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Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem

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ABSTRACT

Various ocean-climate models driven by increased greenhouse gases and higher temperatures predict a decline in oceanic dissolved oxygen (DO) as a result of greater stratification, reduced ventilation below the thermocline, and decreased solubility at higher temperatures. Since spreading of low oxygen waters is underway and predicted to increase, understanding impacts on higher trophic levels is essential. Within the California Current System, shoaling of the oxygen minimum zone (OMZ) is expected to produce complex changes. Onshore movement of the OMZ could lead to habitat compression for species with higher oxygen requirements while allowing expansion of species tolerant of low bottom DO. As part of annual groundfish surveys, we sampled catch across a range of conditions from the upper to the lower limit of the OMZ and shoreward across the continental shelf of the US west coast. DO ranged from 0.02 to 4.25 mL L⁻¹ with 642 stations (of 1020 sampled) experiencing hypoxic conditions in 2008–2010. Catch and species richness exhibited significant and positive relationships with near-bottom oxygen concentration. The probability of occurrence was estimated for four species (spotted ratfish, petrale sole, greenstriped rockfish and Dover sole)

using a binomial Generalized Additive Model. The models for each species included terms for position, day of the year, salinity, near-bottom temperature and the interaction term between depth and near-bottom DO. Spotted ratfish and petrale sole were sensitive to changes in near-bottom oxygen, while greenstriped rockfish and Dover sole show no changes in probability of occurrence in relation to changes in oxygen concentration.

Key words: bottom dissolved oxygen, demersal fish catch, Dover sole, greenstriped rockfish, Northeast Pacific, petrale sole, probability of occurrence, species richness, spotted ratfish

INTRODUCTION

The California Current large marine ecosystem (CCLME) along the US west coast is a major eastern boundary current upwelling system, and as such is highly productive, but also highly heterogeneous over space and time. The CCLME is part of what may be the world's largest Oxygen Minimum Zone (OMZ), i.e., the eastern North Pacific. The OMZ is defined by dissolved oxygen (DO) concentrations < 0.5 mL L⁻¹ (<22 μM). This naturally occurring OMZ, centered along the upper continental slope in the Eastern North Pacific, results in an extensive hypoxic benthic boundary layer (Levin, 2003). DO concentrations within the OMZ decline from 0.5 to 0.25 mL L⁻¹ (~12 μM) as depth increases from ~500 to ~720 m and then increases above 0.5 mL L⁻¹ at greater depths (~900 m) (Levin, 2003). Numerous factors control oxygen concentrations of near bottom water, including when a water mass was last in contact with the atmosphere, oxygen concentration at that point of contact, the rate of oxygen consumption as well as various biological and oceanographic features (e.g., circulation, temperature and productivity) (Seibel, 2011). Recent findings suggest expansions of OMZs are occurring on a global basis, with both shoaling and deepening apparent (Stramma *et al.*, 2008, 2010). Within the CCLME, shoaling of the OMZ has shifted its upper

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boundary, causing naturally occurring low DO water to move shoreward onto the continental shelf and into coastal areas (Bograd *et al.*, 2008; Chan *et al.*, 2008; Pierce *et al.*, 2012). Connolly *et al.* (2010) further suggest that severe shelf hypoxia, in part, is caused by seasonal upwelling of the deep, low DO water combined with depletion of DO owing to biochemical processes, resulting in a distinction between the deep OMZ and the shallower low-oxygen shelf waters.

Bograd *et al.* (2008) recently noted large decreases in DO concentration throughout the southern portion of the CCLME (southern California Bight region) whereas Chan *et al.* (2008) described similar declines in bottom DO within the northern CCLME (off central Oregon). In the shelf waters off Oregon, severe hypoxic ($\text{DO} < 0.5 \text{ mL L}^{-1}$) events caused high mortality in demersal and benthic fauna including commercially harvested species (Chan *et al.*, 2008). Consequences from encroachment of hypoxia onto the continental shelf are expected as organisms at these depths, unlike those in the OMZ, are not adapted to low DO. Transient hypoxic events within the shelf zone are coupled to onshore movement of the OMZ but vary in intensity and extent, whereas DO levels within the OMZ are persistently low across geological time scales. On a global scale, the intensification of OMZs is most likely tied to climate change resulting in greater water-column stratification, reduced ventilation of waters below the thermocline and decreased oxygen solubility at higher temperatures (Stramma *et al.*, 2008, 2010). Within the northern CCLME the shoaling of the OMZ results from a still to-be-determined combination of climate-influenced changes in upwelling and other 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). Within the southern CCLME the underlying causes of the decline in oxygen appear linked to basin-scale or perhaps global climate processes (Koslow *et al.*, 2011) including decreased DO in source waters of the north Pacific Ocean (Whitney *et al.*, 2007; Stramma *et al.*, 2008). Changes in primary production could be an additional factor influencing long-term DO changes in the CCLME (Chan *et al.*, 2008).

Despite the general recognition of hypoxia ($\text{DO} < 1.43 \text{ mL L}^{-1}$) as a potential threat to worldwide fish production, little is known about its effects on upper trophic levels (Diaz *et al.*, 2004). However, direct effects of severe hypoxia ($\text{DO} < 0.5 \text{ mL L}^{-1}$) are expected on demersal fish and benthic invertebrate species, depending on their oxidic requirements, where

the OMZ contacts the continental margin (Koslow *et al.*, 2011; Seibel, 2011). Such effects range from increased mortality to physiological impairment, avoidance, habitat compression, alterations in predator–prey relationships and changes in foraging dynamics (Chan *et al.*, 2008; Keller *et al.*, 2010; Koslow *et al.*, 2011; Seibel, 2011). Because of the apparent expansion and shoaling of the OMZ, we initiated studies in 2007, as part of the Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey (WCGBTS), examining the relationship between demersal biomass and low near-bottom (within 3 m of ocean floor) oxygen concentration (Keller *et al.*, 2010). The survey provides information on a large number of commercially important west coast groundfish species, many of which could potentially be impacted by decreasing near-bottom oxygen levels. Much of the variability associated with survey estimates of population biomass is due to unaccounted processes driven by oceanographic features. There are several studies that have characterized Pacific coast groundfishes in relation to geographic (i.e., depth and latitude) and oceanographic variables (Allen and Smith, 1988; Vetter *et al.*, 1994; Weinberg, 1994; Williams and Ralston, 2002; Tolimieri and Levin, 2006; Allen *et al.*, 2006; Juan Jordá *et al.*, 2009). For fish stock assessment and management purposes, our goal is to build upon these studies by describing the functional relationships that affect the distribution of specific groundfish species (e.g., Vestfals, 2009).

Over time, an expanding array of sensors has been added to the sampling system deployed with the WCGBTS bottom trawl to measure environmental properties known to affect the distribution of groundfish species in the CCLME (e.g., Keller *et al.*, 2010). Prior results suggested an extremely dynamic situation where bottom oxygen concentration explained up to 84% of the variation in biomass for individual species and 31–69% of the depth-specific variation in biomass along a hypoxic gradient off Oregon (Keller *et al.*, 2010). Catch per unit effort (CPUE, kg hectare^{-1}) for eight fish species and five benthic invertebrate species was significantly and positively related to bottom oxygen concentration within the hypoxic region off Oregon in 2007 (Keller *et al.*, 2010). Species richness was also significantly and positively related to oxygen concentration along the hypoxic gradient (Keller *et al.*, 2010). The primary objective of this current study was to examine the relationships between both CPUE and species richness for demersal fishes and benthic invertebrates and near-bottom oxygen concentration coast-wide from 2008–2010. A secondary objective is to define

species–environmental relationships for a selected group of abundant and ecologically contrasting groundfishes that are well sampled by the survey. We focused our analysis on four species of groundfish: Dover sole (*Microstomus pacificus*), petrale sole (*Eopsetta jordani*), spotted ratfish (*Hydrolagus colliei*) and greenstriped rockfish (*Sebastes elongatus*) collected from 2008 to 2010. These species were chosen for their relatively high dominance in the survey catch records, for having contrasting life history strategies, yet each representing those of several other groundfish species, and for being associated with regions of the surveyed area that collectively span the entire CCLME (Allen and Smith, 1988; Tolimieri and Levin, 2006; Juan Jordá *et al.*, 2009). Dover sole is a deep water, benthic species that commonly occurs within the OMZ; petrale sole, spotted ratfish and greenstriped rockfish are typically present in higher oxygen conditions with depth distributions above the OMZ. We examined both the distribution and catch (presence-absence) of the four selected groundfish species and their relationship with environmental variables (depth, near-bottom dissolved oxygen concentration, salinity and temperature) during the 2008 through to 2010 WCG BTS. Similar studies within the CCLME, the Bering Sea and Gulf of Alaska successfully disentangled the effects of environmental and demographic variables on the distribution of canary rockfish (Vestfals, 2009), yellowfin sole (Bartolino *et al.*, 2011) and arrowtooth flounder (Ciannelli *et al.*, 2012).

METHODS

Survey design

Catch and a suite of environmental variables (temperature, dissolved oxygen, salinity, depth and location) were sampled during the Northwest Fisheries Science Center's (NWFSC) annual fishery-independent bottom trawl survey of groundfish resources off the US west coast (Bradburn *et al.*, 2011). The survey design consists of four chartered west coast fishing vessels (20–28 m length) undertaking a series of nominal 15 min tows based on stratified-random sampling locations. Stations fell within 1.5×2 nautical mile grids (Albers Equal Area projection) that span the US west coast from Canada to Mexico (32.5°N to 48.17°N latitude) (Fig. 1). An average of 700 primary cells was randomly selected each year, stratified by geography and depth. Sampling occurred at depths from 55–1280 m and extended from mid-May through to late-October. Vessels used a standard Aberdeen-style trawl with a 3.8-cm mesh (stretch measure) liner in the

codend, a 25.9-m headrope and a 31.7-m foot rope. All fishing operations complied with strict national protocols (Stauffer, 2004).

Biological and environmental sampling

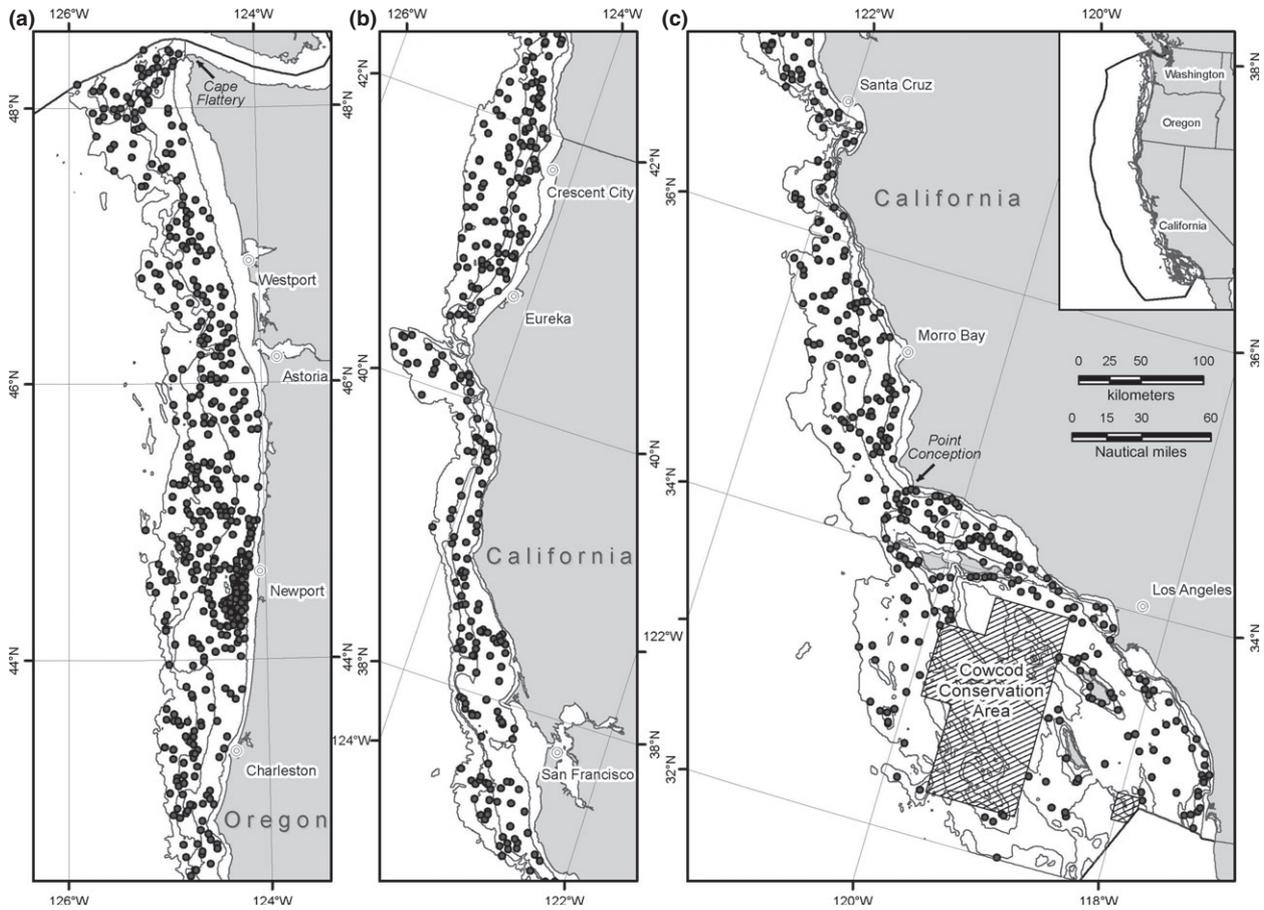
Simrad Integrated Trawl Instrumentation (Simrad Fisheries, Lynnwood, Washington) was used to monitor and record net performance, including mean spread between the trawl wings, mean vertical opening, distance fished and position for each haul. A pair of bottom contact sensors [BCSs, NMFS (Somerton and Weinberg, 2001)] indicated when the net landed on and lifted off the seafloor and were used to determine tow duration. A differential global positioning system (DGPS) navigation unit (Garmin 152; Garmin International Inc., Olathe, KS, USA) was used to monitor towing speed over ground during each haul. Standard survey haul positions were estimated from DGPS coordinates – generally the mid-point between the net touch-down and net lift-off positions. Average net speed over ground and distance fished were calculated from the position data for the trawl and actual bottom time (Wallace and West, 2006; Keller *et al.*, 2008).

Samples were collected by trawling within the randomly selected cells. All fishes and invertebrates were sorted to species (or the lowest possible taxon), and then weighed using an electronic, motion-compensated scale (Marel, Reykjavik, Iceland). Near-bottom temperature (°C), salinity, oxygen (mL L^{-1}) 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 Inc., Bellevue, WA, USA), equipped with a calibrated SBE 43 polarographic membrane type oxygen sensor. Sensors are factory calibrated before and after deployment on an annual basis. These units were attached to the net about 2.8 m behind the headrope where the top wing panel meets the body of the net. Mean depth (m), temperature (°C), salinity and DO concentrations (mL L^{-1}) per tow were averaged over the center 80% of the on-bottom tow duration. Only hauls judged acceptable (based on net performance standards; Stauffer, 2004) were included in the data analyses.

Statistical analysis

Contour plots of near bottom oxygen concentrations (mL L^{-1}) 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

Figure 1. Chart showing geographical extent of the Northwest Fisheries Science Center’s West Coast Groundfish Bottom Trawl Survey and location of 1020 stations sampled for demersal fishes and invertebrates and measurements of near-bottom dissolved oxygen concentrations from 2008 to 2010. The three panels (a, b and c) show different latitudinal ranges.



locations (generalized cross validation). The final rms differences between the data and the surface values are small: 0.018 and 0.003 mL L⁻¹ for 2009 and 2010, respectively. We calculated estimates of species richness as the total number of demersal fishes and benthic invertebrate species taken per trawl sample. CPUE, kg ha⁻¹ was calculated by dividing catch (kg) by area swept (ha) per tow. Area swept was computed from the mean net width for each tow multiplied by the distance fished. The relationships between species richness (n), total CPUE (per tow, kg ha⁻¹) and near-bottom dissolve oxygen concentration (mL L⁻¹) were examined using regression analysis in SAS for Windows (SAS Institute, Inc., Cary, NC, USA). To stabilize the variance, we used the natural logarithms of richness, CPUE, and DO in the analyzes.

To examine variation in latitude and depth distributions among the four species selected for individual analyzes, we calculated mean CPUE-weighted latitude and depth (m) for each species as:

$$X_j = \frac{\sum_{i=1}^n (CPUE_i \times X_{ij})}{\sum_{i=1}^n CPUE_i} \quad (1)$$

where X is the parameter of interest (latitude or depth), j represents an individual species and CPUE is catch per unit effort (kg ha⁻¹) for each station i.

We used a Generalized Additive Model (GAM: Wood, 2006) to correlate the spatial distribution of the four selected groundfish species with co-located environmental and geographic variables. Given the high incidence of zeros in the bottom trawl catches (from 18% of sampled stations for Dover sole to 76% for greenstriped rockfish), the data were analyzed using binomial GAM, fitted to presence-absence data, with a logit link function (Wood, 2006). The same model structure was applied to each species and included the following terms:

$$\text{Logit}(p) = a_y + s_1(\text{lon, lat}) + s_2(d) + s_3(D) + s_4(T) + s_5(S) + \text{te}(\text{DO}, Z) \quad (2)$$

where, for each species p , the inverse logit of the linear predictor, is used to model probability of a non-zero catch, a_y is a year-specific intercept term, lon and lat are longitude and latitude, d is the time of the day, D is the day of the year, T , S , and DO are the near-bottom temperature, salinity, and dissolved oxygen, respectively. Z is depth (m), s_1 and $s_{2,5}$ are two-dimensional and one-dimensional smooth functions, in this case thin plate regression splines (Wood, 2006). In our sampling region, Z and DO are correlated; therefore we modeled their interaction using a tensor product (te), that is a product of two anisotropic smooth functions (cubic regression splines).

RESULTS

Environmental variables

During the 2008 through to 2010 west coast groundfish bottom trawl surveys, we obtained near-bottom oxygen concentrations at 1020 stations out of 2073 sampled along the US west coast (Fig. 1). Samples were well distributed throughout the study region (Fig. 1). Although relatively few measurements were made in 2008 ($n = 39$), the mean, minimum and maximum near-bottom oxygen concentrations were comparable to values seen in later years (2009 and 2010) and we included them in the analysis (Table 1). Sampling expanded over time with near-bottom oxygen measured throughout the survey in 2009 using a single vessel during each section (pass) of the survey ($n = 360$). In 2010, data were collected using both vessels during each pass ($n = 621$). On average 62.9% of the stations sampled were hypoxic ($\text{DO} < 1.43 \text{ mL L}^{-1}$) with a range of 60.5 to 66.7% across years.

Sampling during the 2009 and 2010 groundfish surveys indicated low near-bottom DO in deep water within the OMZ throughout the survey area, as plotted using thin plate smoothing splines (Wahba, 1990) (Fig. 2). Low DO appeared to move shoreward as the

summer progressed and later in the season (August–October) occurred in shallower water off both Washington and Oregon (Fig. 2). The distribution of low oxygen concentrations varied by year, with hypoxic conditions well developed along the shelf offshore of Washington during 2009 relative to 2010 (Fig. 2). In 2009, 79% of the stations in this region exhibited hypoxia versus 41% in 2010. In the southern portion of the study area, low DO appeared more widespread in 2010 with 70% of the stations south of Cape Mendocino, CA (44.43°N) hypoxic in 2010 versus 59% in 2009.

We examined the relationship between near-bottom oxygen and depth and found that it was fairly well described by a quadratic equation (Fig. 3). 60% of the DO variance can be explained as a quadratic function of depth, and the fit is significant ($P < 0.0001$). While the quadratic fit does well showing the shape of the OMZ, at depths < 300 m note the increasing scatter, including some very low oxygen levels.

Catch per unit effort and species richness

For this study, total CPUE (kg ha^{-1}) per tow was calculated as the sum of the CPUE for 1–56 species of demersal fishes and benthic invertebrates per tow [average $26.6 \text{ species tow}^{-1} \pm 7.7$ standard deviation (SD)]. The relationship between total CPUE ($\ln, \text{kg ha}^{-1}$) and near-bottom dissolved oxygen concentration ($\ln, \text{mL L}^{-1}$) was best described by a 2nd order polynomial regression (Fig. 4a). The relationship was highly significant ($P < 0.0001$) and explained 35% of the variance in catch when all data were included in the analysis. If we restricted the data to stations defined as hypoxic ($\text{DO} < 1.43 \text{ mL L}^{-1}$), the amount of variance explained by the relationship increased to 43% (not shown). Further improvements ($r^2 = 0.50$) were noted if the relationship included only catch from stations with $\text{DO} \leq 1.0 \text{ mL L}^{-1}$ (Fig. 4b). Similar results were obtained if the analyses were repeated using CPUE restricted solely to demersal fishes (range: 1–30 species tow^{-1}) rather than total CPUE (which also includes benthic invertebrates) with 48% of the

Table 1. Total number (n) of tows sampled, number with near-bottom dissolved oxygen measurements (total and hypoxic with $\text{DO} \leq 1.43 \text{ mL L}^{-1}$), mean, standard deviation (SD), and range of near-bottom dissolved oxygen concentrations (DO mL L^{-1}) and depth range (m) for 2008–2010.

Year	Total tows (n)	Tows with DO (n)	Hypoxic tows (n)	DO mean ($\pm\text{SD}$) (mL L^{-1})	DO range (mL L^{-1})	Depth range (m)
2008	679	39	26	1.52 ± 1.06	0.04–4.22	59–1100
2009	682	360	240	1.19 ± 0.84	0.08–4.25	59–1204
2010	712	621	376	1.16 ± 0.77	0.02–3.97	57–1256

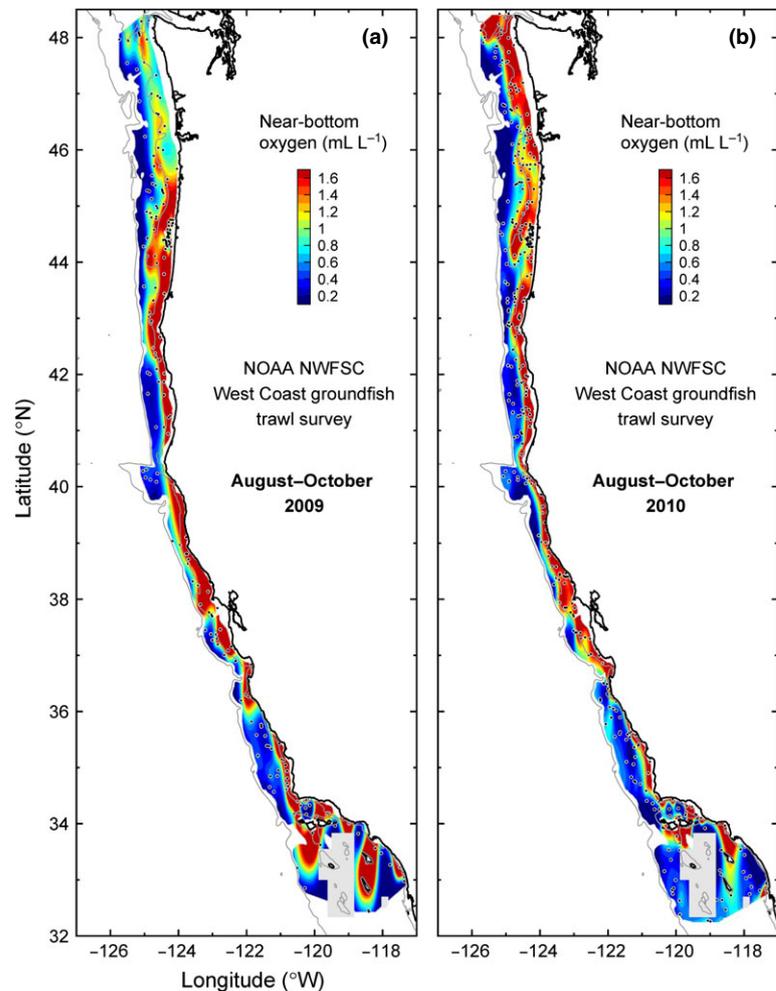


Figure 2. Contour plots of near-bottom oxygen concentrations (mL L^{-1}) along the US west coast at depths of 55–1280 m in (a) 2009; and (b) 2010 (August–October).

variance explained when tows were restricted to those with $\text{DO} \leq 1.0 \text{ mL L}^{-1}$ (results not shown).

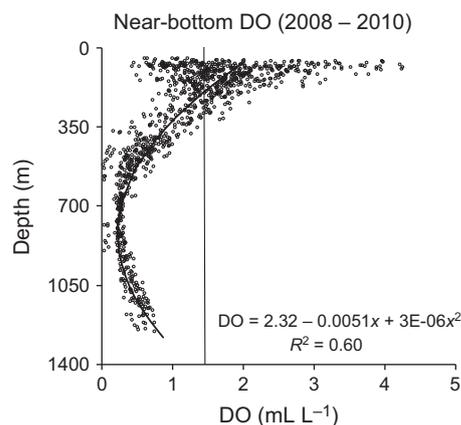
Total-species richness (demersal fishes and benthic invertebrates, $\ln n$) and near-bottom dissolved oxygen concentrations (\ln , mL L^{-1}) exhibited similar relationships to those seen for CPUE. Species richness was best described by a quadratic equation and was a positive function of DO. With all DO data included in the analysis, 15% of the variance in richness was explained as a function of near-bottom oxygen concentration (Fig. 5a). If we used only data from hypoxic stations, then the fit improved to explain 29% of the variance in richness (not shown). Further restricting the data to stations with oxygen concentrations below 1.0 mL L^{-1} increased the amount of variation explained to 36% (Fig. 5b). All relationships were highly significant ($P < 0.0001$).

Individual groundfish species

The mean CPUE (kg ha^{-1}) from 2008 to 2010 varied considerably among the four species selected for

individual analysis, with CPUE for Dover sole considerably higher than the remaining three species (Table 2). However, even though Dover sole is the species with the highest CPUE among the four included in the GAM analysis, it still accounts for only a small fraction of the total CPUE [average $161.5 \text{ kg ha}^{-1} \pm 4.9$ standard error (SE)] used in the regression analysis. Individual species were widely distributed throughout the study area with all four species occurring across a wide latitudinal range (Fig. 6a–d). With the exception of petrale sole (48.42°N), all species extended as far north as 48.45°N , although the southern extent of the latitudinal range was somewhat variable (Table 2). The mean catch-weight latitude was similar for Dover sole, petrale sole and spotted ratfish but the mean catch-weighted latitude for green-striped rockfish indicated a more northerly center of distribution for this species. Dover sole occupied the greatest depth range and had the deepest mean catch-weighted depth relative to the other species. Green-striped rockfish notably did not extend into waters

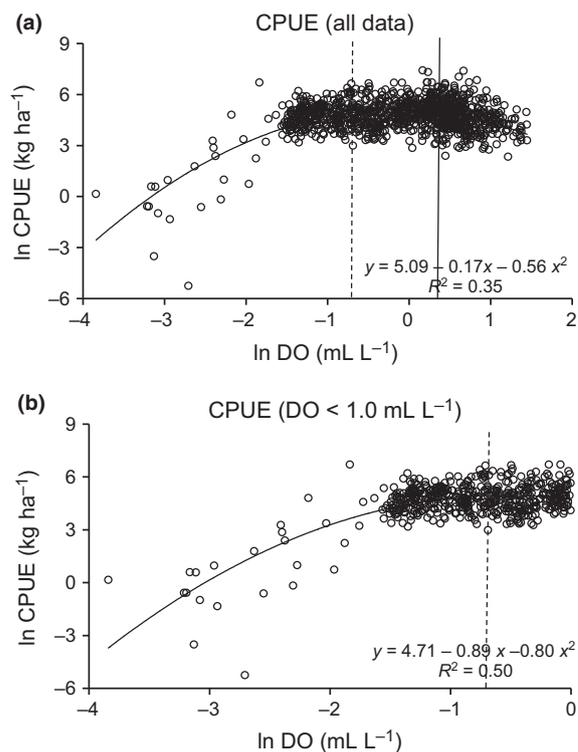
Figure 3. Scatter plot of near-bottom dissolved oxygen concentrations (mL L^{-1}) versus depth (m) for 2008–2010 showing the highly significant ($P < 0.0001$) quadratic relationship between the two variables. The line added to the figure marks the 1.43 mL L^{-1} concentration of near-bottom oxygen defined as hypoxic conditions.



shallower than 73 m while the remaining three species occurred at the shallowest depths sampled (Table 2). Dover sole and spotted ratfish were taken in the greatest number of hauls and greenstriped rockfish in the fewest.

The interaction between depth and DO significantly affected the spatial distribution of species examined (Table 3), although the effects were different among species. Spotted ratfish and to a lesser extent petrale sole (Fig. 7) are the most sensitive species to changes of near-bottom DO, whereas greenstriped rockfish showed no change in probability of occurrence in relation to changes in DO concentration. The probability of occurrence in spotted ratfish decreases sharply once DO goes below 1 mL L^{-1} , and for petrale sole it starts to decrease at 1 mL L^{-1} , but not as sharply as in spotted ratfish. The occurrence probability of Dover sole is high (>0.9) throughout a wide range of DO values, but at depth $<200 \text{ m}$ the probability of occurrence decreases sharply in relation to shallower depth and higher DO values. Greenstriped rockfish, petrale sole and spotted ratfish are mostly found in the upper slope region (depth $<400 \text{ m}$), whereas the probability of catching Dover sole increases in the deeper slope areas (depth $>200 \text{ m}$), even when DO values are $<0.5 \text{ mL L}^{-1}$ (Fig. 7). The s_1 (lon, lat) function had a significant effect on each species (Table 3). A significant variation of species occurrence over space may be related to factors not included in the analysis, such as overall limit on a species range imposed, for example, by the proximity to spawning or nursery habitats.

Figure 4. Total catch per unit effort (demersal fishes and benthic invertebrates, $\ln \text{CPUE}$, kg ha^{-1}) as a function of near-bottom oxygen concentration ($\ln \text{DO}$, mL L^{-1}) from 2008 to 2010 for: (a) all sites studied (Fig. 1 and Table 1); and (b) hypoxic stations with near-bottom oxygen concentrations $<1.0 \text{ mL L}^{-1}$. Highly significant ($P < 0.0001$) quadratic regressions are shown for both data sets. The lines added to the figure mark the 1.43 mL L^{-1} concentration of near-bottom oxygen defined as hypoxic conditions (solid line, Fig. 4a) and the 0.5 mL L^{-1} concentration defined as severe hypoxia (dashed lines, Fig. 4a, b).

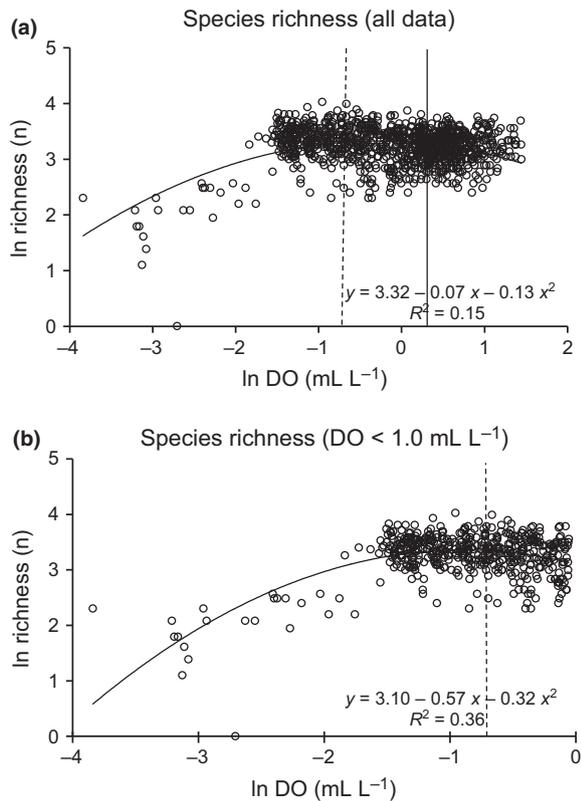


From an analytical perspective, including lat and lon (Table 3) allowed us to examine the effect of habitat variables (e.g., DO) conditional on the species average distribution pattern. Of the other hydrographic variables included in the analysis, near-bottom salinity was the only environmental covariate found to have a significant and mostly positive effect on the probability of occurrence for both petrale sole and spotted ratfish (Fig. 8).

DISCUSSION

This study examined the impact of low, near-bottom DO concentrations on the availability of demersal fishes to a groundfish bottom trawl survey and by extension their distribution along the US west coast at depths from 55 to 1280 m. The survey extended from

Figure 5. Total species richness (demersal fishes and benthic invertebrates, $\ln n$) as a function of the near-bottom oxygen concentration ($\ln \text{DO}$, mL L^{-1}) from 2008 to 2010 for: (a) all stations with near-bottom DO measurements; and (b) hypoxic stations with near-bottom oxygen concentrations $<1.0 \text{ mL L}^{-1}$. Highly significant ($P < 0.0001$) quadratic regressions are shown for both data sets. The lines added to the figure mark the 1.43 mL L^{-1} concentration of near-bottom oxygen defined as hypoxic conditions (solid line, Fig. 5a) and the 0.5 mL L^{-1} concentration defined as severe hypoxia (dashed lines, Fig. 5a,b).



the upper to the lower limit of the OMZ as well as across the boundaries of the OMZ and shoreward to inner shelf waters. The study was motivated by the

observation that low near-bottom oxygen conditions are expanding in distribution along the west coast of North America and the incursion of low DO into shallow shelf waters is increasing in frequency (Bograd *et al.*, 2008; Chan *et al.*, 2008; Pierce *et al.*, 2012). There is an established oxygen minimum zone within the California Current System along the eastern margin of the Pacific basin (Levin, 2003) with a core of low oxygen water ($0.25\text{--}0.5 \text{ mL L}^{-1}$) normally occurring off the continental shelf at depths of $\sim 500\text{--}900 \text{ m}$. The lowest DO values are centered around $700\text{--}800 \text{ m}$ and DO increases above the minimum at both greater and shallower depths (Kamykowski and Zentara, 1990; Levin, 2003). Historical records of the OMZ are consistent with the pattern of low DO we observed in this study, although occasionally even lower ($<0.25 \text{ mL L}^{-1}$, see Fig. 3) DO levels, typical of deep basins of the southern California Bight (Berelson, 1991; Hyland *et al.*, 1991), were observed here. Recently, global expansions of OMZs have been noted (Stramma *et al.*, 2008) with a shoaling of the upper boundary of the OMZ specifically described for waters off California, Oregon and Washington (Bograd *et al.*, 2008; Chan *et al.*, 2008; Bjorkstedt *et al.*, 2011). Although hypoxic waters can generally occur as shallow as 350 m there has been a recent increase in the frequency of low oxygen events in shallower shelf waters ($55\text{--}80 \text{ m}$) within the CCLME (Chan *et al.*, 2008). These shallower hypoxic events are associated with mortality of near-bottom organisms, including commercially important species (Chan *et al.*, 2008), and decreased species richness and overall catch of demersal fishes and benthic invertebrates (Keller *et al.*, 2010).

Wind-driven changes in the intensity of summertime upwelling, tied to changing ocean climate conditions, may be responsible for the initial emergence of hypoxia off the Oregon coast in 2002 (Freeland *et al.*, 2003; Grantham *et al.*, 2004). As water temperatures increase, oxygen levels will decrease owing to both the lower solubility of DO in warmer water and increased

Table 2. Mean catch per unit effort (CPUE, kg ha^{-1}) \pm standard error (SE), catch-weighted mean, minimum and maximum latitude (decimal degree N) and depth (m), and total number of positive hauls (n) for four common groundfish species collected during the 2008–2010 West Coast Groundfish Bottom Trawl Survey.

Species	CPUE (\pm SE)	Latitude			Depth			n
		Mean	Min	Max	Mean	Min	Max	
Dover sole	24.58 (0.93)	41.85	32.03	48.45	431.4	56.7	1217.0	1699
Spotted ratfish	2.04 (0.15)	41.16	32.32	48.45	184.4	56.7	537.7	1009
Greenstriped rockfish	1.86 (0.27)	44.59	32.58	48.45	154.9	73.2	474.3	503
Petrale sole	1.83 (0.11)	41.87	32.72	48.42	142.1	56.7	540.9	860

Figure 6. Extent of the Northwest Fisheries Science Center’s West Coast Groundfish Bottom Trawl Survey showing distribution and relative abundance (catch per unit effort, kg ha^{-1}) from the 2009 and 2010 surveys for: (a) greenstriped rockfish; (b) Dover sole; (c) petrale sole; and (d) spotted ratfish.

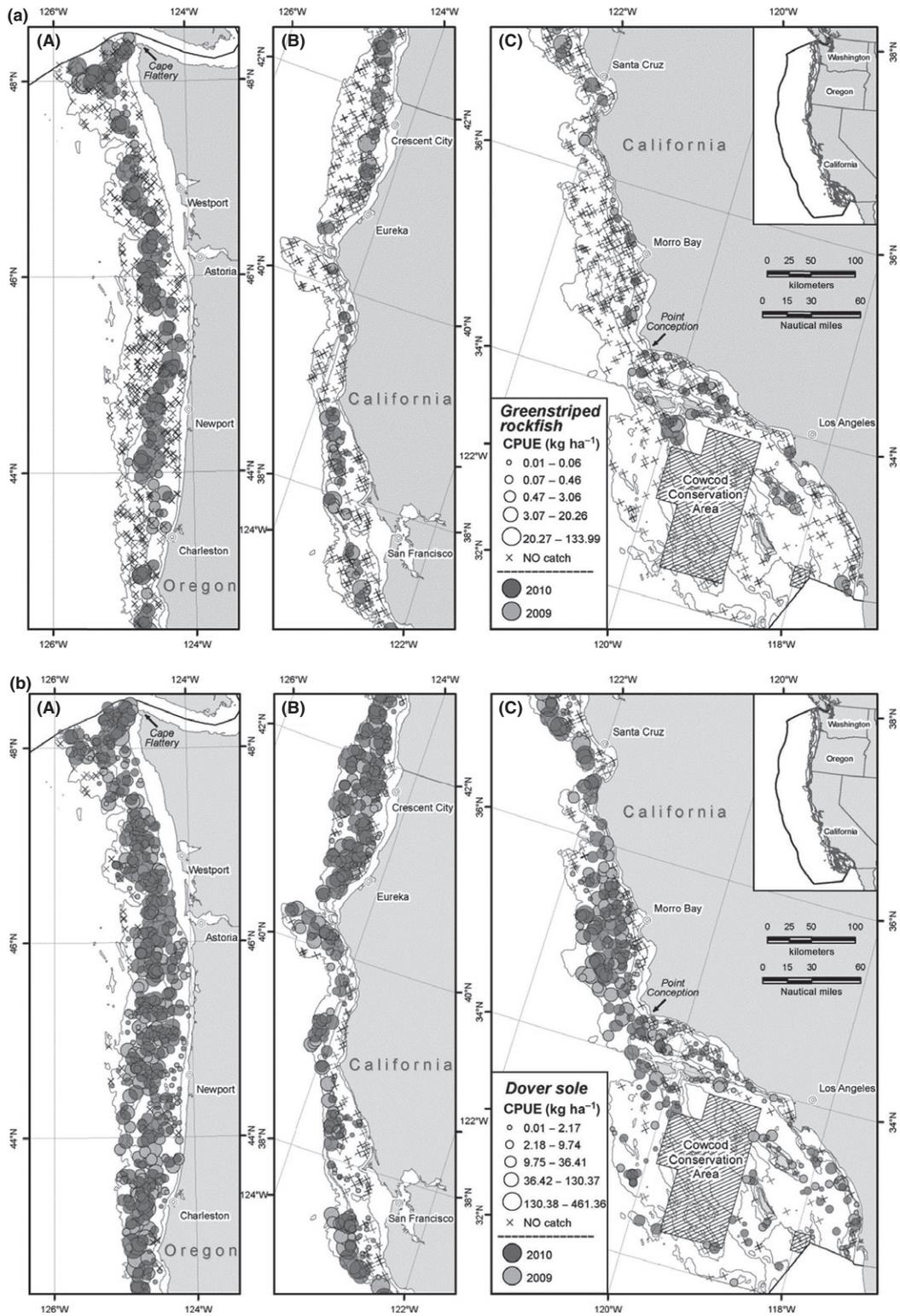


Figure 6. Continued.

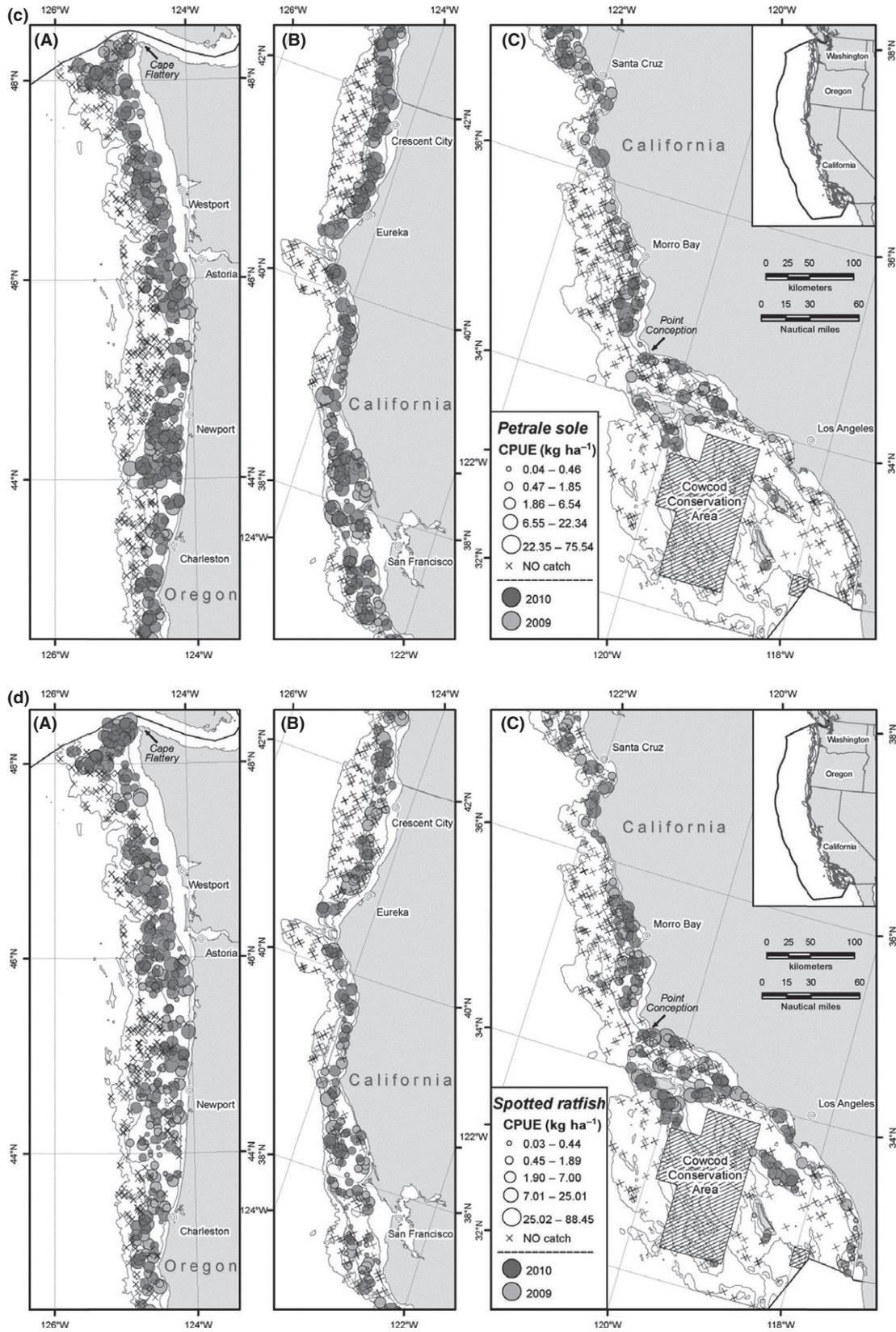


Table 3. Significance (P -value) of the smooth functions for each covariate included in the binomial Generalized Additive Model (GAM) by species.

Species	$s_1(\text{lon, lat})$	$s_2(d)$	$s_3(D)$	$s_4(T)$	$s_5(S)$	te (DO, Z)	Dev
Dover sole	<0.001	0.051	0.951	0.476	0.817	<0.001	59.7
Spotted ratfish	0.009	0.133	0.945	0.133	0.023	<0.001	58.1
Greenstriped rockfish	<0.008	0.720	0.798	0.857	0.578	<0.001	60.6
Petrale sole	<0.002	0.787	0.869	0.062	0.001	<0.001	71.2

Lon and lat are longitude and latitude, d is the time of the day, D is day of the year, T , S , and DO are the near-bottom temperature, salinity, and dissolved oxygen, respectively, Z is depth and s_1 and s_{2-5} are two-dimensional and one-dimensional smooth functions, in this case thin plate regression splines. As Z and DO are correlated, their interaction was modeled using a tensor product (te), that is a product of two anisotropic smooth functions (cubic regression splines). Bold-face values indicate a significant covariate effect at $\alpha = 0.05$. Sample size for all models was 975. Dev is the deviance explained by each model.

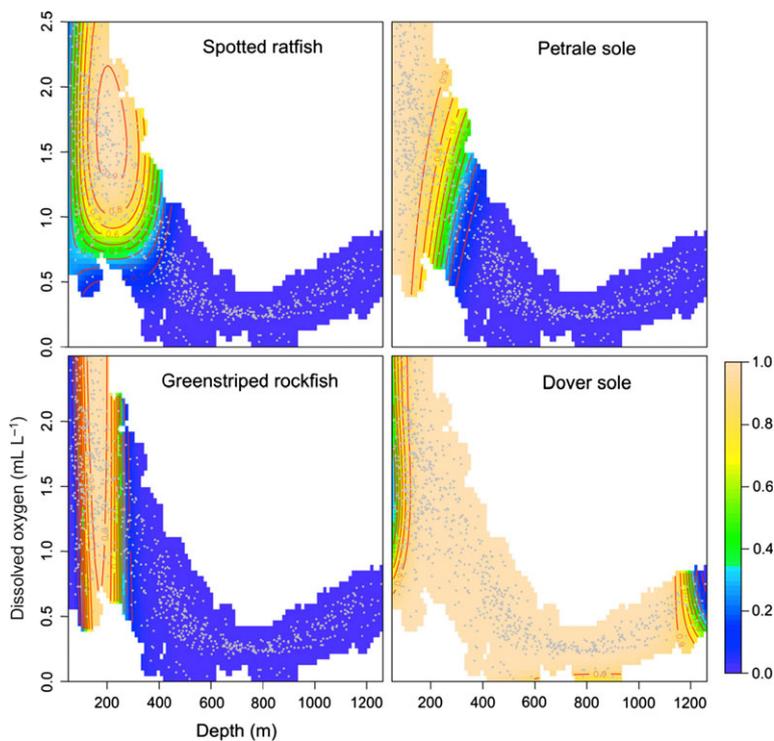


Figure 7. Probability of occurrence of the four selected species in relation to bottom depth (m) and near-bottom dissolved oxygen (DO, mL L^{-1}). Probability values are estimated from a binomial Generalized Additive Model fit to the presence/absence data of the 2008–2010 NWFSC West Coast Groundfish Bottom Trawl Survey. For each examined species, in addition to the interaction term between depth and DO the models also included terms for: position (longitude and latitude), time of day, day of the year, salinity, and water temperature ($^{\circ}\text{C}$) near the bottom. In each plot, the grey dots indicate the occurrences of the observed DO and temperature values.

stratification reducing the supply of DO to depth (Pierce *et al.*, 2012). Similar occurrences of hypoxia in other eastern boundary current systems are linked to changes in ocean climate (Bailey *et al.*, 1985; Morales *et al.*, 1999; Diaz and Rosenberg, 2008; Monteiro *et al.*, 2008). Impacts from low oxygen in bottom waters off Oregon in 2002 included significantly reduced densities of rockfishes, 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). An 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).

Our earlier research, based on a limited number of stations within the inner-shelf hypoxic zone off Oregon, revealed the extent of the response by bottom organisms to low oxygen concentrations (Keller *et al.*, 2010). De Leo *et al.* (2102) recently reported that dissolved oxygen was an important predictor variable related to changing fish assemblage structure off Hawaii at slope sites whereas Breitburg (2002) and others (Howell and Simpson, 1994; Baden and Pihl, 1996; Eby, 2001) previously noted that hypoxia can lead to large reductions in diversity in a number of

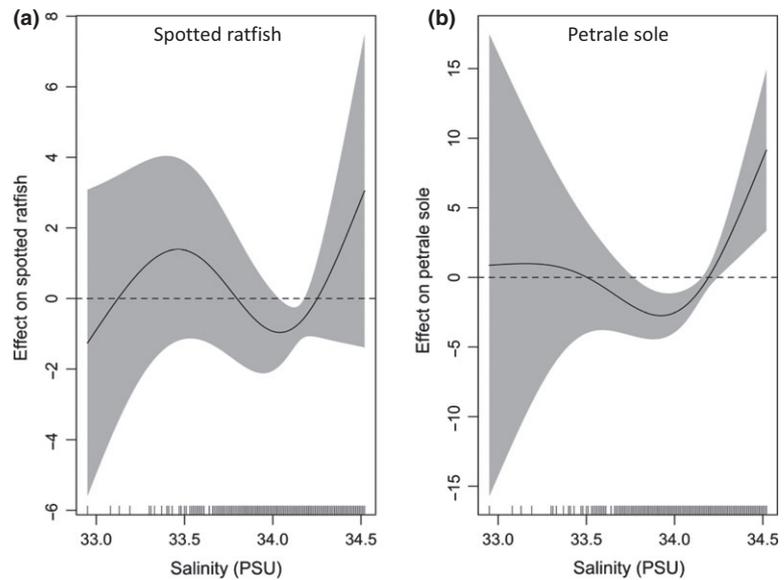


Figure 8. Effect of near-bottom salinity on probability of occurrence of (a) spotted ratfish and (b) petrale sole. The y-axis is in logit units and represents deviation from the yearly logit mean. The smoothed probability of occurrence is scaled by its coefficient from the Generalized Additive Model (GAM) model versus salinity for each species. The shaded area represents the upper and lower twice-standard-error curves.

marine systems. Our current results confirmed these findings and further indicate that demersal fishes and benthic invertebrates inhabiting the US west coast are increasingly impacted as levels of near-bottom DO decrease from moderate ($\text{DO} \sim 1.43 \text{ mL L}^{-1}$) to severe ($\text{DO} < 0.5 \text{ mL L}^{-1}$) hypoxia.

When we examined catch relative to DO at levels defined as hypoxic ($< 1.43 \text{ mL L}^{-1}$), 43% of the variation in overall catch could be explained based on oxygen concentrations. As the level of oxygen decreased from 0.5 to 0.3 mL L^{-1} (severe hypoxia, $n = 130$) we saw an increasing percent (from 50 to 70%) of the variation in demersal fish catch explained by DO concentrations. In the Gulf of Mexico, fish appear to move from hypoxic areas to regions with greater oxygen concentration when oxygen levels dropped below 2 mg L^{-1} (1.43 mL L^{-1}) (Craig *et al.*, 2001). In Hood Canal, Washington, exposure to low DO resulted in rockfish avoidance behavior, when DO similarly dropped below 1.43 mL L^{-1} , although this response was primarily attributed to movement of copper rockfish to shallower waters (Palsson *et al.*, 2008). When compared with impacts of low oxygen on fish distribution in other regions, the overall distribution of demersal fishes along the US west coast appears less likely to be affected by moderately hypoxic waters. The overall response we observed to low oxygen conditions is attributed to species-specific effects based on their physiology and the rate at which they adapt. A second subsequent focus of our study was to examine how four demersal fish species responded to low oxygen conditions.

Distribution patterns of the four individual species used in this study were derived from trawl data

collected during the 2008–2010 trawl surveys. Based on depth of capture relative to the OMZ, Dover sole, a flatfish that undergoes ontogenetic migration moving deeper with age, was the only one of these species occupying the core of the OMZ. Petrale sole, spotted ratfish and greenstriped rockfish are distinctly shallower species, typically occurring in higher oxygen waters, with depth distributions centered above the OMZ ($< 450 \text{ m}$). During the present study the average concentration of oxygen at depths $< 450 \text{ m}$ was $1.58 \pm 0.73 \text{ mL L}^{-1}$ ($n = 704$) whereas the concentration at greater depths ($450\text{--}1280 \text{ m}$) averaged $0.39 \pm 0.17 \text{ mL L}^{-1}$ ($n = 358$). Here we were mainly focusing on general bio-diversity patterns rather than species-specific ontogenetic changes of habitat. Based on depth distribution and whether a species was typically an OMZ-dweller, our expectation was that the probability of occurrence for spotted ratfish, petrale sole and greenstriped rockfish would respond to decreased oxygen levels whereas Dover sole would not. However, our results indicated that neither Dover sole nor greenstriped rockfish reacted to low oxygen conditions by altering their distribution, supporting our expectations for Dover sole, petrale sole and spotted ratfish but not greenstriped rockfish.

In addition to vertical or horizontal migration, demersal fish species have several physiological mechanisms which allow them to cope with hypoxia. Friedman *et al.* (2012) noted that fishes cope with low oxygen through two mechanisms that are not mutually exclusive: increased oxygen extraction from the environment (continued normal behavior) and reduced oxygen demand (i.e., either reduced activity levels or

elevated anaerobic metabolism; Childress and Seibel, 1998). The first method involves enhanced extraction of DO via increased gill surface areas, increased efficiency of hemoglobin and increased hemoglobin concentration. The increased ventilator surface area has repeatedly been reported for fishes living in OMZs (Yang *et al.*, 1992; Childress and Seibel, 1998; Friedman *et al.*, 2012), whereas anaerobic metabolism is considered unlikely, based on documented aerobic enzyme activities (Yang *et al.*, 1992; Childress and Seibel, 1998; Seibel, 2011; Friedman *et al.*, 2012). Species able to regulate oxygen consumption down to very low concentrations include black hagfish (Drazen *et al.*, 2011), shortspine thornyhead (Yang *et al.*, 1992) and Dover sole (Friedman *et al.*, 2012), all OMZ inhabitants. The OMZ-dwelling Dover sole had a two to three times larger gill surface area than comparably-sized flatfishes from higher-oxygen waters, suggesting a morphological adaptation to low oxygen (Friedman *et al.*, 2012).

Unlike flatfishes, Friedman *et al.* (2012) found low aerobic activities and small gills in two thornyhead species (*Sebastes*), suggesting a low oxygen demand commensurate with a more sedentary behavior compared to other fishes. Although very few rockfishes from the genus *Sebastes* have been examined for response to low oxygen, Friedman *et al.* (2012) found that splitnose rockfishes had greater gill surface area and higher aerobic enzyme activities relative to the OMZ-dwelling thornyheads. However, they cautioned that direct comparison with other species of scorpaenids should be avoided because of the wide interspecific variation in body form and biology. As greenstriped rockfishes are often described as sedentary, commonly observed sitting on rock, mud or sand substrate (Love *et al.*, 1990, 2002; Jagielo *et al.*, 2003), we hypothesize that their lack of response to low oxygen conditions is due to their sedentary habit, similar to the activity level of thornyhead species. If activity decreased as DO levels declined this would increase the catchability of greenstriped rockfish. Alternatively, we suggest that greenstriped rockfish, which sometimes occur suspended in mid-water above soft bottoms and reefs (Love *et al.*, 2002), could move off bottom to avoid low DO concentrations but not so far off bottom to avoid capture by the Aberdeen trawl (net height ~5 m) used by the survey. As these are demersal fishes, their response to the net may be to dive downward, suggesting they could be even further than 5-m off-bottom and still be caught by the net. DO profiles indicate that within 5 m of the bottom, oxygen concentrations can increase up to 0.3 mL L⁻¹ over near-bottom levels. Future research on

greenstriped rockfish, focused on gill surface area and aerobic enzyme activities, may reveal why this species was not impacted by the low oxygen conditions seen along the US west coast in 2008–2010.

Our research further indicates the importance of understanding species-specific responses to low near-bottom DO when considering impacts on the overall ecosystem. Recent research suggests that synergistic impacts from climate-related changes in temperature, ocean acidification and reduced DO availability could lead to habitat compression with resultant altered ecological interactions (Seibel, 2011). Such impacts should be taken into account when evaluating the consequences of expanding OMZs within the CCLME, particularly as encroachment of expanding hypoxia and associated acidification onto the continental shelf is impacting organisms not adapted to such conditions. At the species level, variations in mortality rate, physiological impairment, avoidance and habitat compression or expansion could lead to changes in predator–prey relationships and foraging dynamics thus altering the underlying structure of an ecosystem (Chan *et al.*, 2008; Koslow *et al.*, 2011; Seibel, 2011).

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