.05 | 148.7 | 92.9 | 68.6 |
| **Slope rockfishes** | | | | | | | | | |
| Aurora rockfish | *Sebastes aurora* | 37.89 | 122.37 | 0.58 | 34.20 | 6.30 | 462.0 | 86.3 | 26.6 |
| Blackgill rockfish | *Sebastes melanostomus* | 34.66 | 120.78 | 0.55 | 34.23 | 6.81 | 429.6 | 93.6 | 47.7 |
| Darkblotched rockfish | *Sebastes crameri* | 44.56 | 124.71 | 1.27 | 34.01 | 6.55 | 263.0 | 83.3 | 31.0 |
| Pacific ocean perch | *Sebastes alutus* | 47.25 | 125.31 | 1.42 | 33.97 | 6.40 | 247.0 | 92.2 | 37.2 |
| Redbanded rockfish | *Sebastes babcocki* | 44.98 | 124.64 | 1.41 | 33.96 | 6.96 | 245.3 | 91.9 | 52.8 |
| Rougheye rockfish | *Sebastes aleutianus* | 45.98 | 124.77 | 1.08 | 34.04 | 5.96 | 364.6 | 96.3 | 71.6 |
| Splitnose rockfish | *Sebastes diploproa* | 39.38 | 123.11 | 1.19 | 34.09 | 7.41 | 289.7 | 79.4 | 10.9 |
| **Thornyheads** | | | | | | | | | |
| Longspine thornyhead | *Sebastolobus altivelis* | 40.84 | 123.82 | 0.32 | 34.35 | 4.30 | 856.3 | 64.5 | 4.0 |
| Shortspine thornyhead | *Sebastolobus alascanus* | 41.40 | 123.58 | 0.71 | 34.19 | 5.49 | 570.6 | 49.0 | 11.1 |

For example, near-bottom DO was retained in the optimal models for curlfin sole, petrale sole and rex sole based on $\Delta_i = 0$, despite approximate p-values >0.05. Because p-values generated by GAM analyses are approximate (Daskalov 1999), we based our final decisions to retain covariates (including DO) in optimal models on AIC values. Although the relation between expected CPUE and DO (positive versus negative) is not shown for the 8 rockfish species without DO in optimal models, 6 secondary models (with $\Delta_i < 2$) for these species displayed positive relationships between CPUE and DO (over the range of DO values experienced or at hypoxic levels) and one negative. Note that no equivalent model was found for shortbelly rockfishes.

Since this study focused on the impact of low near-bottom oxygen concentrations on species-specific CPUE, the functional form of the relationship be-

Table 3. Suite of optimal models (n = 11) that included near-bottom dissolved oxygen (DO) based on species-specific generalized additive model (GAM) analyses of 34 groundfish species. Although year ($a_y$), latitude (°N) and longitude (°W) (long, lat) were included in all optimal models, a variable subset of significant covariates (day of year [DOY], DO, ml $l^{-1}$; salinity [S], ppt; temperature [$T$], °C; and bottom depth [$Z$], m) was selected for each species during model exploration via backward stepwise elimination. Covariates were removed from the analysis based on their significance (i.e. the variable with the highest p-value was removed first) until an optimal model for each species was chosen based on the lowest Akaike's information criterion (AIC) value. Optimal models without DO not shown

| Model | Equation |
|---|---|
| 1 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_3(\mathrm{S}) + s_4(\mathrm{DOY}) + s_5(T) + s_6(Z)$ |
| 2 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_4(\mathrm{DOY}) + s_5(T) + s_6(Z)$ |
| 3 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_3(\mathrm{S}) + s_5(T) + s_6(Z)$ |
| 4 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_3(\mathrm{S}) + s_4(\mathrm{DOY}) + s_6(Z)$ |
| 5 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_3(\mathrm{S}) + s_4(\mathrm{DOY}) + s_5(T)$ |
| 6 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_5(T) + s_6(Z)$ |
| 7 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_4(\mathrm{DOY}) + s_6(Z)$ |
| 8 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_4(\mathrm{DOY}) + s_5(T)$ |
| 9 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_3(\mathrm{S}) + s_5(T)$ |
| 10 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_6(Z)$ |
| 11 | $\ln \mathrm{CPUE}_j = a_y + s_1(\mathrm{long, lat}) + s_2(\mathrm{DO}) + s_4(\mathrm{DOY})$ |

tween predicted CPUE and near-bottom DO in final models for species that showed significant relationships with DO (n = 26) is shown (Fig. 3). Overall, we observed positive slopes between predicted CPUE and DO within hypoxic (DO < 1.43 ml $l^{-1}$) or severely hypoxic (DO < 0.5 ml $l^{-1}$) waters for 19 of 34 species, indicating that catch decreased as DO declined. We saw opposite responses for 7 additional species and no significant relationship for the remaining 8 species.

As revealed through GAMs, the relationships between DO and catch varied by species and were often complicated—both increasing and decreasing over portions of the DO range encountered *in situ* (Fig. 3). To further explore the relationship between low DO and catch, we plotted the restricted range of DO values over which species exhibited significantly increased CPUE versus their overall range (Fig. 4a) for the 19 species with positive relationships. The restricted range was also examined relative to catch-weighted depth (Fig. 4b). In both cases, DO values with non-significant trends (i.e. encompassing zero across a wide range of catch) were excluded from the images. In general, species exhibiting increased catch over a narrower (and lower) range of DO concentrations were significantly deeper ($p < 0.05$) relative to those with increased catch over a wider range of DO values (Fig. 4).

### Subgroups

By examining similarities and differences in the response of various subgroups to low DO levels we hoped to reveal underlying ecological inferences that might otherwise not be apparent. Within life history subgroups, near-bottom DO played a significant role in the distribution for all flatfishes (n = 10), roundfishes (n = 5) and thornyheads (n = 2), and was incorporated in the optimal models for 6 of 10 shelf rockfish species and 3 of 7 slope rockfishes. Various patterns were revealed when subgroups based on life history, depth or latitude were graphed versus percentage of positive, negative on non-significant DO trends (Fig. 5). Relationships exhibiting positive interactions between expected CPUE and DO declined from 100% for thornyheads to 29% for slope rockfishes; negative relationships were greatest for flatfishes (40%) and slope rockfishes displayed the highest percent of non-significant responses (57%). When examined by depth, the deepest depth category (800 to 900 m) displayed the highest percent of positive relationships between catch and DO, while shelf (55 to 180 m) and lower slope (300 to 700 m) species also exhibited a relatively high percentage of positive relationships (Fig. 5b). Negative relationships were confined to species within depth categories <300 m and the percent of species with non-significant interactions was evenly disbursed among depth categories >800 m. Latitudinal subgroups revealed a clear pattern of positive relationships between DO and CPUE at mid-latitudes (38 to 44° N) versus species found in the most northern and southern regions of the survey (Fig. 5c).

### Total CPUE and species richness

To further examine community response to low DO and other environmental variables, the shape of the functional forms of the relationships for predicted total CPUE and species richness and significant covariates were plotted for all demersal fishes combined (Figs. 6 & 7). We show partial GAM plots identifying the additive effects of DOY, bottom depth (m), and near bottom environmental vari-

Table 4. Species-specific Akaike's information criterion ($\Delta$AIC) values for generalized additive models (GAMs; defined in Table 3) as covariates with approximate p-values >0.05 were removed until an optimal model ($\Delta_i = 0$) was developed for each species. Covariates removed from optimal modes for each species included dissolved oxygen (DO; ml $l^{-1}$), day of the year (DOY), salinity (S; ppt) temperature ($T$; °C) and depth ($Z$; m). Optimal models without DO are not shown for 8 rockfish species but acceptable models ($\Delta_i < 2$) for 7 of these species are shown. Similar results are shown for total catch per unit effort (CPUE) and richness

| Common name | Model | | | | | | | | | | | Covariates removed |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | |
| **Flatfishes** | | | | | | | | | | | | |
| Arrowtooth flounder | 1.0 | 0.0 | 2.7 | 4.2 | 149.6 | 2.0 | 2.8 | 14.9 | 157.1 | 175.4 | 175.5 | S |
| Curlfin sole | 0.0 | 0.4 | 1.1 | 6.4 | 55.1 | 1.1 | 19.6 | 7.2 | 62.5 | 28.9 | 92.2 | None |
| Deepsea sole | 1.7 | 0.0 | 1.5 | 1.8 | 24.1 | 1.2 | 1.1 | 2.7 | 23.3 | 3.0 | 100.2 | S |
| Dover sole | 0.0 | 26.3 | 11.2 | 30.6 | 185.1 | 38.2 | 63.0 | 43.4 | 201.1 | 77.6 | 437.9 | None |
| English sole | 1.5 | 10.5 | 0.0 | 7.6 | 47.0 | 10.4 | 10.5 | 6.8 | 47.7 | 9.1 | 77.9 | DOY |
| Flathead sole | 4.8 | 3.5 | 6.8 | 3.8 | 3.0 | 5.4 | 1.9 | 5.0 | 5.1 | 3.8 | 0.0 | S, $T$, $Z$ |
| Pacific sanddab | 0.0 | 1.3 | 3.1 | 17.0 | 134.3 | 4.3 | 16.1 | 15.2 | 133.8 | 14.2 | 144.5 | None |
| Petrale sole | 2.4 | 0.0 | 32.9 | 39.4 | 73.5 | 31.2 | 41.0 | 59.6 | 91.0 | 60.6 | 104.1 | S |
| Rex sole | 0.7 | 0.0 | 4.1 | 7.7 | 226.2 | 2.4 | 7.1 | 11.9 | 239.5 | 10.0 | 305.7 | S |
| Slender sole | 2.1 | 0.1 | 1.5 | 65.5 | 104.9 | 0.0 | 69.1 | 63.6 | 112.3 | 69.5 | 234.3 | S, DOY |
| **Roundfishes** | | | | | | | | | | | | |
| Lingcod | 2.2 | 2.1 | 1.5 | 2.5 | 3.8 | 0.7 | 1.9 | 0.8 | 2.6 | 0.0 | 4.7 | S, DOY, $T$ |
| Pacific hake | 0.5 | 0.0 | 35.0 | 3.3 | 117.1 | 37.0 | 2.2 | 42.5 | 184.4 | 43.1 | 171.0 | S |
| Sablefish | 0.0 | 1.7 | 12.1 | 4.2 | 160.5 | 16.0 | 5.2 | 16.6 | 168.5 | 19.1 | 198.2 | None |
| Spiny dogfish | 1.5 | 0.0 | 52.3 | 4.7 | 19.2 | 51.9 | 4.9 | 64.6 | 65.5 | 71.3 | 18.4 | S |
| Spotted ratfish | 1.3 | 7.9 | 8.0 | 0.0 | 31.9 | 11.8 | 6.1 | 12.2 | 34.7 | 11.4 | 24.0 | $T$ |
| **Shelf rockfishes** | | | | | | | | | | | | |
| Bocaccio | 3.1 | 3.9 | 1.8 | 2.8 | 1.7 | 2.9 | 5.1 | 5.9 | 0.0 | 4.4 | 6.2 | DOY, $Z$ |
| Canary rockfish | 3.0 | 4.4 | 1.9 | 2.4 | 8.7 | 3.0 | 3.4 | 1.8 | 7.7 | 2.3 | 12.1 | DO, DOY, $T$ |
| Chilipepper | 4.0 | 10.3 | 2.2 | 4.0 | 2.0 | 9.8 | 8.8 | 2.6 | 0.0 | 8.1 | 7.1 | DOY, $Z$ |
| Greenspotted rockfish | 3.0 | 1.3 | 5.6 | 1.8 | 14.8 | 4.2 | 0.6 | 4.6 | 18.7 | 4.3 | 11.1 | DO, S, $T$ |
| Greenstriped rockfish | 2.8 | 2.0 | 3.1 | 0.9 | 27.2 | 2.6 | 0.0 | 1.5 | 28.6 | 4.5 | 24.3 | S, $T$ |
| Rosethorn rockfish | 3.2 | 6.1 | 1.7 | 2.0 | 2.3 | 5.5 | 5.0 | 0.0 | 1.7 | 5.0 | 3.4 | DOY, $T$ |
| Sharpchin rockfish | 3.5 | 9.3 | 7.0 | 4.9 | 1.8 | 10.4 | 9.8 | 5.1 | 5.9 | 8.4 | 8.4 | DO, $Z$ |
| Shortbelly rockfish | 3.0 | 2.0 | 6.6 | 9.1 | 37.5 | 4.9 | 10.4 | 7.1 | 35.6 | 9.5 | 49.5 | DO, S |
| Stripetail rockfish | 1.5 | 2.5 | 0.0 | 0.8 | 12.8 | 0.9 | 7.5 | 0.1 | 13.7 | 5.7 | 26.2 | DOY |
| Yellowtail rockfish | 2.3 | 7.1 | 0.0 | 2.2 | 2.3 | 5.5 | 5.3 | 2.8 | 0.7 | 3.7 | 5.7 | DOY |
| **Slope rockfishes** | | | | | | | | | | | | |
| Aurora rockfish | 1.4 | 1.8 | 0.0 | 22.4 | 56.7 | 0.9 | 29.6 | 20.7 | 55.5 | 27.1 | 78.0 | DOY |
| Blackgill rockfish | 2.5 | 1.7 | 2.3 | 2.1 | 12.9 | 1.3 | 1.4 | 2.9 | 12.9 | 1.9 | 8.6 | DO, S, DOY |
| Darkblotched rockfish | 0.2 | 1.9 | 0.0 | 2.0 | 32.5 | 2.0 | 2.4 | 0.1 | 41.1 | 1.4 | 43.3 | DOY |
| Pacific ocean perch | 2.6 | 5.0 | 3.4 | 1.9 | 6.1 | 5.3 | 5.1 | 1.6 | 5.3 | 4.1 | 7.4 | DO, $T$ |
| Redbanded rockfish | 5.7 | 5.8 | 3.9 | 3.7 | 56.4 | 3.8 | 4.0 | 1.9 | 66.8 | 2.0 | 71.7 | DO, S, DOY, $T$ |
| Rougheye rockfish | 6.0 | 4.4 | 4.5 | 4.1 | 43.4 | 3.4 | 2.9 | 3.0 | 41.8 | 1.9 | 45.0 | DO, S, DOY, $T$ |
| Splitnose rockfish | 1.7 | 3.0 | 0.0 | 34.7 | 58.3 | 1.0 | 36.8 | 34.1 | 61.7 | 37.6 | 113.6 | DOY |
| **Thornyheads** | | | | | | | | | | | | |
| Longspine thornyhead | 2.4 | 0.7 | 1.8 | 14.8 | 50.5 | 0.0 | 15.1 | 13.4 | 50.1 | 13.3 | 141.0 | S, DOY |
| Shortspine thornyhead | 0.4 | 0.0 | 4.3 | 37.1 | 43.9 | 5.1 | 57.2 | 39.2 | 44.3 | 61.0 | 49.1 | S |
| Total CPUE | 0.0 | 29.2 | 17.7 | 14.0 | 156.0 | 43.1 | 39.7 | 39.2 | 165.7 | 25.9 | 224.2 | None |
| Richness | 0.0 | 10.3 | 63.7 | 240.1 | 219.8 | 72.6 | 243.3 | 250.4 | 248.5 | 269.3 | 311.5 | None |

ables: salinity, temperature and oxygen on CPUE (Fig. 6) and species richness (Fig. 7). Both total CPUE and species richness showed highly significant positive relationships with low near-bottom oxygen conditions. The shapes of the functional forms of the relationship between total CPUE, species richness and near-bottom DO were highly similar, with both curves increasing at DO levels less than ~1.5 ml $l^{-1}$ before declining slightly, followed by further increases and greater variability in the predicted response at higher DO levels. The additive effects of the additional variables included in the GAM analysis (near-bottom temperature, bottom depth, near-bottom salinity, DOY) were similar for both total demersal fish CPUE (Fig. 6) and species richness (Fig. 7).

Table 5. Final models for each species, total catch per unit effort (CPUE; ln kg ha$^{-1}$) and richness (ln n) (based on the lowest Akaike's information criterion [AIC] value) with covariates retained: dissolved oxygen (DO; ml l$^{-1}$), day of the year (DOY), salinity (S; ppt) temperature ($T$; °C) and depth ($Z$; m). The deviance explained, generalized cross-validation (GCV), $r^2$, number of hauls (n), relationship of expected CPUE and richness to DO as positive (+), negative (–) or not significant (NS) and approximate p-values for relationships with low DO are also shown. Note that latitude and longitude were retained in all models

| Common name | Covariates retained | Deviance (%) | GCV | $r^2$ | Hauls (n) | Relation to DO | p-value (DO) |
|---|---|---|---|---|---|---|---|
| **Flatfishes** | | | | | | | |
| Arrowtooth flounder | DO, DOY, $T$, $Z$ | 47.0 | 1.853 | 0.44 | 684 | – | 0.0005 |
| Curlfin sole | All | 46.4 | 0.710 | 0.43 | 708 | – | 0.12 |
| Deepsea sole | DO, DOY, $T$, $Z$ | 42.8 | 0.866 | 0.40 | 505 | + | <0.0001 |
| Dover sole | All | 54.8 | 1.510 | 0.53 | 1529 | + | 0.0008 |
| English sole | DO, S, $T$, $Z$ | 27.5 | 2.979 | 0.25 | 1312 | + | 0.01 |
| Flathead sole | DO, DOY | 46.0 | 1.340 | 0.40 | 331 | – | 0.08 |
| Pacific sanddab | All | 63.7 | 2.062 | 0.62 | 1031 | + | 0.03 |
| Petrale sole | DO, DOY, $T$, $Z$ | 28.4 | 1.891 | 0.26 | 1032 | + | 0.08 |
| Rex sole | DO, DOY, $T$, $Z$ | 49.5 | 1.600 | 0.48 | 1532 | + | 0.06 |
| Slender sole | DO, $T$, $Z$ | 42.2 | 1.380 | 0.40 | 1069 | – | 0.002 |
| **Roundfishes** | | | | | | | |
| Lingcod | DO, $Z$ | 17.5 | 3.113 | 0.15 | 1071 | + | 0.007 |
| Pacific hake | DO, DOY, $T$, $Z$ | 35.3 | 2.949 | 0.33 | 1208 | – | 0.05 |
| Sablefish | All | 33.9 | 2.071 | 0.32 | 1491 | + | 0.0002 |
| Spiny dogfish | DO, DOY, $T$, $Z$ | 42.9 | 3.581 | 0.40 | 534 | + | 0.17 |
| Spotted ratfish | DO, S, DOY, $Z$ | 25.8 | 2.030 | 0.24 | 1372 | + | 0.01 |
| **Shelf rockfishes** | | | | | | | |
| Bocaccio | DO, S, $T$ | 24.7 | 2.444 | 0.20 | 353 | – | 0.007 |
| Canary rockfish | S, $Z$ | 22.9 | 2.844 | 0.20 | 458 | NS[a] | 0.46 |
| Chilipepper | DO, S, $T$ | 49.6 | 5.530 | 0.39 | 183 | + | 0.10 |
| Greenspotted rockfish | DOY, $Z$ | 19.7 | 1.409 | 0.15 | 487 | NS[a] | 0.59 |
| Greenstriped rockfish | DO, DOY, $Z$ | 40.1 | 2.841 | 0.36 | 538 | + | 0.08 |
| Rosethorn rockfish | DO, S, $Z$ | 27.9 | 1.477 | 0.25 | 844 | + | 0.06 |
| Sharpchin rockfish | S, DOY, $T$ | 53.7 | 3.323 | 0.45 | 233 | NS[a] | 0.62 |
| Shortbelly rockfish | DOY, $T$, $Z$ | 29.7 | 2.668 | 0.24 | 373 | NS | 0.79 |
| Stripetail rockfish | DO, S, $T$, $Z$ | 42.0 | 3.736 | 0.38 | 247 | + | 0.11 |
| Yellowtail rockfish | DO, S, $T$, $Z$ | 36.0 | 3.926 | 0.32 | 484 | + | 0.09 |
| **Slope rockfishes** | | | | | | | |
| Aurora rockfish | DO, S, $T$, $Z$ | 57.8 | 1.557 | 0.54 | 350 | + | <0.0001 |
| Blackgill rockfish | $T$, $Z$ | 62.4 | 1.964 | 0.57 | 241 | NS[a] | 0.67 |
| Darkblotched rockfish | DO, S, $T$, $Z$ | 38.1 | 3.094 | 0.32 | 358 | – | 0.04 |
| Pacific ocean perch | S, DOY, $Z$ | 77.7 | 2.710 | 0.70 | 113 | NS[a] | 0.62 |
| Redbanded rockfish | $Z$ | 20.9 | 1.113 | 0.19 | 405 | NS[a] | 0.89 |
| Rougheye rockfish | $Z$ | 32.8 | 1.966 | 0.27 | 215 | NS[a] | 0.56 |
| Splitnose rockfish | DO, S, $T$, $Z$ | 49.0 | 3.406 | 0.45 | 346 | + | 0.05 |
| **Thornyheads** | | | | | | | |
| Longspine thornyhead | DO, $T$, $Z$ | 75.5 | 0.612 | 0.74 | 642 | + | <0.0001 |
| Shortspine thornyhead | DO, DOY, $T$, $Z$ | 47.4 | 1.495 | 0.46 | 1367 | + | <0.0001 |
| Total CPUE | All | 39.5 | 0.849 | 0.39 | 3274 | + | <0.0001 |
| Richness | All | 38.4 | 0.655 | 0.39 | 3274 | + | <0.0001 |

[a] There is an equivalent model ($\Delta_i < 2$) which includes DO (data not shown)

For comparison with our earlier research (Keller et al. 2015), we also described the relationship between total CPUE for demersal fishes (ln, kg ha$^{-1}$) and near-bottom DO concentration (ln, ml l$^{-1}$) for the 2008 to 2014 timeframe via a quadratic regression (Fig. 8a). The highly significant ($p < 0.0001$) relationship explained 28% of the variance in catch with all data included in the analysis. When we restricted data to stations defined as hypoxic (DO < 1.43 ml l$^{-1}$), the amount of variance explained increased to 40% (Fig. 8b). Further improvements ($r^2 = 0.62$) occurred when only catch from severely hypoxic stations (DO ≤ 0.5 ml l$^{-1}$) were included in the analysis ($y = 3.12 - 2.74x - 1.42x^2$; n = 954, $p < 0.0001$).

Total species richness (demersal fishes) and near-bottom DO concentrations exhibited relationships

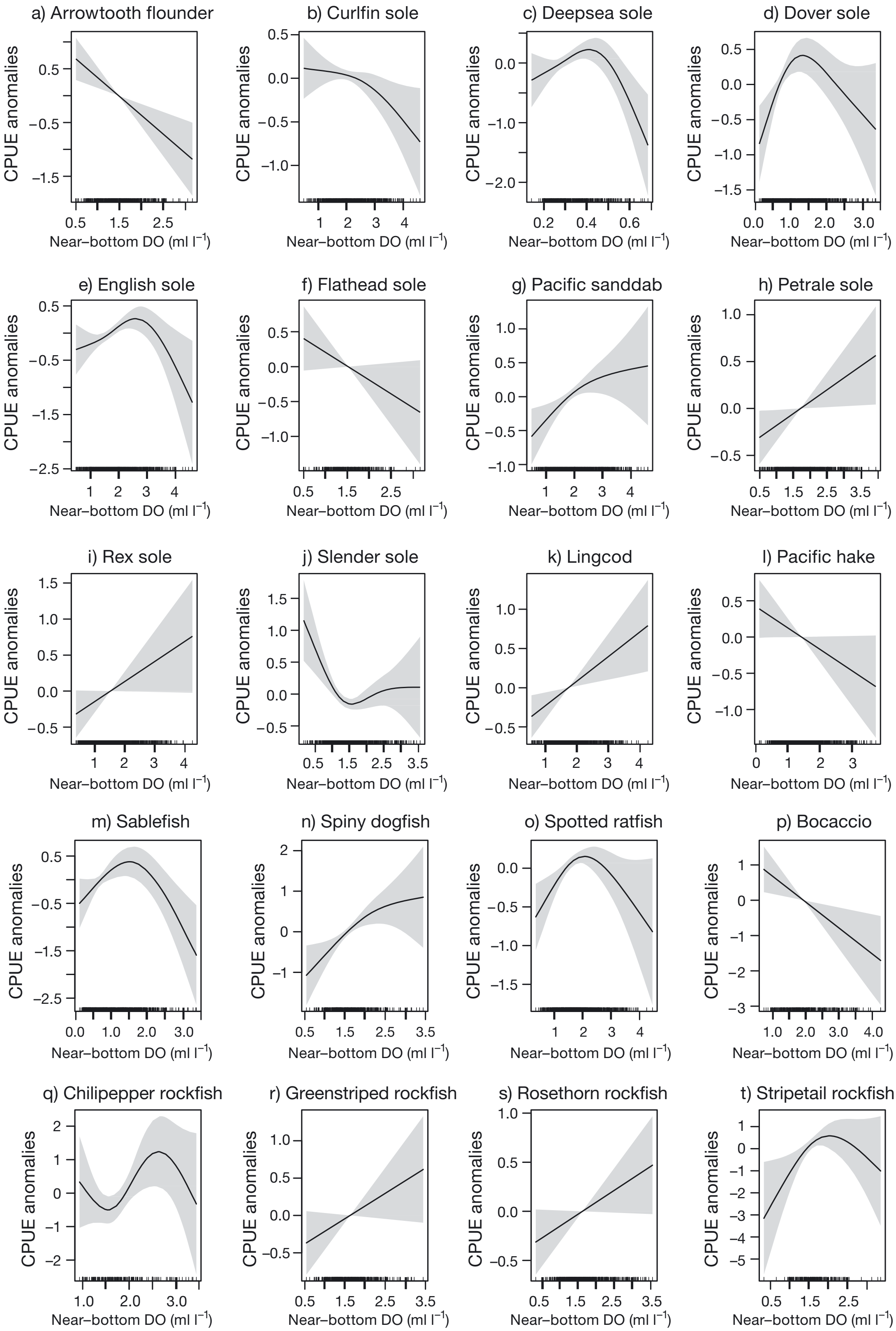
a) Arrowtooth flounder
b) Curlfin sole
c) Deepsea sole
d) Dover sole
e) English sole
f) Flathead sole
g) Pacific sanddab
h) Petrale sole
i) Rex sole
j) Slender sole
k) Lingcod
l) Pacific hake
m) Sablefish
n) Spiny dogfish
o) Spotted ratfish
p) Bocaccio
q) Chilipepper rockfish
r) Greenstriped rockfish
s) Rosethorn rockfish
t) Stripetail rockfish

Fig. 3. (Above and following page) Generalized additive model (GAM) plots identifying the additive effects of near-bottom dissolved oxygen (DO) on catch per unit effort (CPUE; kg ha$^{-1}$) for species that showed significant relationships with DO: (a) arrowtooth flounder; (b) curlfin sole; (c) deepsea sole; (d) Dover sole; (e) English sole; (f) flathead sole; (g) Pacific sanddab; (h) petrale sole; (i) rex sole; (j) slender sole; (k) lingcod; (l) Pacific hake; (m) sablefish; (n) spiny dogfish; (o) spotted ratfish; (p) bocaccio; (q) chilipepper rockfish; (r) greenstriped rockfish; (s) rosethorn rockfish; (t) stripetail; (u) yellowtail rockfish; (v) aurora rockfish; (w) darkblotched rockfish; (x) splitnose rockfish; (y) longspine thornyhead; and (z) shortspine thornyhead

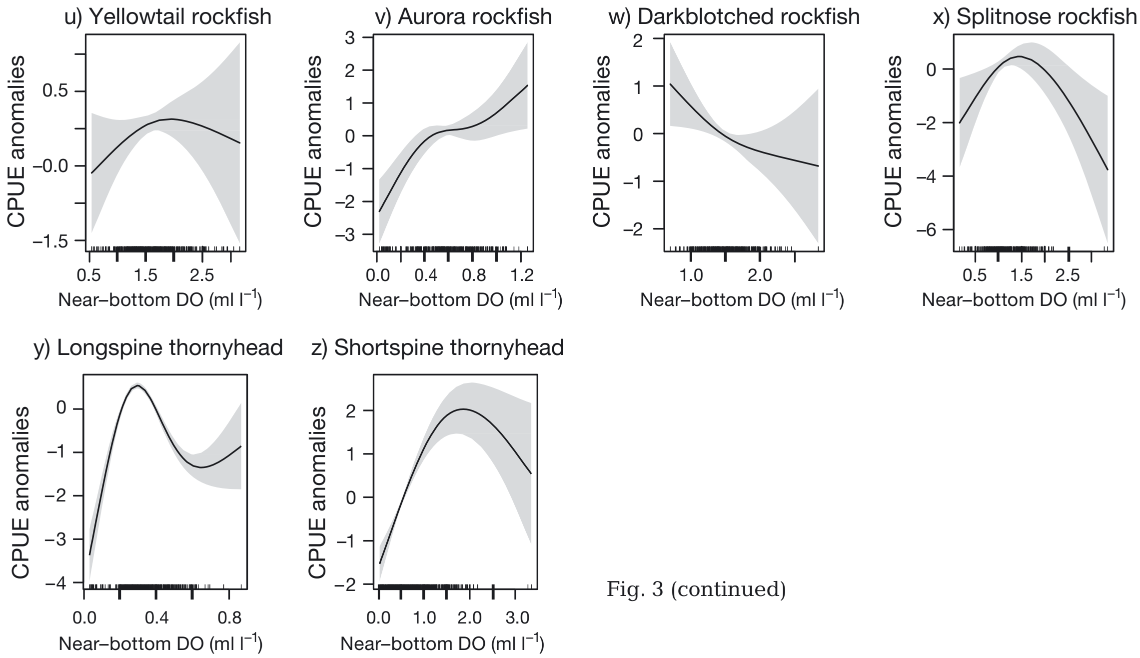

Fig. 3 (continued)

similar to those seen for CPUE. Species richness was also best described by a quadratic equation. With all DO data included in the analysis, 32% of the variance in richness was explained as a function of near-bottom DO concentration (Fig. 9a). If we used only data from hypoxic stations, then the fit improved to explain 41% of the variance in richness (Fig. 9b). Further restricting the data to stations with oxygen concentrations below 0.5 ml $l^{-1}$ increased the amount of variation explained to 59% ($y = 2.45 - 0.58x - 0.35x^2$; $n = 954$, $p < 0.0001$). All relationships were highly significant ($p < 0.0001$). The relationship between DO and both CPUE and species richness was positive, with catch and richness increasing as near-bottom DO levels increased, particularly in hypoxic waters. The higher variance explained in the regression analysis by DO alone (see above) does not reflect the significant influence of the other environmental variables that co-vary with DO, which was accounted for by the GAM analysis (Table 5).

## DISCUSSION

Based on a GAM approach relating catch of multiple groundfish species to a suite of environmental variables, including near-bottom DO, we saw considerable variability in the response of individual species to low near-bottom DO levels ranging from significantly positive (n = 19 species) to significantly negative (n = 7) to no significant response (n = 8). After examining covariate plots, the effect of DO was frequently non-linear for multiple species. The primary pattern indicated that increasing DO within the lower range inhabited by each species had a positive effect on CPUE (for deep-sea sole, Dover sole, English sole, sablefish, yellowtail rockfish, stripetail rockfish, splitnose rockfish, longspine thornyhead and shortspine thornyhead) followed by a decreasing effect at higher DO values (Fig. 3).

Non-linear but generally increasing trends across the entire range of DO inhabited by each species were less common (Pacific sanddab, spiny dogfish and aurora rockfish) (Fig. 3), while linear increasing trends occurred for petrale sole, rex sole, lingcod, greenstriped rockfish and rosethorn rockfish (Fig. 3). Chilipepper rockfish exhibited a complex non-linear pattern with a positive impact observed across a mid-range of DO values where the density of catch was highest and negative impacts at lower and higher DO levels where catch appeared sparse (Fig. 3).

Negative impacts of DO on catch similarly exhibited non-linear (curlfin, slender sole and darkblotched rockfish) and linear patterns (arrowtooth flounder, flathead sole, Pacific hake and bocaccio). Even though bocaccio and darkblotched rockfish exhibited negative relationships with DO, these species, unlike others observed here, rarely occurred at DO levels <1.0 ml $l^{-1}$. Based on the 95% confidence intervals for covariate plots of DO for petrale sole, rex sole, greenstriped rockfish and rosethorn rockfish, the influence of DO appears marginal (i.e. encompasses zero across a wide range of catch). We attribute the variable responses of 34 demersal fish species

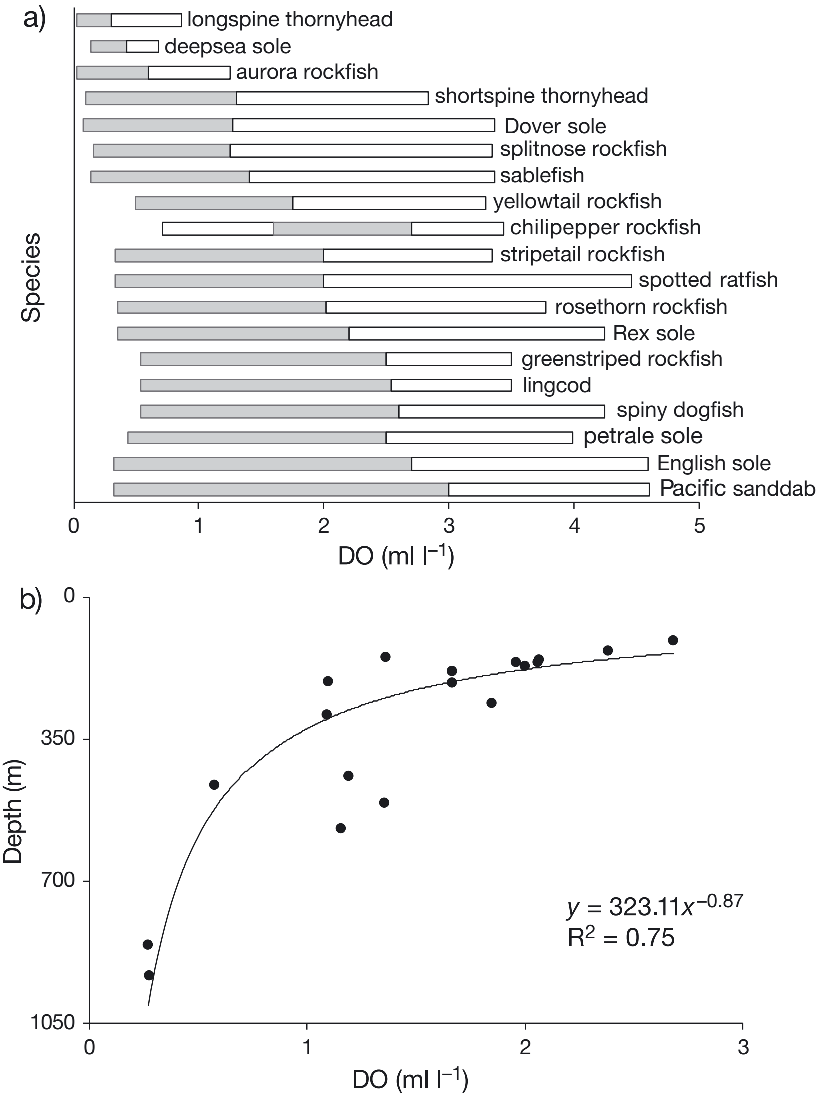

Fig. 4. (a) Overall range (open + shaded bars) and restricted range (shaded bars) of near-bottom dissolved oxygen (DO) for individual species (n = 19) with significant positive relationships between DO and catch per unit effort (CPUE; ln CPUE + 0.1; kg ha$^{-1}$); and (b) the restricted range (DO) versus catch-weighted depth (m) demonstrating a highly significant ($p < 0.0001$) curvilinear relationship between DO and predicted CPUE. Restricted range indicates where CPUE increased with increasing DO based on generalized additive models (GAMs) and excludes DO levels with non-significant trends (i.e. trends that encompassed zero across a wide range of catch); species are arranged in order of increasing restricted range from top to bottom in (a)

to low oxygen in part to their individual physiology. For species not significantly related to DO, habitat has been suggested to be an important factor controlling distribution (e.g. canary rockfish, Vestfals 2009; darkblotched rockfish, Shelton et al. 2014). In general, our results suggest that there is a threshold effect for multiple demersal fish species where small changes in oxygen lead to large changes in CPUE (Figs. 3 & 4). The threshold effect is also reflected in the community response, where total demersal fish catch and richness similarly increased at lower DO levels (Figs. 6 & 7).

Our continued motivation for examining the role of hypoxia in fish distribution and catch is fueled by increasing reports of changing environmental conditions within the California Current System (Bond et al. 2015, Somero et al. 2016), increased occurrence of hypoxia worldwide (Stramma et al. 2008, Bakun et al. 2015) and regionally (Bograd et al. 2008, Chan et al. 2008, Pierce et al. 2012) as well as global expansions of OMZs (Stramma et al. 2008). From 2008 to 2014 we noted a range of tows within hypoxic (60.9 to 66.3% tows yr$^{-1}$) and severely hypoxic (27.4 to 30.6% tows yr$^{-1}$) areas over time but no increasing trend. The relatively consistent range in the percent of tows within hypoxic and severely hypoxic waters is partially related to the spatial overlap between the survey and a well-established OMZ characterized by historical DO levels from 0.25 to 0.5 ml l$^{-1}$ (Kamykowski & Zentara 1990, Levin 2003).

The results from the present study also extend and support our earlier research examining the ties between fish distribution and near-bottom oxygen levels (Keller et al. 2010, 2015). We previously reported that catch, species diversity and condition factors for demersal fishes were significantly correlated with near-bottom oxygen levels both within a known hypoxic area off the central Oregon coast (Keller et al. 2010) and to a more variable extent, coast-wide from the upper to the lower limit of the OMZ and shoreward across the continental shelf (US–Canada to US–Mexico) (Keller et al. 2015). We also extended our prior work by utilizing the same suite of environmental covariates previously incorporated in binomial GAMs for 4 widespread demersal fish species (Keller et al. 2015). Based on data from 2008 to 2010, the probability of occurrence for 4 groundfish species varied in relation to changing DO concentrations, with 2 species exhibiting sensitivity to change while 2 did not (Keller et al. 2015). The current research

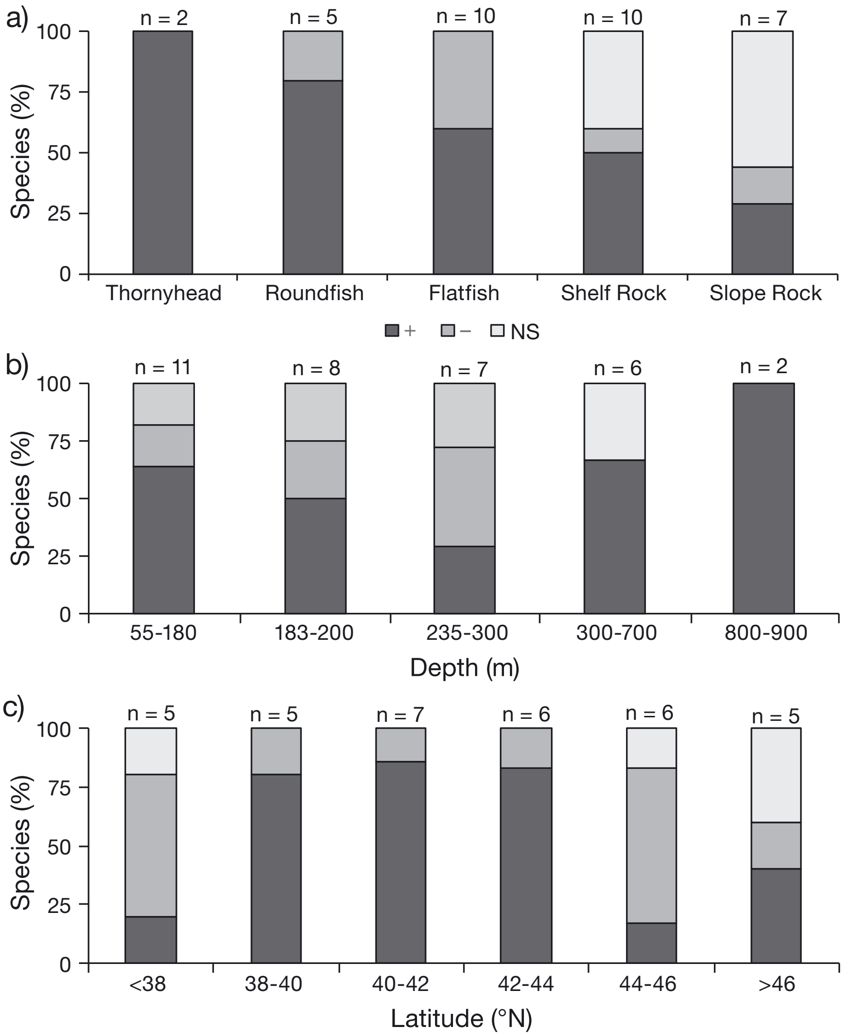

Fig. 5. Subgroups comparing the percentage of species with positive (+), negative (–), and non-significant (NS) relationships between catch per unit effort (CPUE; ln CPUE+0.1, kg ha$^{-1}$) and near-bottom dissolved oxygen (DO; ml l$^{-1}$) by (a) life-history category; (b) depth; and (c) latitude, where n is the total number of species in each subgroup

improved on the prior studies by focusing on species-specific relationships for a greater number of groundfish species based on catch (rather than presence–absence) over a longer time period (2008 to 2014). The use of GAMs for analyzing fisheries-independent data is gaining traction as managers attempt to move towards ecosystem-based models that incorporate environmental, spatial and biological information (Murase et al. 2009, Drexler & Ainsworth 2013, Thorson et al. 2015b). The value of GAM analysis is further supported here via our analysis of total CPUE and richness, which we compared using 2 approaches (GAM and regression analyses). The higher variance explained in the regression analysis by oxygen alone does not reflect the significant influence of the other environmental variables (depth and temperature) that co-vary with oxygen, as revealed through the GAM analysis. Our results also indicate the value of long-term time series, which support the application of more sophisticated analyses as data accumulate over time.

Based on our study, DO levels were consistently low within the OMZ for all years; however, the annual occurrence of shallower, hypoxic events was variable in extent and duration (Fig. 1). Generally, incursion of low DO waters onto the inner shelf (55 to 80 m) along the US west coast has expanded in extent and frequency in recent years (Bograd et al. 2008, Chan et al. 2008, Pierce et al. 2012). Analysis of historical data revealed little evidence of low oxygen along the inner shelf prior to 2002 and no occurrence of anoxia dating back to 1950 (Chan et al. 2008). Impacts from low oxygen in bottom waters off Oregon in 2002 included observation of dead or moribund fishes and invertebrates in reef areas, elevated crab mortality in commercial pots and reports of dead organisms washed ashore (Grantham et al. 2004). As previously noted, these shallower hypoxic and anoxic events are associated with significantly reduced densities of rockfishes, mortality of near-bottom organisms (including commercially important species; Chan et al. 2008) and decreased species richness and overall catch of demersal fish (Keller et al. 2010). Other potential impacts of increased coastal hypoxia and/or expansion of the offshore OMZ include avoidance, habitat compression (or expansion), physiological impairment, changes in foraging behavior and alterations in predator–prey relationships (Chan et al. 2008, Koslow et al. 2011, Seibel 2011, Gallo & Levin 2016).

As in our previous study, we noted a distinct difference in the average DO levels within and outside the OMZ. Here, the average concentration of oxygen at depths <450 m was 1.66 ± 0.77 ml l$^{-1}$ (n = 2120), whereas the concentration at greater depths (450 to 1280 m) averaged 0.38 ± 0.17 ml l$^{-1}$ (n = 1169). One particularly interesting outcome of this study was the observation that even for species known to regularly inhabit the OMZ there appears to be a preference for

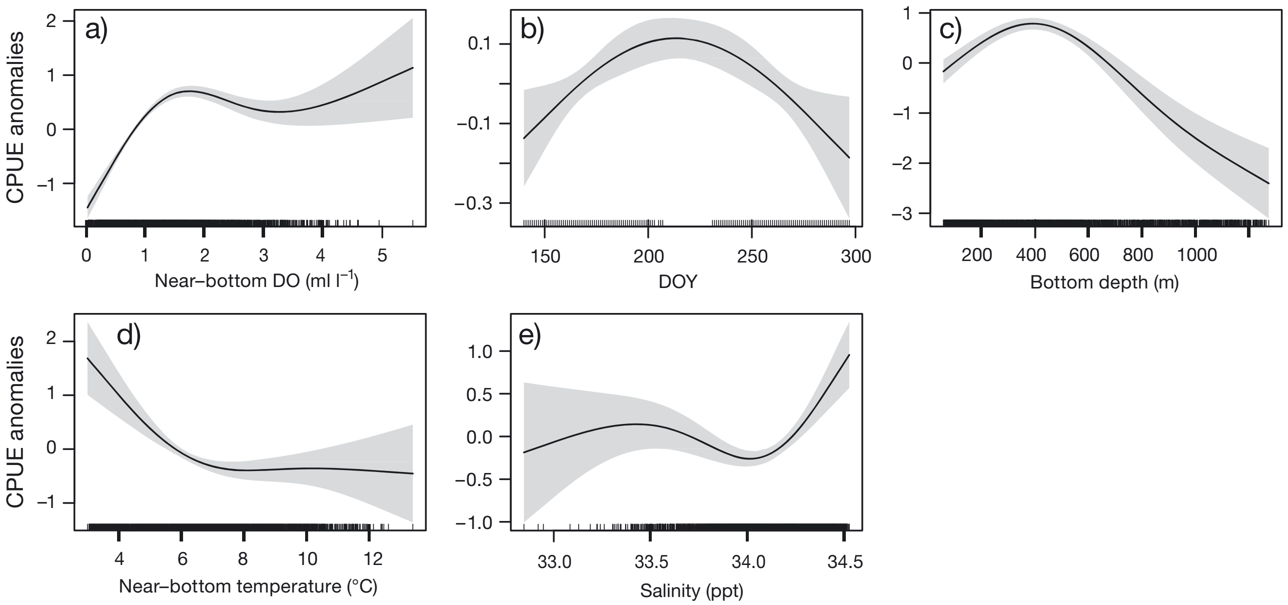

Fig. 6. Generalized additive model (GAM) plots identifying the additive effects of significant covariates: (a) near-bottom dissolved oxygen (DO); (b) day of the year (DOY); (c) bottom depth; (d) near-bottom temperature; and (e) near-bottom salinity on total catch per unit effort (CPUE; ln kg ha$^{-1}$) for all demersal fishes. Shaded areas reflect the 95 % confidence intervals around response curves. Note that ranges on *x*- and *y*-axes differ among panels. The *y*-axis reflects the effect of each covariate on CPUE. The relative density of data is shown by the 'rug' along the *x*-axis

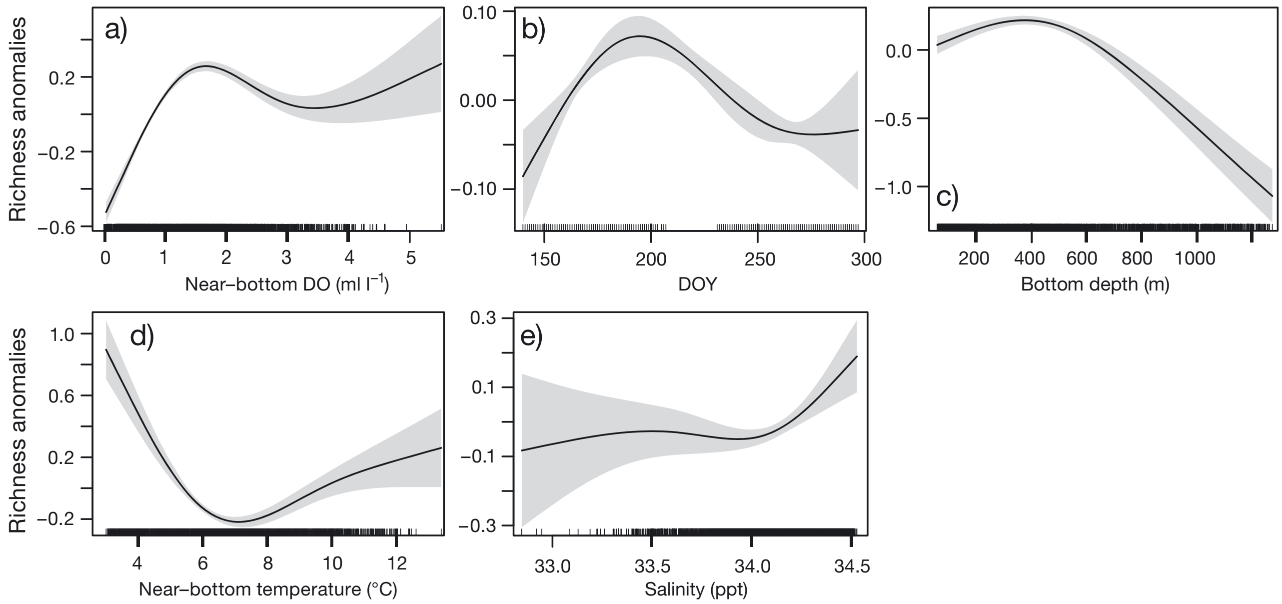

Fig. 7. Generalized additive model (GAM) plots identifying the additive effects of significant covariates: (a) near-bottom dissolved oxygen (DO); (b) day of the year (DOY); (c) bottom depth; (d) near-bottom temperature; and (e) near-bottom salinity on total species richness (ln n) for demersal fishes. Shaded areas reflect 95 % confidence intervals around response curves. Note that ranges on *x*- and *y*-axes differ among panels. The *y*-axis reflects the effect of each covariate on richness. The relative density of data is shown by the 'rug' along the *x*-axis

a higher range of DO levels both within the OMZ and/or extending beyond the OMZ to shallower or deeper depths. As noted previously, there is an apparent threshold effect being observed at lower oxygen levels. Although our earlier modeling efforts indicated little impact of low DO on Dover sole, a species that inhabits the OMZ after undergoing ontogenetic migration as it ages, the present study surprisingly revealed that within low DO waters (DO < 1.5 ml l$^{-1}$) there is a significant and positive relation-

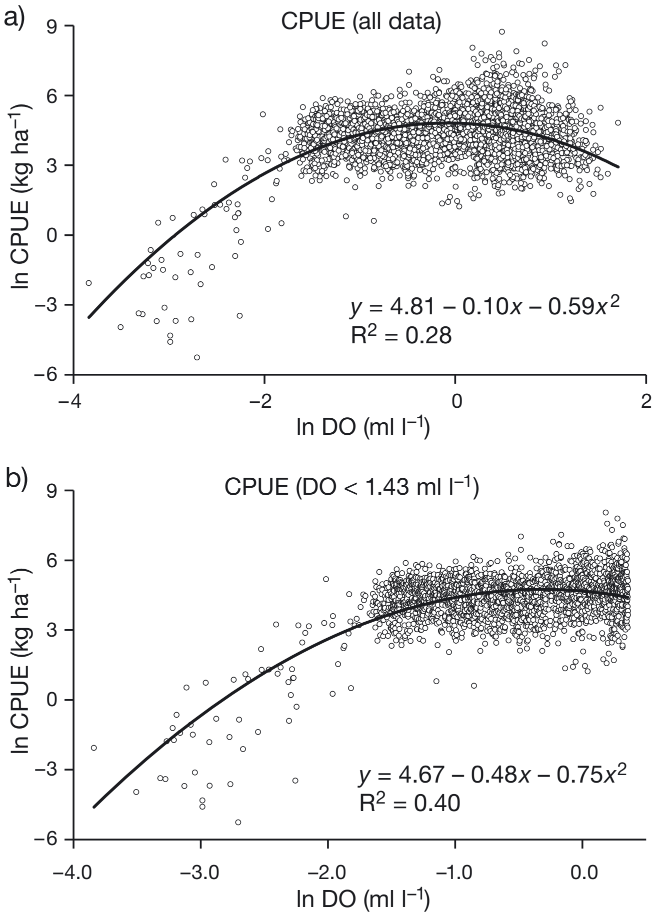

Fig. 8. Total catch per unit effort (demersal fishes; ln CPUE as a function of near-bottom dissolved oxygen (DO) concentration (ln DO) from 2008 to 2014 for (a) all stations and (b) hypoxic stations with near-bottom oxygen concentrations <1.43 ml l$^{-1}$. Highly significant ($p < 0.0001$) quadratic regressions are shown for both datasets

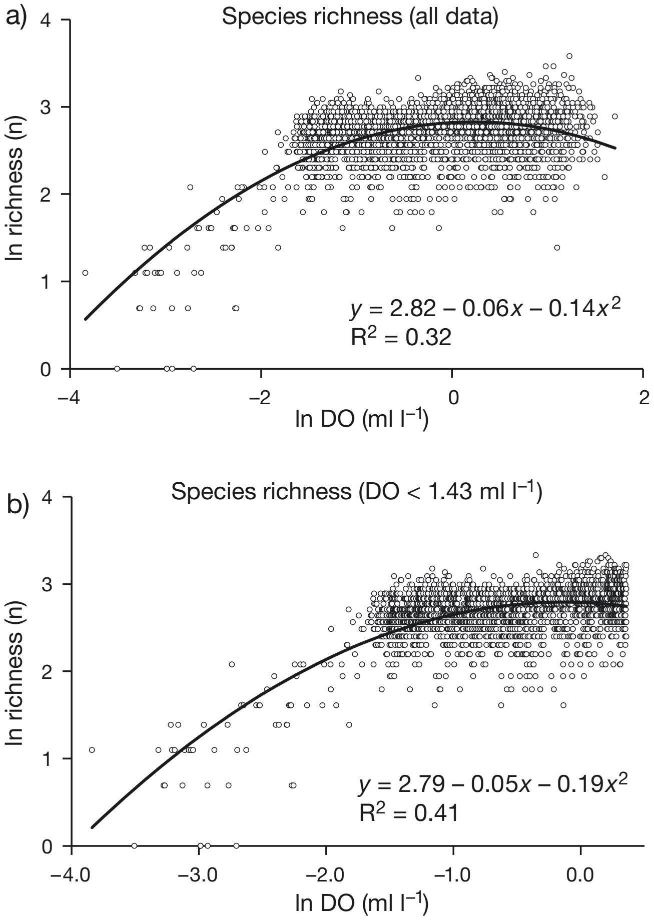

Fig. 9. Total species richness (demersal fishes; ln n) as a function of near-bottom dissolved oxygen (DO) concentration (ln DO, ml l$^{-1}$) from 2008 to 2014 for (a) all stations and (b) hypoxic stations with near-bottom oxygen concentrations <1.43 ml l$^{-1}$. Highly significant ($p < 0.0001$) quadratic regressions are shown for both datasets

ship between expected CPUE for Dover sole and near-bottom DO. Five additional species included here had catch-weighted depths indicating common occurrence within the OMZ (deepsea sole, sablefish, aurora rockfish, longspine thornyhead and shortspine thornyheads) (Table 2). Catch for these deepwater species increased over a relatively narrow band of DO values, particularly when compared to species at shallower depths (Fig. 4a). With the exception of aurora rockfish, catch for these other deepwater species either declined after reaching an upper limit and/or the relationship with DO was no longer significant (Fig. 3). Our study revealed that species-specific responses for fish with positive relationships between catch and DO tended to exhibit a wider range over which catch increased as depth decreased. In addition, the range of DO values over which catch increased was significantly and inversely related to depth (Fig. 4b). As noted in our prior study, deep water species have several physiological mechanisms which allow them to cope with hypoxia (Yang et al. 1992, Childress & Seibel 1998, Friedman et al. 2012) that ultimately lead to the patterns observed here. Fish found within persistently hypoxic slope waters generally display adaptations such as low productivity, high-affinity hemoglobin, low aerobic capacity, high water content, increased gill surface area, loss of a swim bladder and enzymatic adaptations to OMZ conditions (Vetter et al. 1994, Jacobson & Vetter 1996, Vetter & Lynn 1997, Friedman et al. 2012, Gallo & Levin 2016).

Although the species-specific response to low near-bottom DO was variable, the within subgroup response showed some similarities. Not unexpectedly, latitude and longitude played a primary role in the distribution of all subgroups examined here, as evidenced by retention in models for all species and subgroups. Other covariates most often retained for flatfishes, roundfishes and thornyheads in decreasing order included depth, near-bottom DO and temperature. DOY appeared more important for flatfish and roundfishes, suggesting a seasonal component to their distribution relative to rockfish and thornyheads. Depth was retained in all models for slope but not shelf rockfishes, while DOY was rarely retained for slope rockfishes. Overall, salinity appeared more important for rockfishes versus other subgroups.

We saw patterns relating the percentage of species with positive, negative or insignificant relations between DO and CPUE by life history, depth and latitudinal subgroups (Fig. 5). The percent of positive relationships was greatest for the thornyhead subgroup (n = 2). Both longspine and shortspine thornyheads displayed increased catch with increasing DO within a restricted band of DO values. Despite this positive relationship, thornyheads are adapted to low DO waters and commonly occur with the OMZ. Friedman et al. (2012) found low aerobic activities and small gills in thornyheads, suggesting a low oxygen demand commensurate with a more sedentary behavior compared to other fishes. Within the CCLME, expansion of hypoxic bottom waters is not likely to compress the distribution of either longspine or shortspine thornyheads.

A relatively high percentage of roundfishes, flatfishes and shelf rockfishes studied here displayed positive relationships with DO. Although found across a variety of depths and latitudes, these subgroups generally lack specific adaptations to low DO and are more likely to shift distributions, suffer physiological stress or move to less preferred habitats if near-bottom oxygen declines within the CCLME. In particular, highly mobile fishes, such as the roundfish subgroup, are most likely able to detect decreasing DO and move to more oxygenated waters as suggested by prior studies in estuarine waters and off Japan (Breitburg 2002, Gray et al. 2002, Ono et al. 2010). Previously reported impacts of hypoxia on flatfishes include changes in catchability (Sadorus et al. 2014) and negative effects on growth (Youcef et al. 2015). Several flatfish species studied here are commercially important, and in general, our results indicate that many of these species may be vulnerable to decreased oxygen levels.

Impacts of hypoxia on rockfish are less well studied. A moderate decrease in home range occurred for copper rockfish as DO levels declined off Oregon (Rankin et al. 2013), but a definitive movement away from hypoxic bottom waters was reported for copper rockfish in Hood Canal, Washington (Palsson et al. 2008). As noted by Rankin et al. (2013), the level of impact observed may be modified by site fidelity and temperature as well as DO concentration. McClatchie et al. (2010) suggested that cowcod, an important management species, and other depleted rockfishes that do not display hypoxia adaptations may suffer physiological stress or be forced out of preferred habitats if reductions in bottom DO continue within the Southern California Bight. They further noted that oxygen demands of brooding females within the highly diverse rockfishes *Sebastes* spp. are a likely added risk if expansion of hypoxic conditions occurs. Our results reiterate their findings and further suggest that shelf rockfishes are less well adapted to low DO than the deeper slope rockfish species, the majority of which displayed non-significant relations between catch and DO (Fig. 5). As previously noted, negative relationships are difficult to interpret and suggest that other factors may be important in controlling fish distribution for these species, or alternatively, that complete avoidance of low oxygen waters may obscure relationships with catch.

Based on subdivision by depth (Fig. 5), we were somewhat surprised by the high percentage of lower slope and deep-water species exhibiting positive relationships between catch and DO, and attribute these results to the complex form of the interactions uncovered by GAMs. In most cases, these species exhibited positive relationships over a restricted band of DO values (termed restricted range) as confirmed by the significant relationship with catch-weighted depth (Fig. 4b). On the other hand, the decreasing percentage of species that exhibited positive relationships between DO and catch from the upper shelf through the upper slope agreed with our hypothesis that these shallower water species are less well adapted to hypoxia.

The results of the present study also confirmed our earlier findings that variability in the relationship between overall catch of demersal fishes progressively decreases as levels of near-bottom DO decline from moderately (DO ~1.43 ml $l^{-1}$) to severely (DO < 0.5 ml $l^{-1}$) hypoxic. Similar results were noted for species richness, with increased variance explained as near-bottom DO decreased in concentration. The influence of co-variates on these relations was further reveled via the GAM analyses. Within other geographic areas such as the Gulf of Mexico, movement of demersal fish away from areas with low DO occurred when concentrations dropped below 2 mg $l^{-1}$ (1.43 ml $l^{-1}$) (Craig et al. 2001). Copper rockfish similarly moved to shallower water when DO levels dropped below 1.43 ml $l^{-1}$ in Hood Canal (Palsson et al. 2008). Given the highly variable response observed here to DO levels at or near hypoxia, the overall distribution of demersal fishes along the US west coast appears less likely than fish from areas, such as the Gulf of Mexico, to be affected by moderately hypoxic waters.

Despite notable difference in characteristics of OMZs world-wide (i.e. temperature, DO concentration, extent, depth, thickness etc.), our results are comparable to the decreased demersal fish catch and/or diversity noted in OMZs off Peru (Rosenberg et al. 1983), the Indian Ocean (Banse 1968), the Arabian Sea (Hunter et al. 2011), the Chilean OMZ (Quiroga et al. 2009) and the Baltic Sea (Berner & Schemainda 1957). Other studies indicate variability in the influence of DO on fish density with many areas understudied (see Gallo & Levin 2016 for review).

Recent years have witnessed fluctuating environmental conditions within the CCLME, including changes in temperature, carbonate chemistry, DO concentration and the occurrence of the 'warm blob' (Bond et al. 2015, Somero et al. 2016). Within the CCLME the already occurring impacts of hypoxia and ocean acidification are projected to grow rapidly in intensity and extent (Chan et al. 2016). Recent research suggests a link between warming surface temperature and the expansion of OMZs and further indicates that the response time between warming and expansion is rapid (Praetorius et al. 2015). The observation of unusually strong positive temperature anomalies in the surface waters of the NE Pacific in 2014 and 2015 coincided with a range of biological events with an as yet unknown ecosystem response within the CCLME (Bond et al. 2015). Reduced wind speed, wind stress and wind-generated mixing all coincided with the presence of the warm blob (Bond et al. 2015). Reduced winds and less coastal upwelling translate to decreased coastal hypoxia in the short term (Pierce et al. 2012), but given the link between surface warming and expansion of the OMZ, a temporary decrease in hypoxia may be accompanied by a greater offshore area with low DO in the not too distant future.

It is important for West Coast managers to consider management plans and actions in the context of multi-stressor effects. Research suggests that synergistic impacts from climate-related changes in temperature, ocean acidification and reduced DO availability could lead to habitat changes for demersal fish species (Seibel 2011). Our study further suggests that future habitat expansion may occur for species such as Dover sole and thornyheads, which prefer the upper DO limits within the OMZ, as the OMZ expands and grows. Flatfishes, roundfishes and shelf rockfishes will most likely exhibit opposite effects with movement away from areas with severe hypoxia to less preferred habitat. Both habitat compression and expansion will result in altered ecological interactions as the environment continues to change. At the species level, variations in mortality rate, growth rate, recruitment, and either habitat avoidance or expansion could lead to changes that alter the underlying structure of an ecosystem and influence commercial catch (Koslow et al. 2011, Seibel 2011, Gallo & Levin 2016).

Managers will need to consider multiple impacts when evaluating effects of expanding OMZs within the CCLME, particularly since encroachment of hypoxia and associated acidification onto the continental shelf occurs where organisms are currently less well adapted to such conditions. The expanded species pool examined here allowed us to make inferences on the effect of DO on species with contrasting life history strategies (e.g. shelf versus slope), and therefore come to a greater understanding of species selection gradients in a changing environment.

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## LITERATURE CITED

Allen LG, Pondella DJ, Horn MH (2006) Ecology of marine fishes California and adjacent waters. University of California Press, Berkeley, CA

Allen MJ, Smith GB (1988) Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. NOAA Technical Report NMFS 66. US Department of Commerce, Washington, DC

Bailey MC, Maravelias CD, Simmonds EJ (1998) Changes in the spatial distribution of autumn spawning herring (*Clupea harengus* L.) derived from annual acoustic surveys during the period 1984–1996. ICES J Mar Sci 55: 545–555

Bakun A, Black A, Bograd SJ, García-Reyes M, Miller AJ, Rykaczewski RR, Sydeman WJ (2015) Anticipated effects of climate change on coastal upwelling ecosystems. Curr Clim Change Rep 1:85–93

Banse K (1968) Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fishes. Deep Sea Res Oceanogr Abstr 15:45–48

Bartolino V, Colloca F, Sartor P, Ardizzone G (2008) Modelling recruitment dynamics of hake, *Merluccius merluccius*, in the central Mediterranean in relation to key environmental variables. Fish Res 92:277–288

Bartolino V, Ciannelli L, Bacheler NM, Chan KS (2011) Ontogeny and sex disentangle density-dependent and density-independent spatiotemporal dynamics of a marine fish population. Ecology 92:189–200

Bellido JM, Pierce GJ, Wang J (2001) Modeling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalized additive models. Fish Res 52: 23–39

Berner M, Schemainda R (1957) Über den Einfluss der hydrographischen Situation—insbesondere des Durchlüftungszustandes—auf die vertikale Verteilung und den Fang der Laichdorschschwärme im Bornholmbecken. Z Fisch N F 6:331–342

Bograd SJ, Pozo Buil M, Di Lorenzo E, Castro CG and others (2015) Changes in source waters to the Southern California Bight. Deep-Sea Res II 112:42–52

Bograd SJ, Castro CG, Di Lorenzo E, Palacios DM, Bailey H, Gilly W, Chavez FP (2008) Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys Res Lett 35:L12607

Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys Res Lett 42:3414–3420

Booth JAT, Woodson CB, Sutula M, Micheli F and others (2014) Patterns and potential drivers of declining oxygen content along the southern California coast. Limnol Oceanogr 59:1127–1138

Bradburn M, Keller AA, Horness BH (2011) The 2003 to 2008 US West Coast bottom trawl surveys of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, length and age composition. NOAA Tech Memo NMFS-NWFSC-114. US Department of Commerce, Seattle, WA

Breitburg D (2002) Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25:767–781

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY

Cardinale M, Arrhenius F (2000) The influence of stock structure and environmental conditions on the recruitment process of Baltic cod estimated using a generalized additive model. Can J Fish Aquat Sci 57:2402–2409

Chan F, Barth JA, Lubchenco J, Kirincich A, Weeks H, Peterson WT, Menge BA (2008) Emergence of anoxia in the California Current large marine ecosystem. Science 319: 920

Chan F, Boehm AB, Barth JA, Chornesky EA and others (2016) The West Coast ocean acidification and hypoxia science panel: major findings, recommendations, and actions. California Ocean Science Trust, Oakland, CA

Childress JJ, Seibel BA (1998) Life at low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. J Exp Biol 201:1223–1232

Ciannelli L, Dingsør GE, Bogstad B, Ottersen G and others (2007) Spatial anatomy of species survival: effects of predation and climate-driven environmental variability. Ecology 88:635–646

Ciannelli L, Bartolino V, Chan KS (2012) Nonadditive and nonstationary properties in the spatial distribution of a large marine fish population. Proc Biol Sci 279: 3635–3642

Connolly TP, Hickey BM, Geier SL, Cochlan WP (2010) Processes influencing seasonal hypoxia in the northern California Current System. J Geophys Res 115:C03021

Craig JK, Crowder LB, Gray CD, McDaniel CJ, Henwood TA, Hanifen JG (2001) Ecological effects of hypoxia on fish, sea turtles and marine mammals in the northwestern Gulf of Mexico. In: Rabalais NN, Turner RE (eds) Coastal hypoxia: consequences for living resources and ecosystems. American Geophysical Union, Washington, DC, p 269–291

Daskalov G (1999) Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. Fish Res (Amst) 41:1–23

Denis V, Lejeune J, Robin JP (2002) Spatio-temporal analysis of commercial trawler data using general additive models: patterns of loliginid squid abundance in the north-east Atlantic. ICES J Mar Sci 59:633–648

Diaz RJ, Rosenberg R (2008) Spreading dead zone and consequences for marine ecosystems. Science 321:926–929

Drexler M, Ainsworth C (2013) Generalized additive models used to predict species abundance in the Gulf of Mexico: an ecosystem modelling tool. PLOS ONE 8:e64458

Friedman JR, Condon NE, Drazen JC (2012) Gill surface area and metabolic enzyme activities of demersal fishes associated with the oxygen minimum zone off California. Limnol Oceanogr 57:1701–1710

Gallo ND, Levin LA (2016) Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. Adv Mar Biol 74:117–198

Gao K, Xu J, Gao G, Li Y and others (2012) Rising $CO_2$ and increased light exposure synergistically reduce marine primary productivity. Nat Clim Chang 2:519–523

Gilly WF, Beman JM, Litvin SY, Robison BH (2013) Oceanographic and biological effects of shoaling of the oxygen minimum zone. Annu Rev Mar Sci 5:393–420

Grantham BA, Chan F, Nielsen KJ, Fox DS and others (2004) Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in northeast Pacific. Nature 429:749–754

Gray JS, Wu RS, Or YY (2002) Effects of hypoxia and organic enrichment on the coastal marine environment. Mar Ecol Prog Ser 238:249–279

Green PJ, Silverman BW (1994) Nonparametric regression and generalized linear models: a roughness penalty approach. Chapman & Hall, London

Gunderson DF (1993) Surveys of fisheries resources. John Wiley & Sons, New York, NY

Hastie T, Tibshirani R (1990) Generalized additive models. Chapman & Hall, London

Hunter WR, Oguri K, Kitazato H, Ansari ZA, Witte U (2011) Epi-benthic megafaunal zonation across an oxygen minimum zone at the Indian continental margin. Deep-Sea Res I 58:699–710

Jacobson LD, Vetter RD (1996) Bathymetric demography and niche separation of thornyhead rockfish: *Sebastolobus alascanus* and *Sebastolobus altivelis.* Can J Fish Aquat Sci 53:600–609

Juan Jordá MJ, Barth JA, Clarke ME, Wakefield WW (2009) Groundfish species associations with distinct oceanographic habitats off the Pacific Northwest Coast. Fish Oceanogr 18:1–19

Kamykowski D, Zentara SJ (1990) Hypoxia in the world ocean as recorded in the historical data set. Deep-Sea Res 37:1861–1874

Keeling RF, Körtzinger A, Gruber N (2010) Ocean deoxygenation in a warming world. Annu Rev Mar Sci 2: 199–229

Keller AA, Horness BH, Fruh EL, Simon VH and others (2008) The 2005 US West Coast bottom trawl survey of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, and length composition. NOAA Tech Memo NMFS-NWFSC-93. US Department of Commerce, Washington, DC

Keller AA, Simon VH, Chan F, Wakefield WW and others (2010) Demersal fish and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. Fish Oceanogr 19:76–87

Keller AA, Ciannelli L, Wakefield WW, Simon V, Barth J, Pierce SD (2015) Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. Fish Oceanogr 24: 162–176

Koslow JA, Goericke R, Lara-Lopez A, Watson W (2011) Impact of declining intermediate-water oxygen on deep-water fishes in the California Current. Mar Ecol Prog Ser 436:207–218

Levin LA (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr Mar Biol Annu Rev 41:1–45

Maravelias CD, Reid DG, Swartzman G (2000) Modelling spatio-temporal effects of environment on Atlantic herring using GAMs. Environ Biol Fishes 58:157–172

McClatchie S, Goericke R, Cosgrove R, Auad G, Vetter R (2010) Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fishes. Geophys Res Lett 37:L19602

Murase H, Nagashima H, Yonezaki S, Matsukura R, Kitakado T (2009) Application of a generalized additive model (GAM) to reveal relationships between environmental factors and distributions of pelagic fish and krill: a case study in Sendai Bay, Japan. ICES J Mar Sci 66: 1417–1424

Ono T, Ito M, Hattori T, Narimatsu Y, Kitagawa D (2010) Oxygen decline in the continental slope waters off Japan and its potential influence on groundfishes. In: PICES-2010 Annual Meeting, 22–31 October, Portland, OR. www.pices.int/publications/presentations/PICES-2010/2010-S1/S1-day2/S1-1425-Ono.pdf

Palsson WA, Pacunski RE, Parra TR, Beam J (2008) The effects of hypoxia on marine fish populations in southern Hood Canal, Washington. Am Fish Soc Symp 64:255–280

Peterson JO, Morgan CA, Peterson WT, Di Lorenzo E (2013) Seasonal and interannual variation in the extent of hypoxia in the northern California Current from 1998–2012. Limnol Oceanogr 58:2279–2292

Pierce SD, Barth JA, Shearman RK, Erofeev AY (2012) Declining oxygen in the Northeast Pacific. J Phys Oceanogr 42:495–501

Praetorius SK, Mix AC, Walczak MH, Wolhowe MD, Addison JA, Prahl FG (2015) North Pacific deglacial hypoxic events linked to abrupt ocean warming. Nature 527: 362–366

Quiroga E, Sellanes J, Arntz WE, Gerdes D, Gallardo VA, Hebbeln D (2009) Benthic megafaunal and demersal fish assemblages on the Chilean continental margin: the influence of the oxygen minimum zone on bathymetric distribution. Deep-Sea Res II 56:1112–1123

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rankin PS, Hannah RW, Blume MT (2013) Effect of hypoxia on rockfish movements: implications for understanding the roles of temperature, toxins and site fidelity. Mar Ecol Prog Ser 492:223–234

Rosenberg R, Arntz WE, Chuman de Flores E, Flores LA, Carbjal G, Finger I, Tarazona J (1983) Benthos biomass and oxygen deficiency in the upwelling system off Peru. J Mar Sci 41:263–279

Sadorus L, Mantua N, Essington T, Hickey B, Hare S (2014) 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. Fish Oceanogr 23:225–241

Sagarese SR, Frisk MG, Cerrato RM, Sosebee KA, Musick JA, Rago PJ (2014) Application of generalized additive models to examine ontogenetic and seasonal distributions of spiny dogfish (*Squalus acanthias*) in the Northeast (US) shelf large marine ecosystem. Can J Fish Aquat Sci 71:847–877

Sakamoto Y, Ishiguro M, Kitagawa G (1986) Akaike information criterion statistics. D. Reidel Publishing, Dordrecht

SAS Institute (1999) SAS/STAT user's guide, version 8. SAS Institute, Cary, NC

Seibel BA (2011) Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. J Exp Biol 214:326–336

Shelton AO, Thorson JT, Ward EJ, Feist BE (2014) Spatial semiparametric models improve estimates of species abundance and distribution. Can J Fish Aquat Sci 71: 1655–1666

Somero GN, Beers JM, Chan F, Hill TM, Klinger T, Litvin SY (2016) What changes in the carbonate system, oxygen and temperature portend for the Northeastern Pacific Ocean: a physiological perspective. Bioscience 66:14–26

Stauffer G (2004) NOAA protocols for groundfish bottom trawl surveys of the nation's fishery resources. NOAA Tech Memo NMFS-F/SPO-65. US Department of Commerce, Washington, DC

Stramma L, Johnson GC, Sprintall J, Mohrholz V (2008) Expanding oxygen-minimum zones in the tropical oceans. Science 320:655–658

Stramma L, Schmidtko S, Levin LA, Johnson GC (2010) Ocean oxygen minima expansions and their biological impacts. Deep-Sea Res 57:587–595

Stramma L, Prince ED, Schmidtko S, Luo J and others (2012) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat Clim Chang 2:33–37

Swartzman G, Stuetzle W, Kulman K, Powojowski M (1994) Relating distribution of pollock schools in the Bering Sea to environmental factors. ICES J Mar Sci 51:481–492

Swartzman G, Silverman E, Williamson N (1995) Relating trends in walleye pollock (*Theragra chalcogramma*) abundance in the Bering Sea to environmental factors. Can J Fish Aquat Sci 52:369–380

Thorson JT (2015) Spatio-temporal variation in fish condition is not consistently explained by density, temperature, or season for California Current groundfishes. Mar Ecol Prog Ser 526:101–112

Thorson JT, Stewart I, Punt A (2011) Accounting for fish shoals in single- and multi-species survey data using mixture distribution models. Can J Fish Aquat Sci 68: 1681–1693

Thorson JT, Skaug HJ, Kristensen K, Shelton AO, Ward EJ, Harms JH, Benante JA (2015a) The importance of spatial models for estimating the strength of density dependence. Ecology 96:1202–1212

Thorson JT, Scheuerell MD, Shelton AO, See KE, Skaug HJ, Kristensen K (2015b) Spatial factor analysis: a new tool for estimating joint species distributions and correlations in species range. Methods Ecol Evol 6:627–637

Tolimieri N, Levin PS (2006) Assemblage structure of eastern Pacific groundfishes on the US continental slope in relation to physical and environmental variables. Trans Am Fish Soc 135:317–332

Vestfals C (2009) Identifying habitat factors for canary rockfish (*Sebastes pinniger*) off Washington and Oregon using environmental data and trawl logbooks. MSc thesis, Oregon State University, Corvallis, OR

Vetter RD, Lynn EA (1997) Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes* and *Sebastolobus*): paradigms revisited. Mar Ecol Prog Ser 155:173–188

Vetter RD, Lynn EA, Garza M, Costa AS (1994) Depth zonation and metabolic adaptation in dover sole, *Microstomus pacificus*, and other deep living flatfishes: factors that affect the sole. Mar Biol 120: 145–159

Wahba G (1990) Spline models for observational data. CBMS-NSF Regional Conference Series in Applied Mathematics. Society for Industrial and Applied Mathematics, Philadelphia, PA

Weinberg K (1994) Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington. Fish Bull 92:620–632

Welsh AH, Cunningham RB, Donnelly CF, Lindenmayer DB (1996) Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecol Modell 88: 297–308

Whitney FA, Freeland HJ, Robert M (2007) Decreasing oxygen levels in the interior waters of the subarctic Pacific. Prog Oceanogr 75:179–199

Williams EH, Ralston S (2002) Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. Fish Bull 100:833–855

Winter A, Coyle KO, Swartzman G (2007) Variations in age-0 pollock distribution among eastern Bering Sea nursery areas: a comparative study through acoustic indices. Deep-Sea Res II 54:2869–2884

Wood SN (2006) Generalized additive models — an introduction with R. Chapman & Hall, London

Yang TH, Lai NC, Graham B, Somero GN (1992) Respiratory, blood, and heart enzymatic adaptations of *Sebastolobus alascanus* (Scorpaenidae; Teleostei) to the oxygen minimum zone: a comparative study. Biol Bull 183:490–499

Youcef WA, Lambert Y, Audet C (2015) Variations in length and growth of Greenland halibut juveniles in relation to environmental conditions. Fish Res 167:38–47

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