



Original Article

Gauging oxygen risk and tolerance for the megafauna of the Southern California shelf based on *in situ* observation, species mobility, and seascape

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Oxygen decline poses increasing risks to global shelf communities. This study was conducted to measure species oxygen exposures *in situ* and to assess risks of low oxygen based on the hypothesis that species risk varies spatially and is dependent on the interaction of shelf oxygen dynamics with habitat pattern, species mobility, and tolerance to low oxygen. Here, we report concomitant observations of oxygen, depth, and habitat for the most common benthic and epibenthic megafauna on the southern California shelf (30–125 m). The study was conducted when oxygen concentrations were the lowest observed within the previous 30 years off southern California (2012–2014), yet hypoxic conditions ($<1.42 \text{ ml l}^{-1}$) were not observed. No significant oxygen exposure differences were observed among highly mobile, mobile, and sessile species due to the dynamic nature of the oxycline. Habitat affinities for the most abundant benthic megafauna (53 taxa) were discriminated among four different habitats. Highly mobile rockfish (Sebastidae) exhibited distributions suggesting less tolerance to low oxygen than most other taxa. Given the mosaic of consolidated and coarse-grained habitats that rockfish prefer, the onset of hypoxic conditions near the shelf break (~ 90 – 120 m) would likely compress local rockfish populations into less favourable habitat in a non-linear fashion.

Keywords: behaviour, habitat, hypoxia, oxygen, rockfish, seascape

Introduction

Recent downward trends in oceanic dissolved oxygen have affected the functioning of regional coastal ecosystems (e.g. Rabalais *et al.*, 2001; Grantham *et al.*, 2004; Levin *et al.*, 2009; Breitbart *et al.*, 2018). Dissolved oxygen concentrations have declined globally since the middle of the 20th century (Keeling *et al.*, 2010; Levin, 2018) and within the California Current System (CCS) since the 1980s (Bograd *et al.*, 2015; Ren *et al.*, 2018). Globally, dissolved oxygen concentrations have declined $\sim 2\%$ over the last half century (Schmidtko *et al.*, 2017). Regional decreases have been greater in some areas including the CCS where oxygen levels have declined at a rate of $\sim 2.1 \mu\text{mol kg}^{-1} \text{ year}^{-1}$ (Bograd *et al.*, 2008), and the shelf marginal oxygen minimum zone (OMZ) has shoaled over the last several decades (Netburn and Anthony Koslow, 2015) due to the shoaling and intensification of the California

Undercurrent (Bograd *et al.*, 2015). These secular changes are expected to continue within the CCS due to global warming, which strengthens the stratification between surface and interior waters, thus increasingly limiting the ventilation of interior waters both within the CCS and its source waters (Ren *et al.*, 2018). Hypoxia-induced risks to coastal ecosystems also vary temporally due to seasonal and interannual climate forcing modes such as ENSO. La Niña events on the shelf of the Southern California Bight are associated with increased hypoxia (SCB; Nam *et al.*, 2011).

Intrusions of hypoxic water masses onto shelf marginal habitats present potential ecological challenges to the species that occupy these habitats. Ecological effects of decreasing oxygen concentrations within the CCS include mass mortality events (Chan *et al.*, 2008), compression of breeding habitats (Navarro *et al.*, 2018), decreased abundances of mesopelagic fishes

(Koslow *et al.*, 2011), and a potential partial loss of protected rockfish habitat (McClatchie *et al.*, 2010). De-oxygenation of marine environments also negatively affects human uses of aquatic ecosystems, including fisheries (e.g. Gunderson, 1998; Breitburg *et al.*, 2009).

Habitat complexity likely influences species diversity and the potential species responses to hypoxia. The degree to which shelf species and communities are affected by declining levels of dissolved oxygen likely depends on (i) the nature of the underlying habitat patches, (ii) how species occupy patches along habitat-induced diversity gradients, and (iii) how patches are distributed with respect to depth since dissolved $[O_2]$ generally decreases with increasing water depth. The spatial distribution of characteristic habitats along the southern California shelf varies with depth and distance alongshore due to the complex topography resulting from repeated sea-level transgressions and the tectonic complexity of the southern California borderlands (Le Dantec *et al.*, 2010). These geological processes have resulted in a complex mosaic of benthic habitat patches of varying sizes and configurations that affect habitat occupancy, utilization, and species diversity (e.g. Switzer *et al.*, 2016). Local effects of periodic hypoxia on species and individuals are thus likely influenced by the interaction of the severity (amplitude and period) of dissolved oxygen limitation with seascape, species mobility, and species-specific sensitivities to low oxygen. Generally, finer grained sediments dominate with increasing depth, but this pattern can vary because the depths of sediment deposits vary alongshelf. Sediment deposition (def., depocenters) depths are forced by resuspension due to surface gravity waves (Clarke *et al.*, 1982) and high amplitude internal waves propagating up onto the shelf (Cacchione and Southard, 1974). The depth distribution of consolidated outcrops can also vary alongshelf due to tectonic forcing resulting in outcrops that vary in size and depth. Thus, the response of highly mobile species, such as rockfish to low oxygen exposure, likely depends on the patterns of local habitat that support sheltering, foraging, and perhaps even reproduction.

An important first step in determining the effects of de-oxygenation is the identification of regional and local habitats and species that are most at risk or sensitive (*sensu* Hughes *et al.*, 2018) to increasing oxygen stress. Knowledge of how oxygen interacts with habitat characteristics such as bedform, grain, rugosity, and patch structure can provide initial insights into which shelf communities will be most likely affected regionally and locally by declining trends in oxygen, and what these effects might include. Some highly mobile species exhibit distributional changes in response to episodic (Chu and Tunnicliffe, 2015; Pihl *et al.*, 1991), seasonal (Roberts *et al.*, 2009), and interannual (Eby and Crowder, 2002; Limburg *et al.*, 2011) oxygen variability. Such large-scale migration is not possible for less mobile species, suggesting that less mobile species are more vulnerable to stress from extreme hypoxic events. Oxygen tolerances and the physiological effects of hypoxia are being reported for a growing number of species and settings, yet most of these are for individual species or small sets of species.

Here, we report oxygen exposures (defined as the oxygen concentration at the site and time of animal observation) for some of the most abundant megafauna on the inner shelf off southern California across a spectrum of species mobility and habitat types. The motivating questions addressed here include: (i) are there identifiable species differences in oxygen exposure

on the southern California shelf and shelf break and (ii) could the interaction of benthic habitat configuration (i.e. seascape), species mobility, and sensitivity to hypoxia interact with oxygen dynamics to affect species and community responses to de-oxygenation? The data gathered provide baseline information on oxygen and depth exposures for southern California benthic shelf megafauna. These data also contribute shelf oxygen data in southern California over high-resolution space and time scales. Such field observations are needed to complement studies of laboratory-based species-specific hypoxic thresholds (e.g. Vaquer-Sunyer and Duarte, 2008) for hypothesis testing (i.e. tests based on empirical shelf oxygen values), and to better assess specific hypoxia risk across space and among habitats.

Methods

ROV surveys of the nearshore shelf (depths ~30–125 m) off San Diego, CA, USA, were conducted to yield concomitant observations of benthic and epibenthic megafauna, sediment and bottom characteristics, and dissolved oxygen concentrations. The San Diego marine shelf is complex due to tectonic faulting and transgressive sea-level forcing of sediments (Hogarth *et al.*, 2007; Le Dantec *et al.*, 2010). Survey areas were chosen to span a range of shelf widths and slopes, habitat types (Parnell, 2015; Switzer *et al.*, 2016), and proximity to submarine canyons. The areas studied ranged along ~45 km of shoreline from Coronado to Del Mar (Figure 1). The shelves off Del Mar and La Jolla were repeatedly surveyed using an ROV for surveys of squid spawning and embryo deposition (Navarro *et al.*, 2018) and the effects of tectonically forced habitat patch structure on macro and megafaunal diversity (Switzer *et al.*, 2016). Surveys were also conducted further south on the shelves off Pt. Loma and Coronado. Every effort was made to seasonally stratify the surveys enabling coverage of both the spring/summer upwelling season and fall/winter periods when stratification is greatly reduced. ROV surveys were conducted between August 2012 and January 2014.

The ROV used in this study was a SeaBotix LBV-150 ROV equipped with a SeaBird SBE 37 MicroCAT CTD (SBE 37SMP-IDO), 2 external LED lights (1080 lumen, 140° beam angle), and red scaling lasers (5 cm separation). Temperature, conductivity, depth, and $[O_2]$ were measured at 1-min intervals. The main ROV video camera (520 line, dynamic range 90 mm to infinity, colour, 0.1 lx) provided an analogue composite NTSC video signal that was converted to digital using a Canopus ADVC110 converter. A GoPro camera, housed within a Golem Gear LCD_150 housing, was mounted on the ROV and recorded high definition video (1280 × 960 resolution, 48 frames s^{-1}) to aid taxonomic identification in the main video. The remotely operated vehicle (ROV) was deployed off of a small (~8 m) vessel; the vessel track was recorded using a Hemisphere V110 inertial GPS. Survey velocities averaged ~0.75 $m s^{-1}$. Vessel track, digital video, and conductivity, temperature, depth sensor (CTD) data were recorded onto a laptop computer.

ROV videos were analysed by sampling still captured images at 5-s intervals to identify habitat characteristics and quantify conspicuous megabenthos. Habitat factors included 5 levels of grain size and 11 levels of bedform (see Table 1). These two habitat factors characterize important differences among benthic habitats on the San Diego shelf (Switzer *et al.*, 2016). Bedform

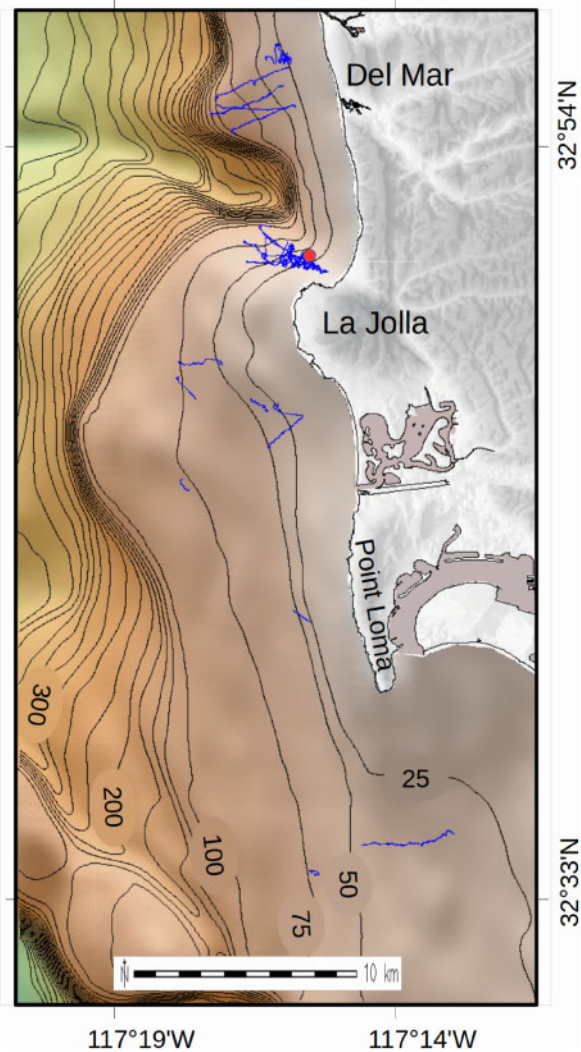


Figure 1. Map of the ROV study area off San Diego, CA, USA. Blue lines indicate ROV survey tracks, and red circle indicates the position of the SeapHOx instrument deployed on the bottom (~ 32 m deep). Depth units are metres.

characteristics of unconsolidated sediments provide information on the interaction between grain size and near-benthic hydrodynamic forcing such as oscillatory flows due to surface gravity waves and bottom current orientation and strength. Hard bottom bedform included “outcrops” (attached hard bottom) and “boulders” (>1 m largest dimension). Bedforms of mixed hard and soft bottom included “sediment veneer” (a layer of unconsolidated sediment $< \sim 1$ cm thick covering outcropped features), “rocks with sand” (rocks < 1 m in largest dimension mixed with sand), and cobble (~ 2.5 – 25 cm). Soft bottom bedform levels included “parallel waves”, “hatched waves”, “parallel ripples”, “hatched ripples”, “linguloid ripples”, and “flat”. Sediment waves were defined as undulations having amplitudes $> \sim 5$ cm, and ripples were $< \sim 5$ cm. Grain size levels included “consolidated” for hard bottom and “shell hash” (shell and gravel debris ~ 2.5 cm to 2 mm), “coarse sand” (~ 0.5 to 2 mm), “fine sand” (~ 0.5 to 0.05 mm), and “mud” ($\sim < 0.05$ mm) for sediments. All benthic

megafauna (within view of the ROV while it was $< \sim 2$ m off the bottom) were enumerated to the lowest possible taxonomic level.

Habitat factors were analysed using multiple correspondence analysis [MCA; Venables and Ripley, 2002; MASS package in R (R Core Team, 2018)] to identify and classify major habitat categories. MCA enables dimensional reduction for categorical data in a manner similar to principal component analysis for numerical data. For this application, MCA identifies combinations of the most important habitat characteristics (MCA factors) that account for the greatest variability, and which are orthogonal to each other.

Oxygen was measured continuously near the bottom off La Jolla to gauge oxygen variability over longer time scales than individual ROV deployments, which typically lasted < 8 h. Longer-term and more continuous oxygen measurements were necessary for contextualizing the representativeness of shelf oxygen conditions during the ROV survey observations. Oxygen was recorded using a SeapHOx instrument (Martz *et al.*, 2010) mounted ~ 0.5 m from the bottom off North La Jolla at a depth of 32 m (see Figure 1). Data were recorded at 15-min intervals from 30 August 2012 to 21 October 2013 across four deployments.

Results

ROV-based observations of oxygen and benthic megafauna ranged in depth from 30 to 120 m, with a mode ~ 35 m deep (Figure 2a). Comparisons of oxygen as a function of seawater density (σ_T) between the ROV CTD and SeapHOx indicate broad overlap between them (Figure 2b) indicating that the spatially distributed ROV-based observations of oxygen concentration exhibited variability similar to that measured by the bottom-mounted SeapHOx at a single location off La Jolla over longer time scales. However, an ANOVA comparison of slope models (all SeapHOx data compared with ROV CTD data at the same depth as the SeapHOx instrument) was significant (Figure 2b, $p \ll 0.001$) indicating differences between the two sets of observations. The model slope for continuous SeapHOx observations was steeper, but model slopes converged near the uppermost range of seawater density. The shallower slope of ROV-based oxygen observations indicates that the ROV surveys were disproportionately conducted during periods when lower oxygen waters bathed the nearshore shelf. Boxplots of oxygen concentrations binned by depth and for the bottom-mounted SeapHOx instrument (Figure 3) indicate decreasing trends in both oxygen concentration and variability with increasing depth, with a median asymptote located at ~ 35 m deep. Median oxygen concentrations did not decrease deeper than ~ 75 m because not all ROV missions extended to depths > 75 m. ROV CTD measurements at these depths evidently occurred when oxygen concentrations were relatively elevated on the shelf, possibly due to breaking internal waves. This result was likely due to the highly dynamic nature of the oxycline and the episodic timing of ROV surveys. Hypoxic oxygen concentrations (< 1.5 ml l^{-1}) as per McClatchie *et al.* (2010) were not observed during either the ROV surveys or the SeapHOx deployments. Oxygen concentrations < 2.0 ml l^{-1} were observed for only $\sim 1.6\%$ of ROV images and $< 0.2\%$ of SeapHOx observations (32 m deep).

Boxplots of depth and concomitant oxygen observations for highly mobile (def., free-swimming epibenthic fish), low mobility (sedentary epibenthic fish and motile invertebrates), and sessile species are presented in Figures 4–6, respectively. Boxplots were

Table 1. MCA loadings of habitat factor levels ($\times 10^3$ for ease of readability).

Habitat factor	Consolidation	Levels	MCA1 factor loadings	MCA2 factor loadings
Grain size	Hard bottom	Consolidated	-37	1.42
		Soft bottom	7.3	17.3
	Soft bottom	Coarse sand	4.11	19.3
		Fine sand	2.9	-15.83
		Mud	3.64	-10.9
Bedform	Hard Bottom	Outcrop	-36.2	0.84
		Boulders	-26.1	0.79
	Mixed	Sediment veneer	2.29	-6.3
		Rocks with sand	5.33	17.7
		Cobbles	-9.12	15.6
	Soft Bottom	Parallel waves	5.61	29.8
		Hatched waves	5.81	35.3
		Parallel ripples	6.31	30.2
		Hatched ripples	5.21	18.3
		Linguloid ripples	5.34	19.2
		Flat	4.55	-17.1

Loadings whose scaled absolute values > 1 standard deviation among loadings by factor (i.e. most important factor levels for each MCA factor) are indicated in bold.

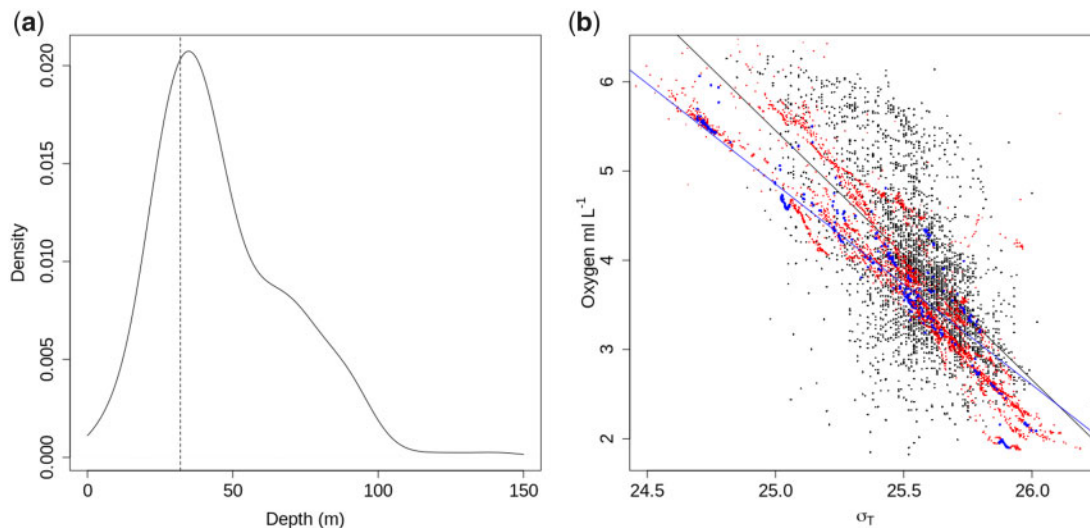


Figure 2. (a) Depth distribution (probability density function) of ROV CTD observations; dotted line indicates the depth of the SeapHOx instrument. (b) Oxygen plotted as function of seawater density ($\sigma\text{-T}$) between the SeapHOx instrument (black) and ROV CTD observations at the same depth as the SeapHOx instrument (~ 32 m, blue circles), and all other ROV CTD depth observations (red). Regression lines indicate linear model fits for SeapHOx (black line) and all ROV CTD (blue line) observations.

created for species and group complexes observed in at least ten still frames captured from the survey videos. Means and ranges of oxygen, temperature, and depths for all species observed at least once are listed in Tables 2 and 3. Generalized linear models of species abundance (species included in Figures 4–6) as a function of oxygen and mobility were not significant due to the highly variable nature of oxygen among survey days, and there were no discernible correlations between oxygen and depth for any species. The only species with a clear water mass affinity was the pelagic tunicate (*Pegea confederata*), which was only observed in relatively shallow waters and only during periods of elevated oxygen concentrations (Figure 4).

Habitats were categorized from the first two MCA factors, which accounted for 31 and 60% of the cumulative variance

among the habitat factor levels. Loadings for MCA1 characterized consolidated, outcrop, and boulder habitats (Table 1). Negative loadings for MCA factor 2 characterized fine sands and mud distributed across flat (\sim smooth) bedforms. Positive MCA2 loadings characterized coarse sand distributed across ripple and wave-type bedforms. MCA loadings were used to plot the local depth distributions of these three different habitats that were characterized as “hard”, “coarse soft”, and “fine soft” habitats. Hard bottom was discriminated as $\text{MCA1} < 0.02$, coarse soft bottom as $\text{MCA2} \geq 0.017$, and fine soft bottom as $\text{MCA2} \leq -0.007$. These values best discriminated the habitats as other values for these two factors were indicative of a mixture of habitat types. Depth distributions for these characteristic habitats are shown in Figure 7. Locally, hard bottom habitats were distributed

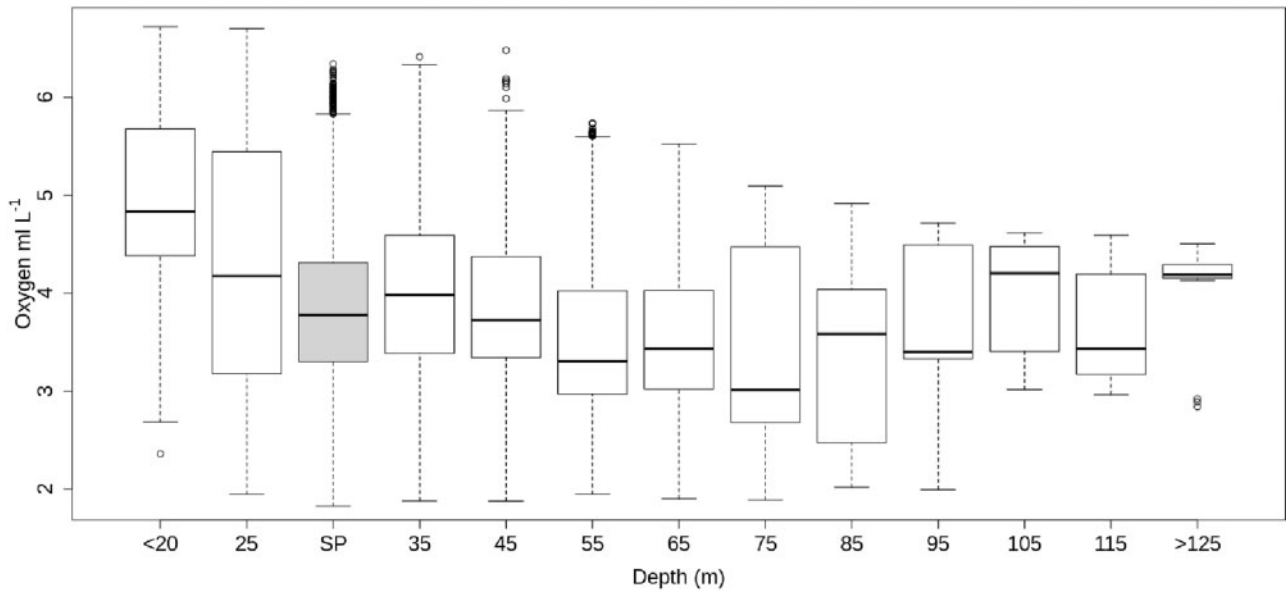


Figure 3. Boxplot of dissolved oxygen concentrations by binned depth for all ROV observations (depth bin indicated) and for the SeapHOx instrument (SP—shaded box) located on the bottom (depth 32 m). Center line indicates median, boxes represent 25th and 75th percentiles, whiskers indicate 5th and 95th percentiles, and open circles indicate outliers.

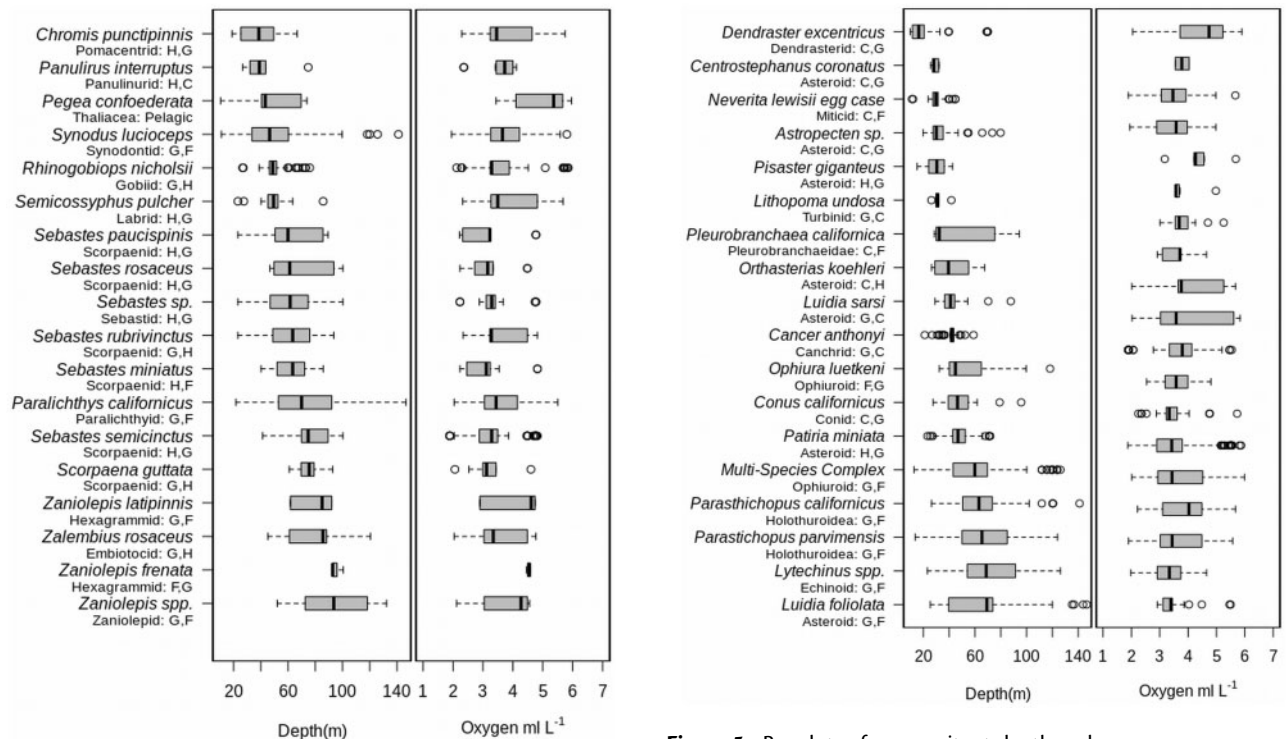


Figure 4. Boxplots of concomitant depth and oxygen concentrations for high-mobility species. Species are ordered by median observation depth. Primary and secondary habitats (see text) where each was observed are listed with major taxonomic group. “H” = hard bottom, “C” = coarse sediment, “F” = fine sediment, and “G” = generalist. Species are ordered by median observation depth (see Figure 3 for the description of boxes and whiskers).

Figure 5. Boxplots of concomitant depth and oxygen concentrations for low-mobility species. Primary and secondary habitats (see text) where each was observed are listed with major taxonomic group. “H” = hard bottom, “C” = coarse sediment, “F” = fine sediment, and “G” = generalist. Species are ordered by median observation depth (see Figure 3 for the description of boxes and whiskers).

throughout the depth range of the entire study but were most abundant between 20 and 40 m. Depth distributions of coarse soft habitats were wide ranging with a mode located at ~50 m

depth. Fine soft habitats were most abundant >60 m deep where smaller patches of hard bottom were also located.

Primary and secondary habitat species affinities are listed in Figures 4–6. Primary and secondary habitat types are defined as

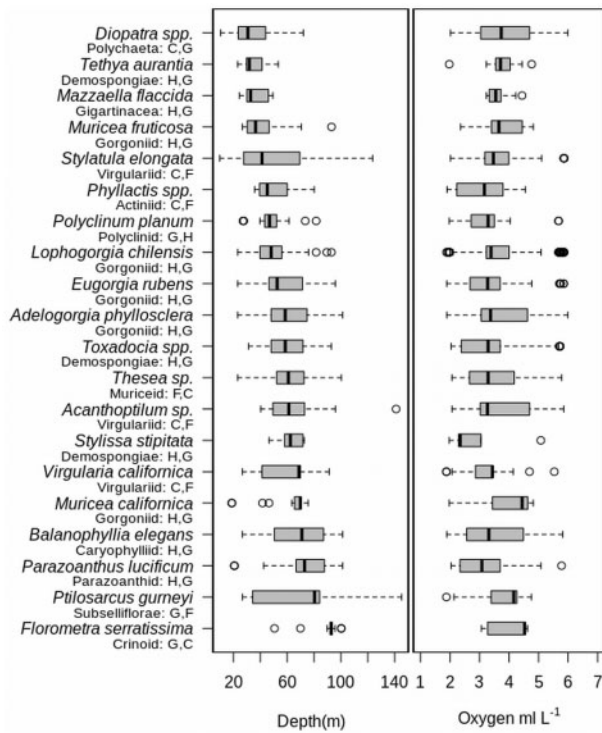


Figure 6. Boxplots of concomitant depth and oxygen concentrations for *sessile species*. Primary and secondary habitats (see text) where each was observed are listed with major taxonomic group. “H” = hard bottom, “C” = coarse sediment, “F” = fine sediment, and “G” = generalist. Species are ordered by median observation depth (see Figure 3 for the description of boxes and whiskers).

the first and second most frequent habitats where each species was observed. A species was considered a generalist, “G”, for either its primary or secondary habitat when it was observed with MCA1 and 2 loadings outside the ranges defined above for hard, coarse soft, and fine soft habitats. Primary habitats for highly mobile species were equally distributed among the hard and generalist categories. Habitat types for lower mobility species mainly consisted of generalist and coarse soft habitats, whereas sessile species were mainly observed among hard and coarse soft habitats.

The depth distribution of habitats observed during the ROV surveys varied considerably alongshore with fine grained unconsolidated habitats dominating most areas deeper than ~60 m. Consolidated habitat dominates the shallower inshore shelf but is also observed at various outcrops as deep as 90 m along a latitudinal dip in a sub-bottom consolidated surface (Switzer *et al.*, 2016) and across much of the shelf break at deeper depths. Coarser-grained habitats with complex wave forms indicating influences from surface gravity and internal tidal driven waves are widely distributed along the shelf and extend quite deep (~100 m). Many areas near the shelf break are dominated by coarser sediments interspersed with rocky outcrops of varying size.

Discussion

Given the rising levels of hypoxia observed in many regions, it has become increasingly important to identify potential and

realized ecological effects across multiple spatial scales. An important first step is the identification of species and ecological processes most sensitive to these changes and which are therefore most likely at the greatest risk of adverse change. The effects of hypoxia can be exacerbated by ocean warming and stratification in some regions (Levin, 2018) due to the decreased solubility of oxygen and increased bacterial metabolism (Sarmiento *et al.*, 2010) associated with higher temperatures. Fundamental poleward shifts in the biogeographic ranges of characteristic regional fauna due to warming have already been observed (e.g. Wernberg *et al.*, 2011; Yamano *et al.*, 2011; Poloczanska *et al.*, 2016). The potential synergism of range shifting and the ecological risks associated with hypoxia have become a fundamental concern (Rosa and Seibel, 2008; Clark *et al.*, 2013). The complex, hierarchical, and interconnected nature of marine ecosystems makes it difficult to predict what the combined effects of hypoxia and warming will be (Vaquer-Sunyer and Duarte, 2011). At higher ecological levels, these effects have already included a loss of biodiversity in some benthic communities (Levin *et al.*, 2009).

Here, we have presented work that (i) provides baseline information on oxygen and depth exposures for some of the most abundant megafauna on the inner shelf off southern California and (ii) relates oxygen exposures to species mobility and habitat occupancy. Field observations such as these are needed to complement studies of laboratory-based species-specific hypoxic thresholds (e.g. Vaquer-Sunyer and Duarte, 2008) throughout species ranges to better assess specific local and regional hypoxic exposure across space and time given the variable nature of habitat depth distribution and configuration.

For context, our study was conducted during a period when negative oxygen anomalies at the 26.4 σ_T isopycnal, observed ~32–38 m deep in this study, within the southern CCS were the greatest observed over the previous 35 years (Wells *et al.*, 2017). This time series indicates not only shoaling of the OMZ but also a decrease in oxygen within isopycnals that is likely driven by changes to source water masses (Stramma *et al.*, 2010; Bograd *et al.*, 2015). Therefore, the oxygen exposures presented here represent a period during which the inner shelf off San Diego was at the greatest risk of hypoxia exposure over at least the last three decades (through 2014) and these exposures were most likely driven by external forcing of the CCS.

Physiological and behavioural responses have been documented for a few of the species or closely related congeners observed in this study (Table 4). Oxygen concentrations observed in this study indicate that these species were not exposed to species/genus-specific hypoxia. Various life stages of *Panulirus interruptus* exhibit hypoxic stress at oxygen concentrations near the minimum observed for this species in the present study. However, the observed temperatures for adult *P. interruptus* in this study (Table 3) were much lower (12 vs. 20°C and 27°C) than temperatures that lobsters were exposed to in a physiological study (Table 4; Ocampo *et al.*, 2003). *Doryteuthis opalescens* exhibits decreased hatch rates at oxygen levels <1.05 ml l⁻¹ (Zeidberg *et al.*, 2012), whereas market squid adults were only observed once in the present study at [O₂] of 3.9 ml l⁻¹. *Doryteuthis opalescens* embryo sacks, however, were observed over a broad range of [O₂] (1.9–6.2, mean 3.6 ml l⁻¹; Navarro *et al.*, 2018), but these values were nonetheless greater than the levels previously observed for decreased hatch rates. Juvenile *Haliotis rufescens* exhibit mortality in combination with decreased pH levels at <3.5 ml l⁻¹ [O₂] (Kim *et al.*, 2013). Minimal [O₂] of *Haliotis*

Table 2. Relative mobility and depth statistics for species observed in this study.

Species	Major taxa	Group	Mobility	Depth		
				Minimum	Maximum	Mean
<i>Acanthoptilum</i> sp.	Cnidaria	Virgulariid	s	40.2	141.0	64.1
<i>Adelogorgia phyllosclera</i>	Cnidaria	Alcyonacea	s	23.1	101.3	61.7
<i>Astropecten</i> sp.	Echinodermata	Asteroid	m	19.9	79.8	32.2
<i>Balanophyllia elegans</i>	Cnidaria	Caryophylliid	s	26.6	101.3	69.7
<i>Beringraja binoculata</i>	Chordata	Rajid	hm	32.3	–	–
<i>Bugula californica</i>	Bryozoa	Bugulid	s	41.3	44.7	43.0
<i>Caulolatilus princeps</i>	Chordata	Malacanthid	hm	42.9	45.4	44.2
<i>Centrostephanus coronatus</i>	Echinodermata	Asteroid	m	25.6	32.3	28.9
<i>Chromis punctipinnis</i>	Chordata	Pomacentrid	hm	18.8	66.7	37.5
<i>Citharichthys sordidus</i>	Chordata	Paralichthyid	hm	37.9	70.2	54.2
<i>Conus californicus</i>	Mollusca	Conid	m	27.6	95.8	50.0
<i>Craniella arb</i>	Porifera	Demospongiae	s	28.6	34.1	32.7
<i>Dendroaster excentricus</i>	Echinodermata	Dendroasterid	m	9.8	69.9	20.0
<i>Dendroaster</i> spp. juveniles	Echinodermata	Dendroasterid	m	17.1	34.3	25.3
<i>Diopatra</i> spp.	Annelida	Polychaeta	s	10.4	72.0	34.1
<i>Doryteuthis opalescens</i>	Mollusca	Loligonid	hm	39.2	–	–
<i>Eugorgia rubens</i>	Cnidaria	Alcyonacea	s	23.1	95.8	58.8
<i>Florometra serratissima</i>	Echinodermata	Crinoid	s	50.5	100.2	89.9
<i>Fusitriton oregonensis</i>	Mollusca	Raneliid	m	40.2	–	–
<i>Gorgonocephalus eucnemis</i>	Echinodermata	Ophiuroid	s	60.9	–	–
<i>Halichoeres semicinctus</i>	Chordata	Labrid	hm	36.9	–	–
<i>Haliclona</i> sp.	Porifera	Demospongiae	s	24.9	32.7	29.5
<i>Haliotis assimilis</i>	Mollusca	Haliotid	m	25.6	40.4	33.0
<i>Henricia leviuscula</i>	Echinodermata	Asteroid	m	46.4	49.3	47.9
<i>Leucilla nuttingi</i>	Porifera	Calcarea	s	34.8	35.2	35.0
<i>Lophogorgia chilensis</i>	Cnidaria	Alcyonacea	s	23.1	92.9	49.0
<i>Loxorhynchus grandis</i>	Arthropoda	Epialtid	hm	23.1	63.8	43.8
<i>Luidia foliolata</i>	Echinodermata	Asteroid	m	25.4	146.5	66.0
<i>Luidia sarsi</i>	Echinodermata	Asteroid	m	29.1	87.7	45.3
<i>Lytechinus</i> spp.	Echinodermata	Echinoid	m	23.1	126.1	69.6
<i>Mazzaella flaccida</i>	Rhodophyta	Gigartinae	s	24.4	49.3	36.9
<i>Megastrea undosa</i>	Mollusca	Turbinid	m	26.2	41.7	31.7
<i>Megathura crenulata</i>	Mollusca	Fissurellid	m	31.8	31.8	31.8
<i>Metacarcinus anthonyi</i>	Arthropoda	Canchrid	m	21.1	58.9	41.5
<i>Metacarcinus gracilis</i>	Arthropoda	Cancrid	m	43.0	–	–
Multi-species complex	Echinodermata	Ophiuroid	m	12.7	126.1	58.9
<i>Muricea californica</i>	Cnidaria	Alcyonacea	s	18.8	75.6	61.7
<i>Muricea fruticosa</i>	Cnidaria	Alcyonacea	s	26.6	93.0	40.5
<i>Neverita lewisii</i> egg case	Mollusca	Mitid	m	11.2	44.8	30.0
<i>Octopus californicus</i>	Mollusca	Octopoda	m	23.8	102.5	66.8
<i>Octopus rubescens</i>	Mollusca	Octopoda	m	55.6	60.9	58.2
<i>Ophiodon elongatus</i>	Chordata	Hexagrammid	hm	19.6	72.9	49.6
<i>Ophiura luetkeni</i>	Echinodermata	Ophiuroid	m	32.4	118.2	53.4
<i>Orthasterias koehleri</i>	Echinodermata	Asteroid	m	26.3	67.5	42.8
<i>Oxyjulis californica</i>	Chordata	Labrid	hm	23.1	49.4	34.0
<i>Pagurus armatus</i>	Arthropoda	Pagurid	m	32.2	50.8	41.5
<i>Panulirus interruptus</i>	Arthropoda	Panulinurid	hm	26.6	74.7	39.9
<i>Paralabrax clathratus</i>	Chordata	Serranid	hm	45.1	–	–
<i>Paralichthys californicus</i>	Chordata	Paralichthyid	hm	21.7	146.5	73.6
<i>Parastichopus californicus</i>	Echinodermata	Holothuroidea	m	26.3	141.0	65.2
<i>Parastichopus parvimensis</i>	Echinodermata	Holothuroidea	m	13.7	123.9	66.3
<i>Parazoanthus lucificum</i>	Cnidaria	Parazoanthid	s	20.7	101.3	72.8
<i>Patiria miniata</i>	Echinodermata	Asteroid	m	23.1	71.8	47.4
<i>Pegea confoederata</i>	Tunicata	Thaliacea	hm	10.4	73.8	45.8
<i>Pelagophycus porra</i>	Phaeophyta	Laminariaceae	s	40.8	–	–
<i>Phacellophora camtschatica</i>	Cnidaria	Phacellophoridae	m	46.8	46.8	46.8
<i>Phyllactis</i> spp.	Cnidaria	Actiniid	s	35.7	80.1	51.4
<i>Pisaster giganteus</i>	Echinodermata	Asteroid	m	15.2	42.6	29.8
<i>Pleurobranchaea californica</i>	Mollusca	Pleurobranchaeidae	m	28.5	94.4	50.7
<i>Polyclinum planum</i>	Tunicata	Polyclinid	s	27.1	81.5	47.7

Continued

Table 2. continued

Species	Major taxa	Group	Mobility	Depth		
				Minimum	Maximum	Mean
<i>Ptilosarcus gurneyi</i>	Cnidaria	Subselliflorae	s	26.7	145.2	66.9
<i>Pyrosoma atlanticum</i>	Tunicata	Thalliaceanae	m	21.1	35.8	26.7
<i>Rhacochilus vacca</i>	Chordata	Embiotocid	hm	23.1	50.4	43.6
<i>Rhinogobiops nicholsii</i>	Chordata	Gobiid	hm	26.6	75.9	50.6
<i>Scorpaena guttata</i>	Chordata	Scorpaenid	hm	60.9	92.7	76.3
<i>Sebastes auriculatus</i>	Chordata	Sebastid	hm	70.7	70.7	70.7
<i>Sebastes melanops</i>	Chordata	Sebastid	hm	63.4	71.5	67.4
<i>Sebastes miniatus</i>	Chordata	Sebastid	hm	40.1	85.8	62.9
<i>Sebastes nigrocinctus</i>	Chordata	Sebastid	hm	70.8	–	–
<i>Sebastes paucispinis</i>	Chordata	Sebastid	hm	23.1	89.3	62.8
<i>Sebastes rosaceus</i>	Chordata	Sebastid	hm	46.6	100.2	69.8
<i>Sebastes rubrivinctus</i>	Chordata	Sebastid	hm	23.1	93.6	63.6
<i>Sebastes semicinctus</i>	Chordata	Sebastid	hm	41.2	100.2	76.1
<i>Sebastes serranoides</i>	Chordata	Sebastid	hm	32.3	58.5	45.4
<i>Sebastes serriceps</i>	Chordata	Sebastid	hm	23.1	100.2	61.7
<i>Sebastes sp.</i>	Chordata	Sebastid	hm	23.1	100.2	63.8
<i>Sebastes umbrosus</i>	Chordata	Sebastid	hm	63.4	69.8	66.6
<i>Sebastes dallii</i>	Chordata	Sebastid	hm	41.2	71.8	65.5
<i>Semicossyphus pulcher</i>	Chordata	Labrid	hm	23.1	85.8	49.7
<i>Styela montereyensis</i>	Urochordata	Styelid	s	30.1	32.3	31.2
<i>Stylatula elongata</i>	Cnidaria	Virgulariid	s	9.8	123.6	47.3
<i>Stylissa stipitata</i>	Porifera	Demospongiae	s	46.4	72.6	62.3
<i>Synodus lucioceps</i>	Chordata	Synodontid	hm	11.0	141.0	50.3
<i>Tethya aurantia</i>	Porifera	Demospongiae	s	23.1	53.3	34.3
<i>Toxadocia spp.</i>	Porifera	Demospongiae	s	31.2	92.9	60.4
<i>Trachurus symmetricus</i>	Chordata	Carangid	hm	23.1	–	–
<i>Virgularia californica</i>	Cnidaria	Virgulariid	s	26.6	91.2	58.5
<i>Xystreureys liolepis</i>	Chordata	Paralichthyid	hm	48.9	–	–
<i>Zalembius rosaceus</i>	Chordata	Embiotocid	hm	45.2	120.6	80.6
<i>Zaniolepis frenata</i>	Chordata	Hexagrammid	hm	92.6	100.6	94.5
<i>Zaniolepis latipinnis</i>	Chordata	Hexagrammid	m	61.7	92.1	79.6
<i>Zaniolepis spp.</i>	Chordata	Zaniolepid	hm	52.1	132.3	93.7
<i>Zapteryx exasperata</i>	Chordata	Rhinobatid	hm	19.3	–	–

Depths for species observed only once are listed in the minimum depth column.

assimilis, a similarly distributed abalone species, was 3.7 ml l^{-1} . *Sebastes caurinus* exhibited decreased home ranges when exposed to $<1.4 \text{ ml l}^{-1} [\text{O}_2]$ (Rankin et al., 2013). Sebastids in the present study were all observed well above this threshold. However, a deeper dwelling species, *Sebastes semicinctus* (mean depth $\sim 76 \text{ m}$), observed in this study was exposed to minimal $[\text{O}_2]$ levels of 1.9 ml l^{-1} .

Highly mobile animals such as rockfish are capable of avoiding hypoxic waters, and many exhibit hypoxic stress at higher oxygen thresholds than less mobile and sessile species (Vaquer-Sunyer and Duarte, 2008). However, animals to avoid hypoxic conditions can come at the cost of elevated exposure to predators, or diminished foraging and nursery space (Navarro et al., 2018), especially when hypoxia is severe or long lasting. Differential alongshelf habitat depth distributions and configuration can limit or enhance the ability of mobile species to respond to hypoxic events by affecting their ability to avoid predators, feed, and reproduce as they move among or within habitats. The highest mobility species observed in this study mainly included fish and were generally associated with hard consolidated bottom or were generalists, having been observed among mixed or variable habitat types. Generalist species included *Synodus lucioceps*, *Rhinogobiops nicholsii*, *Sebastes rubrivinctus*, *Paralichthys californicus*, *Scorpaena*

guttata, *Zalembius rosaceus*, and *Zaniolepis frenata*. These species are likely to be the least impacted by hypoxic events due to their mixed habitat affinities. This is especially true for the shallowest species such as *S. lucioceps* and *R. nicholsii*, which are less likely to experience hypoxia. Many less mobile species, mainly invertebrates, were generalists or associated with coarse-grained habitats. Despite their limited mobility, these species are less at risk of hypoxia due to their shallow distribution. These generalist species included *Lithopoma undosa*, *Luidia sarsi*, *Cancer anthonyi*, *Parastichopus parvimensis*, *P. californicus*, *Lytechinus spp.*, *Luidia foliolata*, and the ophiuroid species complex. Sessile species are most at risk due to their lack of mobility, especially those exhibiting the deepest distributions such as the gorgonians *Adelorgia phyllosclera*, *Eugorgia rubens*, and *Lophogorgia chilensis*. Due to the provisioning of nursery habitat for juvenile rockfish by gorgonians, hypoxia-induced mortality of gorgonians could result in knock on effects for rockfishes (Carlson and Straty, 1981). The local depth distribution of consolidated bottom is a primary determinant of local hypoxic risk for gorgonians. However, regardless of mobility and habitat affinity, risk to low oxygen events increases with increasing amplitude and duration of hypoxia (Levin et al., 2009).

Table 3. Temperature, and oxygen exposure statistics for species observed in this study.

Species	Temperature (°C)			[Oxygen] (ml l ⁻¹)			[Oxygen] (kPa)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean
<i>Acanthoptilum</i> sp.	9.9	14.2	11.3	2.1	5.9	3.7	6.9	21.0	12.6
<i>Adelogorgia phyllosclera</i>	9.6	14.3	11.6	1.9	6.0	3.7	6.2	21.5	12.9
<i>Astropecten</i> sp.	9.9	14.0	11.4	1.9	5.0	3.4	6.5	17.8	11.7
<i>Balanophyllia elegans</i>	9.6	14.1	11.2	1.9	5.8	3.5	6.2	20.9	12.0
<i>Beringraja binoculata</i>	11.6	–	–	3.6	–	–	12.1	–	–
<i>Bugula californica</i>	12.9	13.2	13.1	4.1	4.5	4.3	14.4	15.7	15.0
<i>Caulolatilus princeps</i>	10.4	10.8	10.6	2.5	3.3	2.9	8.2	11.1	9.7
<i>Centrostephanus coronatus</i>	11.6	12.0	11.8	3.6	4.0	3.8	12.1	13.9	13.0
<i>Chromis punctipinnis</i>	10.3	14.0	11.9	2.3	5.7	3.9	7.7	20.6	13.4
<i>Citharichthys sordidus</i>	10.4	12.3	11.8	3.2	4.0	3.8	10.5	14.0	13.1
<i>Conus californicus</i>	10.5	13.5	11.5	2.5	4.8	3.6	8.5	17.0	12.3
<i>Craniella arb</i>	11.5	12.0	11.6	3.4	3.8	3.5	11.5	13.1	12.0
<i>Dendraster excentricus</i>	9.9	15.8	12.9	2.0	5.9	4.5	6.8	21.8	15.9
<i>Dendraster</i> spp. juveniles	10.5	11.6	11.2	3.3	4.7	4.1	11.1	15.9	13.9
<i>Diopatra</i> spp.	9.9	14.3	12.0	2.0	6.0	3.9	6.7	21.5	13.4
<i>Doryteuthis opalescens</i>	13.3	–	–	5.5	–	–	19.5	–	–
<i>Eugorgia rubens</i>	9.6	14.2	11.1	1.9	5.9	3.3	6.2	21.0	11.2
<i>Florometra serratissima</i>	10.7	11.6	11.3	3.1	4.6	4.0	10.4	15.9	13.8
<i>Fusitriton oregonensis</i>	10.5	–	–	3.2	–	–	10.7	–	–
<i>Gorgonocephalus eucnemis</i>	10.2	–	–	2.5	–	–	8.4	–	–
<i>Halichoeres semicinctus</i>	11.9	–	–	4.0	–	–	13.6	–	–
<i>Haliclona</i> sp.	10.0	12.0	11.4	2.1	4.0	3.4	7.0	13.9	11.5
<i>Haliotis assimilis</i>	11.5	12.0	11.7	3.7	3.8	3.7	12.4	13.1	12.8
<i>Henricia leviuscula</i>	9.9	10.7	10.3	2.0	3.3	2.6	6.5	11.0	8.8
<i>Leucilla nuttingi</i>	12.0	12.3	12.2	4.1	4.3	4.2	14.0	14.7	14.4
<i>Lophogorgia chilensis</i>	9.6	14.2	11.6	1.9	5.9	3.7	6.2	21.1	12.6
<i>Loxorhynchus grandis</i>	10.4	14.0	11.9	3.0	4.8	3.7	9.8	17.0	12.9
<i>Luidia foliolata</i>	9.9	12.9	11.1	2.0	4.7	3.3	6.6	16.1	11.2
<i>Luidia sarsi</i>	10.3	14.0	12.1	2.0	5.7	4.1	6.8	20.2	14.1
<i>Lytechinus</i> spp.	10.1	14.0	11.3	1.9	5.6	3.6	6.3	19.8	12.4
<i>Mazzaella flaccida</i>	10.7	13.2	11.5	3.2	4.4	3.6	10.8	15.6	12.3
<i>Megastrea undosa</i>	11.2	14.0	11.9	3.6	5.0	3.8	12.1	17.8	13.1
<i>Megathura crenulata</i>	11.6	11.6	11.6	3.6	3.6	3.6	12.1	12.1	12.1
<i>Metacarcinus anthonyi</i>	9.9	14.5	12.0	2.0	5.8	4.1	6.7	21.1	14.2
<i>Metacarcinus gracilis</i>	10.3	–	–	2.9	–	–	9.5	–	–
Multi-species complex	9.7	14.5	11.2	1.9	5.9	3.4	6.2	21.2	11.5
<i>Muricea californica</i>	9.9	13.2	11.7	2.0	4.8	4.0	6.5	16.7	13.8
<i>Muricea fruticosa</i>	10.2	13.2	11.8	2.4	4.8	3.8	7.9	16.9	13.1
<i>Neverita lewisii</i> egg case	10.1	15.7	11.5	1.9	5.7	3.5	6.3	20.9	12.0
<i>Octopus californicus</i>	10.6	13.2	11.2	2.9	5.5	3.5	9.8	19.4	11.9
<i>Octopus rubescens</i>	10.2	11.4	10.8	2.5	3.5	3.0	8.4	11.9	10.2
<i>Ophiodon elongatus</i>	10.1	11.0	10.6	2.3	3.3	3.0	7.6	11.1	10.0
<i>Ophiura luetkeni</i>	9.9	13.7	11.7	1.9	5.5	3.7	6.2	19.7	12.8
<i>Orthasterias koehleri</i>	10.8	13.1	11.7	2.9	4.6	3.6	9.8	16.3	12.5
<i>Oxyjulis californica</i>	14.0	14.2	14.1	4.8	5.7	5.2	17	20.6	18.6
<i>Pagurus armatus</i>	11.0	11.5	11.3	2.8	3.5	3.1	9.4	11.9	10.7
<i>Panulirus interruptus</i>	10.3	12.3	11.6	2.4	4.1	3.5	7.9	14.2	12.1
<i>Paralabrax clathratus</i>	10.8	–	–	3.4	–	–	11.6	–	–
<i>Paralichthys californicus</i>	10.1	13.1	11.1	2.0	5.5	3.6	6.8	19.4	12.1
<i>Parastichopus californicus</i>	10.1	14.3	11.3	2.0	6.0	3.6	6.8	21.5	12.4
<i>Parastichopus parvimensis</i>	10.4	13.9	11.5	2.2	5.7	3.9	7.4	20.2	13.2
<i>Parazoanthus lucificum</i>	9.9	14.0	11.0	2.0	5.8	3.2	6.8	20.7	10.8
<i>Patiria miniata</i>	10.1	14.0	11.2	2.2	5.7	3.4	7.5	20.5	11.6
<i>Pegea confoederata</i>	11.0	14.9	13.0	3.4	6.0	4.9	11.6	21.7	17.3
<i>Pelagophycus porra</i>	14.0	–	–	5.7	–	–	20.2	–	–
<i>Phacellophora camtschatica</i>	10.7	10.7	10.7	3.2	3.2	3.2	10.8	10.8	10.8
<i>Phyllactis</i> spp.	9.9	13.3	11.0	1.9	4.6	3.1	6.3	16.0	10.5
<i>Pisaster giganteus</i>	11.0	15.6	13.0	3.2	5.7	4.4	10.7	20.9	15.4
<i>Pleurobranchaea californica</i>	10.7	13.6	11.7	3.0	5.3	3.8	10.2	18.6	13.1
<i>Polyclinum planum</i>	9.9	13.9	11.0	2.0	5.7	3.2	6.5	20.3	11.0

Continued

Table 3. continued

Species	Temperature (°C)			[Oxygen] (ml l ⁻¹)			[Oxygen] (kPa)		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean
<i>Ptilosarcus gurneyi</i>	10.1	12.9	11.5	1.9	4.8	3.7	6.2	16.4	12.7
<i>Pyrosoma atlanticum</i>	11.3	12.2	11.7	3.5	4.5	4.0	11.8	15.5	13.6
<i>Rhacochilus vacca</i>	10.7	14.0	11.5	3.2	4.8	3.6	10.9	17.0	12.4
<i>Rhinogobiops nicholsii</i>	10.0	14.2	11.5	2.1	5.9	3.7	7.0	21.0	12.8
<i>Scorpaena guttata</i>	9.9	11.6	10.9	2.1	4.6	3.2	6.9	15.8	10.8
<i>Sebastes auriculatus</i>	11.7	11.7	11.7	3.7	3.7	3.7	12.6	12.6	12.6
<i>Sebastes melanops</i>	12.1	12.2	12.2	4.7	4.8	4.7	16.2	16.7	16.4
<i>Sebastes miniatus</i>	10.1	12.2	10.9	2.2	4.8	3.1	7.4	16.7	10.4
<i>Sebastes nigrocinctus</i>	10.1	–	–	2.4	–	–	7.9	–	–
<i>Sebastes paucispinis</i>	10.1	14	11.0	2.2	4.8	3.2	7.4	17.0	10.8
<i>Sebastes rosaceus</i>	10.1	11.4	10.8	2.2	4.5	3.2	7.4	15.4	10.8
<i>Sebastes rubrivinctus</i>	10.1	14.0	11.1	2.3	4.8	3.5	7.9	17.0	12.0
<i>Sebastes semicinctus</i>	9.6	12.2	11.0	1.9	4.8	3.3	6.2	16.7	11.1
<i>Sebastes serranoides</i>	10.7	11.6	11.1	2.9	3.6	3.2	9.7	12.1	10.9
<i>Sebastes serriceps</i>	11.2	14.0	12.6	3.1	4.8	3.9	10.5	17.0	13.7
<i>Sebastes</i> sp.	10.1	14.0	11.1	2.2	4.8	3.4	7.4	17.0	11.5
<i>Sebastes umbrosus</i>	11.0	12.2	11.6	3.4	4.8	4.1	11.6	16.7	14.2
<i>Sebastes dallii</i>	11.2	11.5	11.3	3.1	3.7	3.2	10.6	12.4	11.0
<i>Semicossyphus pulcher</i>	10.4	14.0	11.8	2.3	5.7	4.0	7.8	20.3	13.8
<i>Styela montereyensis</i>	11.6	11.8	11.7	3.6	3.7	3.6	12.1	12.7	12.4
<i>Stylatula elongata</i>	9.9	14.2	11.4	2.0	5.9	3.6	6.7	21.1	12.3
<i>Stylissa stipitata</i>	9.9	12.7	10.7	2.0	5.1	2.8	6.5	17.8	9.7
<i>Synodus lucioceps</i>	9.9	15.8	11.6	2.0	5.8	3.8	6.5	21.4	13.0
<i>Tethya aurantia</i>	9.9	14.0	11.8	2.0	4.8	3.7	6.5	17.0	12.7
<i>Toxadocia</i> spp.	10.1	14.0	11.2	2.0	5.7	3.4	6.8	20.5	11.6
<i>Trachurus symmetricus</i>	14.0	–	–	4.8	–	–	17.0	–	–
<i>Virgularia californica</i>	9.9	13.4	11.0	1.9	5.5	3.2	6.2	19.6	11.0
<i>Xystreurys liolepis</i>	11.3	–	–	3.4	–	–	11.5	–	–
<i>Zalambius rosaceus</i>	10.3	11.9	11.0	2.0	4.8	3.5	6.8	16.5	12.1
<i>Zaniolepis frenata</i>	11.4	11.5	11.5	4.5	4.6	4.5	15.2	15.7	15.5
<i>Zaniolepis latipinnis</i>	10.6	11.9	11.4	2.9	4.7	4.1	9.7	16.4	14.0
<i>Zaniolepis</i> spp.	10.1	11.5	10.9	2.1	4.6	3.7	7.1	15.6	12.7
<i>Zapteryx exasperata</i>	12.6	–	–	4.4	–	–	15.2	–	–

Oxygen is provided in units of ml l⁻¹ and kPa for intercomparison with units used in other studies. Statistics for species observed only once are listed in the “Minimum” column.

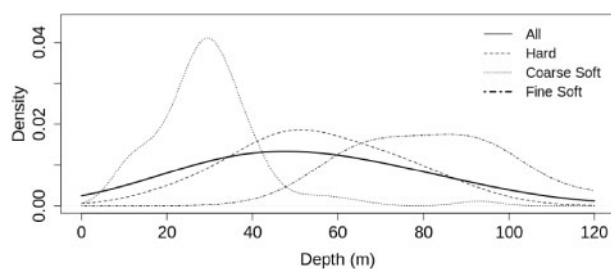


Figure 7. Probability density functions of habitat depths. Habitat types were discriminated using MCA of 16 habitat factors (5 grain size and 11 bedform factors) (see text for a description of the analysis and Table 2 for a list of habitat MCA scores). Hard bottom discriminated as $MCA1 < 0.02$, coarse soft bottom as $MCA2 \geq 0.017$, and fine soft bottom as $MCA2 \leq -0.007$.

Shelf seascape composition, the sizes, shapes, and the arrangement of shelf habitats, will likely affect community responses to anticipated de-oxygenation off southern California in a non-linear fashion. The sizes and patchwork distribution of shelf and shelf break habitats along the tectonically complex shelf off

southern California forces patterns of beta diversity and species abundance (Switzer *et al.*, 2016). Species occupy these patches in a non-linear fashion at scales much larger than the individual patches themselves, and species abundances among the patches vary with patch area in a non-linear fashion (Switzer *et al.*, 2016). Because of this, in addition to the knowledge of oxygen thresholds for individual species, predictions of species and community responses to future de-oxygenation should include knowledge of local and regional seascapes as species utilization of shelf habitats experience compression due to hypoxia. An example is the distribution and arrangement of hard bottom outcrops that are less abundant inshore of the shelf break off southern California where rockfish would have to escape given the onset of severe hypoxia. The alongshore gradient of increasing size and contiguousness of outcrops off San Diego and the concomitant non-linearity in species' utilization of the habitat patches (Switzer *et al.*, 2016) suggests that the effects of habitat compression (i.e. species shoaling patterns) will also be non-linear. Rockfish populations off San Diego would likely be adversely affected by habitat compression in a non-linear fashion relative to the degree of shoaling, increasing risks to their populations in a disproportionate manner relative to the benthic footprint of oxygen stress. Further work is

Table 4. Previously published effects of hypoxia for species and/or congeners observed in the present study.

Species	Life stage	Response	Reference
<i>Panulirus interruptus</i>	Stage 1 phylossoma	Inactive <1.4–1.7 ml l ⁻¹ DO	Belman and Childress (1973)
<i>Panulirus interruptus</i>	4–9 cm carapace length	QO ₂ reduction <2.5 ml l ⁻¹ DO	Winget (1969)
<i>Panulirus interruptus</i>	Adult	P _{crit} at 27°C = 1.86 ml l ⁻¹ DO P _{crit} at 20°C = 1.24 ml l ⁻¹ DO	Ocampo <i>et al.</i> (2003)
<i>Panulirus interruptus</i>	–	Significant increase in lactate under hypoxia (oxygen saturation 15%)	Ocampo <i>et al.</i> (2003)
<i>Haliotis rufescens</i>	5–10 mm shell length	Mortality in combination with decreased pH and DO of 3.5 ml l ⁻¹	Kim <i>et al.</i> (2013)
<i>Haliotis rufescens</i>	5–10 mm shell length	Mortality in combination with decreased pH and O ₂ of 4.46 ml l ⁻¹	Kim <i>et al.</i> (2013)
<i>Doryteuthis opalescens</i>	Paralarvae	Decreased hatch rate <1.05 ml l ⁻¹ DO	Zeidberg <i>et al.</i> (2012)
<i>Doryteuthis opalescens</i>	Adult	Giant axon activity and mantle contractions decreased and neuromuscular latency increased under severe hypoxia <1 ml l ⁻¹ DO	Li and Gilly (2019)
<i>Sebastes</i> sp.	Adult	Reduced home range for <i>Sebastes caurinus</i> <1.4 ml l ⁻¹ DO	Rankin <i>et al.</i> (2013)

Dissolved oxygen units have been converted as needed to ml l⁻¹ dissolved oxygen (DO) for ease of comparison.

needed to address how the effects of declining oxygen on shelf communities are modulated by the interaction of oxygen dynamics with seascape pattern, species mobility, behaviour, and species-specific oxygen tolerance to low oxygen.

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