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Ecophysiological limits to aerobic metabolism in hypoxia determine epibenthic distributions and energy sequestration in the northeast Pacific ocean

Jackson W. F. Chu,[1]* Katie S. P. Gale[2]
[1]Department of Biology, University of Victoria, Victoria, British Columbia, Canada
[2]Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, British Columbia, Canada

Abstract

Expansion of oxygen deficient waters (hypoxia) in the northeast Pacific Ocean (NEP) will have marked impacts on marine life. The response of the resident communities will be a function of their ecophysiological constraints in low oxygen, although this remains untested in the NEP due to a lack of integrative studies. Here, we combine in situ surveys and lab-based respirometry experiments were conducted on three indicator species (spot prawn *Pandalus platyceros*, slender sole *Lyopsetta exilis*, squat lobster *Munida quadrispina*) of seasonally hypoxic systems in the NEP to test if metabolic constraints determine distributions and energy sequestration in a hypoxic setting. These experiments were integrated with a global review of critical oxygen levels (O_2^{crit}; lower threshold of aerobic metabolism) for crustaceans to determine if O_2^{crit}-based hypoxia thresholds are different among ocean basins. Our results show that species-specific differences in O_2^{crit} and standard metabolic rates (1) determine the lowest environmental oxygen ($[O_2]_{env}$) at which in situ populations occur, (2) result in disproportionate shifts in distributions among co-occurring species during summer hypoxia expansion events, and (3) characterize shifts in megafaunal community respiration rates due to marked spatio-temporal variability in $[O_2]_{env}$. Our results show that O_2^{crit}-based hypoxia thresholds are significantly lower in the East Pacific Ocean relative to other major ocean basins, which suggests that the physiological response of local fauna to deoxygenation can be determined by the natural variability and oxygen exposure in a region. In order to establish realistic predictions on the biological consequences of marine deoxygenation, we suggest integrating metabolism-based traits to calculate hypoxia thresholds for marine ecosystems.

In the past 50 years, oxygen deficient waters of oxygen minimum zones (OMZs) (Stramma et al. 2008; Keeling et al. 2010) have expanded their global coverage by 4.5 million km^2 (Stramma et al. 2010). Shoaling of the upper OMZ boundaries is linked to habitat compression, large-scale redistribution of fish communities, and the mass mortality of commercially valuable and other species (Grantham et al. 2004; Koslow et al. 2011; Stramma et al. 2012). Global models predict that a continued linear decrease in oceanic oxygen content will result in a 12–24% reduction in the biomass of global fish stocks by 2050 (Cheung et al. 2013) and a 20% loss of viable habitat by 2100 (Deutsch et al. 2015). However, there is uncertainty in the magnitude of future oceanic oxygen loss (Bopp et al. 2013). Furthermore, lack of field observations at the community level and insufficient integration of physiological principles reduces confidence in the predictions of the ecosystem-level response to deoxygenation (IPCC 2013).

The consequences of multidecadal oxygen deficiency include a decline in local biomass through emigration, decreased growth, altered food-web dynamics, and death. This loss of ecosystem function is furthered by reductions in biologically controlled nutrient cycling and energy transferred to higher trophic levels (Diaz and Shaffner 1990; Ekau et al. 2010). Cumulatively, these negative impacts translate into a net loss in ecosystem services (Diaz and Rosenberg 2008), which is of global societal importance as almost all food provisions created by marine ecosystems require sufficient oxygen levels to sustain the growth and production of organisms (Diaz et al. 2013). To support better projections regarding the magnitude of ecosystem function lost to oxygen deficiency, a standardized approach should integrate

*Correspondence: jwfchu@gmail.com

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metabolism-based measurements made at higher trophic levels and grounded within a multispecies framework.

The mechanism behind the response of marine ecosystems to decreases in environmental oxygen (hereafter termed $[O_2]_{env}$) is directly linked to the physiology of the resident species (Pörtner and Farrell 2008). In aquatic ectotherms, the metabolic relationship between oxygen consumption and $[O_2]_{env}$ is non-linear with an ecophysiological threshold occurring at species-specific critical oxygen levels (Dejours 1975), hereafter termed O_2^{crit}. In $[O_2]_{env}$ above O_2^{crit}, organisms can regulate a constant rate of oxygen consumption that is independent of changes in $[O_2]_{env}$. O_2^{crit} also marks the lowest $[O_2]_{env}$ at which a resting, unfed organism can maintain a constant rate of aerobic metabolism and marks the transition to anaerobic processes. In $[O_2]_{env}$ below O_2^{crit}, oxygen consumption linearly conforms to changes in $[O_2]_{env}$; metabolism is negatively affected through reduction in oxygen transport and delivery efficacy (Pörtner and Farrell 2008). Because aquatic ectotherms naturally occur close to their O_2^{crit} (Childress 1975; Childress and Seibel 1998; Seibel 2011), O_2^{crit} values can: (1) be used as indicators of hypoxia tolerance (Pörtner and Farrell 2008), (2) link changes in $[O_2]_{env}$ with higher-level energy transfer (Pörtner and Knust 2007), and (3) be used to predict large-scale shifts in species distributions in response to deoxygenation (Deutsch et al. 2015).

Current global hypoxia thresholds (e.g., 1.4 mL L^{-1}, Rabalais et al. 2010) used in the literature are uncoupled from the biology of the resident species (Seibel 2011) and do not account for the differences in oxygen content among major ocean basins (Hofmann et al. 2011). As a result, general thresholds are biased toward Atlantic systems, where a majority of past hypoxia research has been performed, and fail to predict in situ species distributions in areas with historically lower oxygen levels such as the northeast Pacific Ocean (Chu and Tunnicliffe 2015a). In such regions, benthic communities are naturally found in lower $[O_2]_{env}$ (Keller et al. 2010, 2015; Chu and Tunnicliffe 2015a) and respond to hypoxia at much lower oxygen levels than what general thresholds would suggest (Sperling et al. 2016). Although the metabolic relationship between oxygen demand and $[O_2]_{env}$ availability is well-established, few studies have applied O_2^{crit} as a tool for assessing ecological response of in situ distributions (Deutsch et al. 2015). O_2^{crit} values remain unknown for most marine species (Seibel and Childress 2013) and are uncoupled from field abundance data which rarely have in situ, concomitant measurements of $[O_2]_{env}$. Furthermore, no integrative datasets exist for the Pacific Ocean—areas of which are the most susceptible to aerobic habitat loss in the future (Deutsch et al. 2015).

Here, we present a study from the northeast Pacific Ocean in which we determine if hypoxia thresholds derived from physiological traits can predict the in situ biological response of benthic communities influenced by oxygen deficiency. First, we combine data from oceanographic oxygen profiles, field distributions, and lab-based respirometry to experimentally test the applicability of using metabolic traits to assess changes in the distributions and aerobic energy sequestration among three co-occurring megafaunal species exposed to seasonally variable oxygen regimes. To account for the scaling relationship between metabolism and body mass (Schmidt-Nielsen 1984), we measure O_2^{crit} and standard metabolic traits across the full range of adult size classes and develop specific metabolic scaling coefficients for each of our focal species. We report on the first measurements of metabolic rate and O_2^{crit} for one of these species, the slender sole *Lyopsetta exilis*. Second, we test if hypoxia thresholds calculated from O_2^{crit} reveal regional differences in hypoxia tolerance that explain why general thresholds fail to predict in situ distributions in the northeast Pacific Ocean. We calculate and compare hypoxia thresholds for major ocean basins using a global meta-analysis based on O_2^{crit} values reported for crustaceans, the most common taxonomic group in hypoxia tolerance studies (Vaquer-Sunyer and Duarte 2008). Ultimately, our results highlight the importance of using metabolism-based traits to assess the biological consequences to oceanic oxygen loss.

Materials and methods

Field mapping animal distributions to $[O_2]_{env}$

Saanich Inlet (Fig. 1a) is a highly productive basin on Vancouver Island, British Columbia, Canada (Grundle et al. 2009). A shallow sill (75 m depth) restricts deep water circulation and exchange with source waters outside the inlet. Near-anoxia ($\sim$ 0 mL L^{-1}) to severe hypoxia ($<$ 0.5 mL L^{-1}) characterizes the deepest parts ($>$ 200 m) of the inlet and normoxia ($>$ 1.4 mL L^{-1}) occurs in the shallower depths ($<$ 60 m). Deoxygenation expands the volume of hypoxic and severely hypoxic deep waters into midwater depths over the course of the summer (Chu and Tunnicliffe 2015a) before renewal of deep waters occurs in the fall (Anderson and Devol 1973). In 2013, remotely operated vehicle (ROV) imagery surveys repeated the same benthic transect line in Saanich Inlet at three times of the hypoxia cycle: before deoxygenation (May), after deoxygenation (September) and at the onset of reoxygenation (October) (Chu and Tunnicliffe 2015a). This $\sim$ 3 km transect begins mid-inlet ($\sim$ 190 m bottom depth), transitions through the zones of severe hypoxia and hypoxia ($<$ 1.4 mL L^{-1}), and ends in the normoxic, shallow depths ($\sim$ 45 m).

Dozens of species common to the northeast Pacific Ocean occur in Saanich Inlet (Chu and Tunnicliffe 2015a). Methods and data on the mapping of the distribution, density, and movement of the associated epibenthic species assemblage observed along transects are published in Chu and Tunnicliffe (2015a, b). Epibenthic animal distributions were mapped to their in situ environmental oxygen ($[O_2]_{env}$),

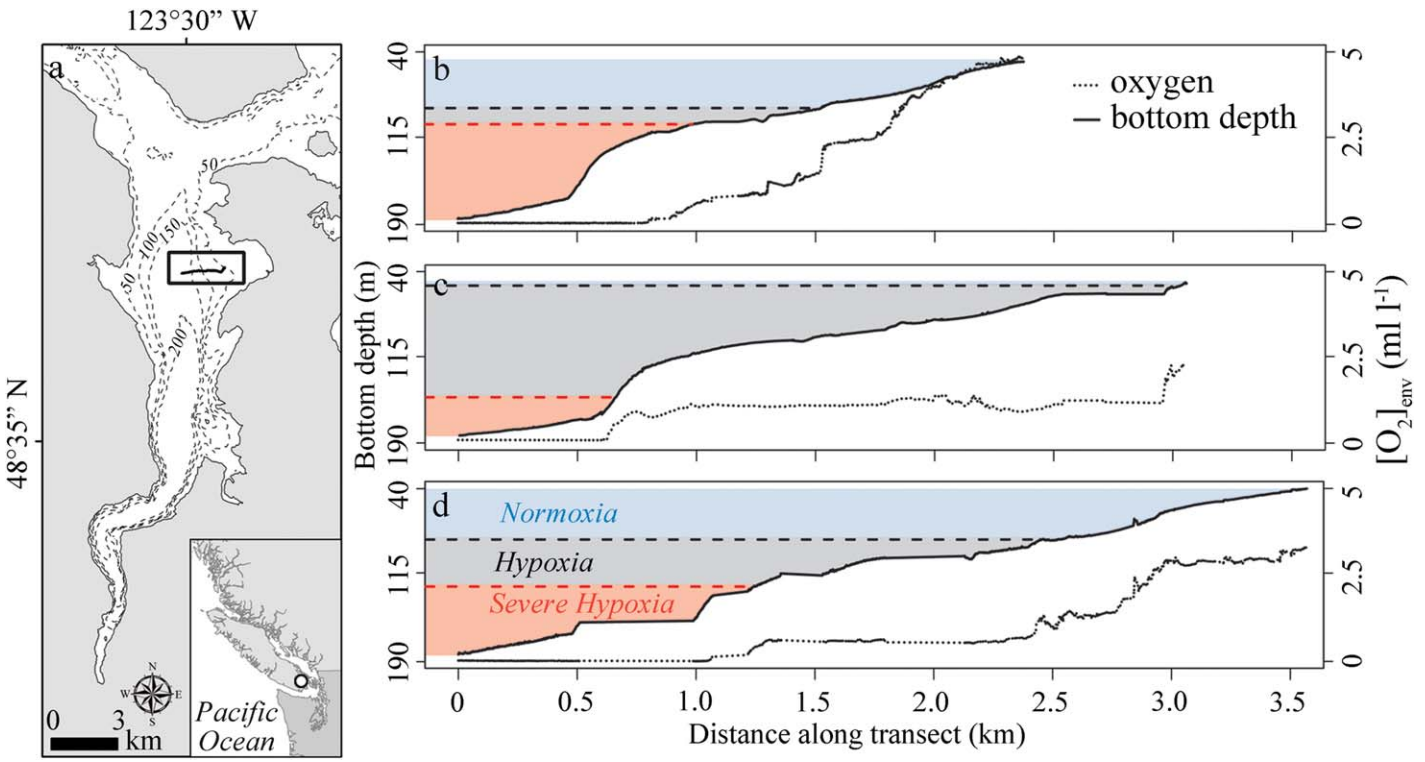

Fig. 1. Seasonal hypoxia cycle of our study site. (**a**) In situ animal abundances relative to environmental oxygen ($[O_2]_{env}$) were measured along a benthic transect line in Saanich Inlet, Vancouver Island, British Columbia, Canada (inset circle). Seasonal deoxygenation events in the inlet creates zones of severe hypoxia (< 0.5 mL L^{-1}), hypoxia (< 1.4 mL L^{-1}), and normoxia (> 1.4 mL L^{-1}) that expand and contract throughout the year. In 2013, remotely operated vehicles equipped with oxygen sensors and cameras repeated a bottom transect at three stages of the hypoxic cycle: (**b**) May, before summer deoxygenation and when steep oxygen gradients were evident, (**c**) September, after deoxygenation-induced expansion of hypoxic waters, and (**d**) October, during re-oxygenation and re-establishment of the steep oxygen gradient at the site. *In situ* oxygen data from Chu and Tunnicliffe (2015*b*).

which was measured within 1 m of the seafloor during transects. Concurrent with the seasonally shifting oxycline, resident species show marked shifts in their density and spatial arrangement within the hypoxia transition zone. Structure of the whole community is primarily driven by the abundance of key mobile species and their fidelity to specific oxygen regimes (Chu and Tunnicliffe 2015a). The commercially important spot prawn *Pandalus platyceros* (Fig. 2a) is strongly associated with normoxic conditions while squat lobster *Munida quadrispina* (Fig. 2b) and slender sole *Lyopsetta exilis* (Fig. 2c) are strongly associated with severely hypoxic conditions. The in situ oxygen occurrence data for these three species at each phase of the 2013 hypoxia cycle were used to assess whether distribution patterns in the field were correlated to species-specific O_2^{crit}, which were experimentally determined in the laboratory. Values of O_2^{crit} are reported in units of concentration ($[O_2]^{crit}$, mL L^{-1}) and the equivalent partial pressure (pO_2^{crit}, kPa).

Lab-based respirometry experiments

Adult spot prawn, squat lobster, and slender sole were captured from Saanich Inlet, British Columbia, Canada. Spot prawns (5–39 g) were caught at 70 m depth by shrimp traps in April 2014. Squat lobsters (wet weight, 2–20 g) and slender sole (6–68 g) were collected by a bottom otter trawl on the CCGS JP Tully at 100 m depth in October 2013 and September 2014. Animals were transported to holding tanks at the Outdoor Aquatics Unit at the University of Victoria within 2 h of capture and acclimated to the recirculating sea water conditions for 1 month before experimentation. For the duration of this study, animals were kept in constant darkness, temperature (9 ± 1°C), and salinity (31–32‰) under oxygen saturated conditions. Spot prawn and squat lobster were fed a weekly diet of frozen fish and cat food. Slender sole were fed a daily mixed diet of fish feed (Skretting GEMMA) supplemented with frozen krill and bloodworms. Animals were caught under a scientific license (XR 356 2013) issued by Fisheries and Oceans Canada. All experiments were conducted according to guidelines set out by the Canadian Council for Animal Care and protocols approved by the University of Victoria Animal Care Committee.

Standard respirometry protocols were used to measure mass-specific oxygen consumption rates (MO_2) and O_2^{crit} (Pörtner et al. 2010). Data were collected per second using a

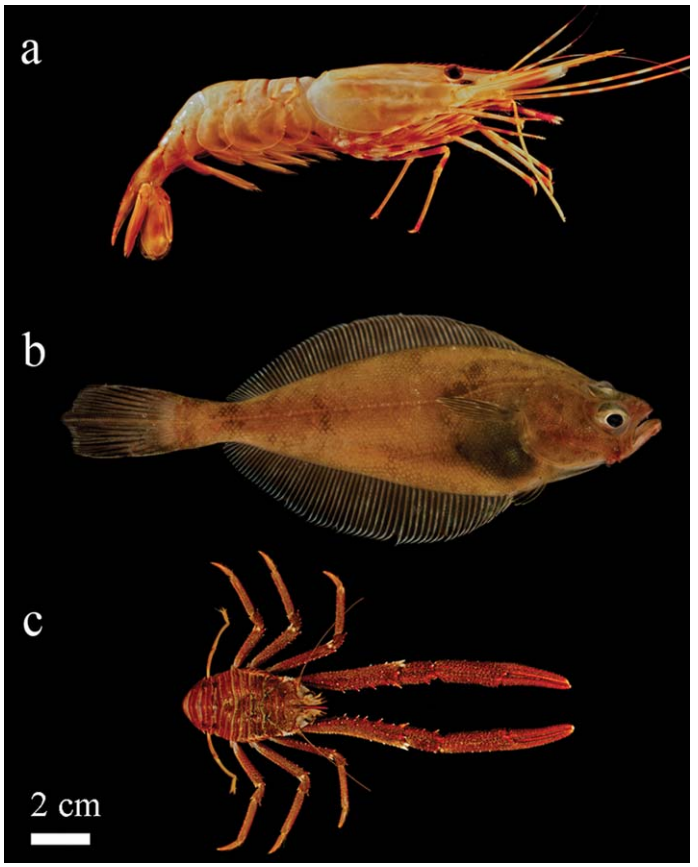

Fig. 2. Focal species of this study: (**a**) spot prawn *Pandalus platyceros*, (**b**) slender sole *Lyopsetta exilis*, and (**c**) squat lobster *Munida quadrispina*.

laptop running Autoresp software and dissolved oxygen was measured using a DAQ-PAC-G4 4-channel respirometry system and MINI-DO galvanic oxygen electrodes (Loligo Systems, Denmark). In all experiments, animals were first removed from the general population and isolated without food for 24 h. Individuals were then weighed and moved into either a 1.7 or 3.5 L respirometry chamber that was submerged in a 60 L aquarium. This larger aquarium functioned as both a water bath and the source of oxygen-saturated seawater for intermittent flushing of the respirometry chamber. Chambers were custom-built to have two pairs of input and output ports to accommodate both closed and flow-through respirometry methods. To prevent the buildup of oxygen gradients, a closed loop connected an external flow-through probe vessel to a submersible pump that continuously recirculated water inside the respirometry chamber during experiments. The entire volume of sea water in the system was exchanged weekly to prevent accumulation of metabolites. To mimic natural habitat conditions, darkness in the respirometry chambers was maintained with black plastic bags, salinity was kept constant at 35‰, and water temperature was kept constant at 9°C using chillers. Following manufacturer protocols, oxygen electrodes were calibrated using a 2-point system: a saturated sodium sulphite solution for 0% oxygen saturation and 100% oxygen saturated sea water fully aerated with air stones. Electrodes were recalibrated every 2 weeks to prevent problems with long-term sensor drift.

Determining O_2^{crit} and standard metabolic rates (SMR)

Species-specific O_2^{crit} values were determined for spot prawn ($n = 19$), slender sole ($n = 34$), and squat lobster ($n = 25$) using closed respirometry. In each O_2^{crit} experiment, an isolated individual was first acclimated to the respirometry chamber in flow-through conditions for 12–24 h. Flow-through was then stopped to begin the experiment. MO_2 (oxygen consumption rate) was calculated from the oxygen consumed over sequential 7 min intervals for spot prawn and 10 min for slender sole and squat lobster. Experiments ended when MO_2 reached zero. Because the three focal species followed the general oxyregulation response curve, O_2^{crit} was calculated from the intersection between the linear regressions of the oxyregulation and oxyconformation phases on the plot of MO_2 vs. $[O_2]_{env}$ for each individual animal (Yeager and Ultsch 1989). O_2^{crit} and the slopes of the two linear regressions were calculated from each experiment using piece-wise regression analysis with the "segmented" package in R (Muggeo 2008).

Because MO_2 can quickly deplete oxygen and limit the duration of an experiment in closed conditions, mass-specific standard metabolic rates (SMR) for spot prawn ($n = 20$), slender sole ($n = 34$), and squat lobster ($n = 32$) were determined using intermittent flow-through respirometry. This method maintains $[O_2]_{env}$ above O_2^{crit} and can extend duration of metabolism-based experiments. In each SMR experiment, an isolated individual was first acclimated to the respirometry chamber under flow-through conditions for 12–24 h before data collection began. Flush/wait/measure intervals were 300/120/420 seconds for spot prawn, 420/120/360 seconds for slender sole, and 300/120/600–900 seconds for squat lobster. Relatively longer measurement periods were required for squat lobster because of their lower MO_2. Experiments lasted for 24 h for slender sole and 24–36 h for spot prawn and squat lobster. Background respiration was measured using one hour blank controls, which were subtracted from animal MO_2 measurements. To prevent brief periods of spontaneous activity from skewing calculations, the percentile method was used to calculate the SMR associated with each individual experiment. This method takes the average of the lowest 10% of the MO_2 measurements in an experiment after exclusion of outliers. Outliers were defined as mean $2 \pm$ s.d. of the lowest 10% of MO_2 values (Clark et al. 2013).

To account for the variance associated with each individual trial (closed and intermittent), the variability associated with metabolism measurements, and the linear scaling relationship of body size with SMR, random-effects meta-analyses were used with body mass as a moderator to determine average O_2^{crit}, oxyconformation slope, oxyregulation slope, mass-specific SMR, and mass-corrected SMR for each species.

Restricted maximum-likelihood estimation was used in the mixed-effects models; mean and standard error for O_2^{crit}, slope of the oxyconformation phase, slope of the oxyregulation phase, and SMR were used as random effects and wet weight was used as a moderator. Meta-analyses were done using the "metafor" package in R (Viechtbauer 2010). Two metabolic scaling relationships were calculated for each species using the formula $Y = aM^b$, where Y is either mass-specific (mg O_2 kg^{-1} h^{-1}) or mass-corrected (mg O_2 h^{-1}) oxygen consumption rates and M = wet body mass (kg). The constant *a* and scaling exponent *b* are calculated as the intercept and slope of a least squares linear regression after logarithmic transformation of both variables (Clarke and Johnston 1999). Scaling exponents are typically −0.25 (mass-specific MO_2) and 0.75 (mass-corrected MO_2) for most animals (Schmidt-Nielsen 1984).

Mapping aerobic habitat in the field

Lab-derived metabolic measurements were integrated with the in situ distributions mapped for each of the three focal species (Chu and Tunnicliffe 2015b) to assess if their metabolic traits could be used to predict population-level responses to expanding hypoxia. For each focal species, bootstrap resampling tests were used to test if field populations were constrained to $[O_2]_{env}$ above their species-specific O_2^{crit}. For a bootstrap test, a resampled distribution of differences ($n = 1000$ samples) was generated by taking a randomly chosen value from the vector of in situ oxygen occurrences in an ROV survey period (May, Sep, Oct) and subtracting it from the vector of lab-determined O_2^{crit} values for each focal species. The distribution of differences was then compared with a null distribution (centred on zero) to determine if in situ oxygen occurrences for each species at each phase of the hypoxia cycle were significantly different from its O_2^{crit}; that is whether the O_2^{crit} were lower than the $[O_2]_{env}$ at which field populations occurred. For each species, bootstrap tests were done at each survey period to determine if field populations were also redistributing according to the spatially shifting $[O_2]_{env}$ profile. In comparisons where the null was rejected ($p < 0.05$), the mean-value of the distribution of differences was interpreted as the average "oxygen distance" or the difference between the $[O_2]_{env}$ where populations occurred relative to their species-specific O_2^{crit}.

To illustrate the impact of expanding hypoxia on aerobic respiration in the field, the standard metabolic rates and O_2^{crit} measured for each focal species were integrated with their in situ distributions and oxygen occurrences at each phase of the 2013 hypoxia cycle. Species-specific, mass-corrected SMR calculated from the meta-analyses were converted to units of energy using 20.1 kJ of energy sequestered per liter of oxygen consumed during aerobic respiration (Schmidt-Nielsen 1984). Energy values were used to represent the individual-based "average aerobic respiration rate," which was then multiplied by the in situ count data for each species to calculate the aerobic respiration rate for each field population. Individuals occurring in $[O_2]_{env}$ below their species-specific O_2^{crit} were considered functionally anaerobic and excluded from the aerobic respiration rate calculated for their respective field populations. Calculations were done for each species at each ROV survey period (May, Sep, Oct) and then spatially mapped to the $[O_2]_{env}$ profile to determine the proportional contribution of each population to the total aerobic respiration rate (sum total of the three focal species) at each phase of the hypoxia cycle.

Regional hypoxia thresholds

Hypoxia thresholds were calculated using O_2^{crit} values from major ocean basins to empirically assess if hypoxia tolerance is different among regions. A global dataset of O_2^{crit} values was compiled for marine crustaceans, which builds on data and methods provided in similar meta-analyses (Vaquer-Sunyer and Duarte 2008; Storch et al. 2014; Deutsch et al. 2015). However, unlike past studies that aimed to compare among taxa, the primary objective of this meta-analysis was to assess if differences in hypoxia tolerance exist among regions. Thus, only crustaceans were used because (1) large differences in hypoxia tolerance occur between major taxonomic groups, and (2) a majority of metabolism studies has historically been performed on crustaceans (Vaquer-Sunyer and Duarte 2008). Web of Science was searched with the Boolean parameters: (crustacea* or crab or lobster or shrimp) AND (pcrit or "critical oxygen" or oxyconform* or oxyregulat* or o2crit or "o2 crit") OR [(LC50 or LD50 or "lethal dose" or "lethal concentration") AND (oxygen or o2 or anoxi* or hypoxi*)]. Because O_2^{crit} values were often not linked to keywords in older literature, keyword searches were supplemented with manual methods that included searching through reference lists from metabolic scaling meta-analyses (Glazier 2005; Brey 2010) and respirometry equipment manufacturers (www.loligosystems.com). Temperature, salinity, animal weight, life stage, and location of animal collection were recorded with each associated O_2^{crit} record.

All O_2^{crit} values were converted into $pO2^{crit}$ (kPa) or $[O_2]^{crit}$ (mL L^{-1}) and in cases where salinity was not reported, a value of 32 PSU was adopted for unit conversions (mean from all reports ≥ 30 PSU, Storch et al. 2014). O_2^{crit} values were spatially grouped into seven major oceanic regions: East Pacific, West Pacific, East Atlantic, West Atlantic, South Pacific, Indian, and Southern (Antarctic); no values were available for the Arctic. All O_2^{crit} values extracted from the literature are reported (Supporting Information Table 1). However, to compare O_2^{crit} between ocean basins, only one O_2^{crit} per species per study location was used. In cases where a study measured multiple O_2^{crit} for the same population, only the lowest reported O_2^{crit} was used (Storch et al. 2014) because higher O_2^{crit} in a species were usually the result of responses to cumulative stressors.

Because species harvested in fisheries (hereafter, "exploited species") are often targeted for their relatively larger size, uneven representation of exploited species among regions may result in a bias when calculating regional hypoxia thresholds based on metabolic traits. Therefore, separate analyses were run for exploited and non-exploited species to determine if exploited species had generally higher O_2^{crit} thresholds (are more hypoxia sensitive) and if exploitation status could influence potential differences in hypoxia thresholds among oceans. Species were queried in the Food and Agriculture Organization of the United Nations (FAO) Global Capture Production database (www.fao.org), which includes annual weights, by country or region, for all species reported in commercial, recreational, industrial, or subsistence fisheries; species with any reported catch since 1950 were designed as "exploited". For all species not in the FAO database, exploitation status was assessed using SeaLifeBase (www.sealifebase.org) and a brief literature search.

Pairwise permutation tests were used to assess if O_2^{crit} differed between ocean basins; *p*-values were adjusted for multiple comparisons using the false discovery rate method (Mangiafico 2015). The 95% confidence intervals were generated for each region using bias-corrected and accelerated (BCa) bootstrap resampling. This comparison was separately done for the $[O_2]^{crit}$ and pO_2^{crit} values to determine if results were dependent on choice of oxygen units. Separate comparisons among major ocean basins were also done with the subsets of exploited and non-exploited species.

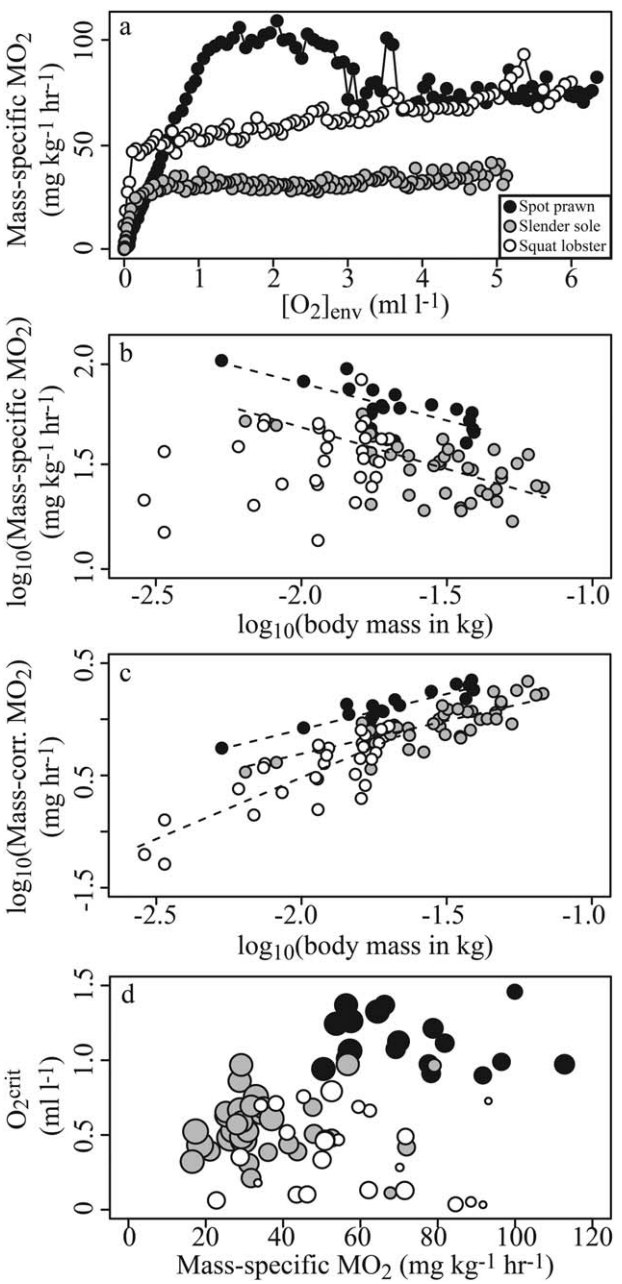

Fig. 3. Lab-derived species-specific relationships between oxygen consumption and environmental oxygen ($[O_2]_{env}$). (**a**) Examples of a single oxyregulation curve for spot prawn (14.3 g, wet weight), slender sole (20.3 g), and squat lobster (14.8 g). Each species regulated oxygen consumption (mass-specific MO_2) independently of changes in ambient oxygen in the $[O_2]_{env}$ range above their species-specific O_2^{crit}. (**b–c**) Linear relationships between oxygen consumption and body mass. (b) Mass-specific MO_2 decreased with increasing body mass for spot prawn and slender sole ($p < 0.05$) but not squat lobster. (c) Mass-corrected MO_2 increased with increasing body mass in all three species ($p < 0.05$). Table 1 summarizes species-specific scaling formulas and Table 2 summarizes metabolic scaling coefficients. (**d**) Relationship between O_2^{crit}, mass-specific MO_2, and body mass. Regulated MO_2 was calculated as the mean of the regulated MO_2 measurements for each O_2^{crit} trial. Circle size scales to body mass. No significant relationships were resolved between O_2^{crit} and regulated (mass-specific) MO_2 or O_2^{crit} and body mass (plot not shown) for any of the three species (all $p > 0.05$).

Results

Species-specific hypoxia tolerance and oxygen requirements

Each species was able to regulate oxygen consumption (MO_2) within a range of $[O_2]_{env}$ and O_2^{crit} was resolved in each species (Fig. 3a). In general, mass-specific MO_2 linearly decreased with increasing body mass (Fig. 3b) and mass-corrected MO_2 increased with increasing body mass (Fig. 3c) for all three species. Linear relationships between mass-specific MO_2 and body mass were significant for spot prawn ($p < 0.001$, $R^2 = 0.57$) and slender sole ($p < 0.001$, $R^2 = 0.52$) but not for squat lobster ($p > 0.05$, $R^2 = 0.04$) (Table 1). Relationships between mass-corrected MO_2 and body mass were significant for spot prawn ($p < 0.001$, $R^2 = 0.79$), slender sole ($p < 0.001$, $R^2 = 0.66$), and squat lobster ($p < 0.001$, $R^2 = 0.64$) (Table 1). Metabolic scaling exponents were summarized as 95% confidence intervals (95CI) to assess if metabolism of each focal species scaled to the general −0.25 (mass-specific MO_2) and 0.75 (mass-corrected MO_2) exponents known for

Table 1. Scaling relationships between oxygen consumption rates and body mass. Goodness of fit (R^2) for each scaling relationship is in parentheses next to each formula. Asterisks denote a significant linear relationship between a response variable and body mass ($\alpha = 0.05$).

			†Response variable (Y)	
Species	*n*	Body mass range (g)	Mass specific MO_2 (mg O_2 kg^{-1} h^{-1})	Mass corrected MO_2 (mg O_2 h^{-1})
Spot prawn	20	5.3–39.2	$1.17M^{-0.37}$ (0.57)*	$1.17M^{0.63}$ (0.79)*
Slender sole	34	6.4–67.8	$0.87M^{-0.41}$ (0.52)*	$0.87M^{0.59}$ (0.66)*
Squat lobster	32	2.3–20.0	$2.01M^{0.24}$ (0.04)	$1.68M^{\dagger 1.1}$ (0.64)*

†Calculated using formula $Y = aM^b$, where Y is either mass specific (mg O_2 kg^{-1} h^{-1}) or mass-corrected (mg O_2 h^{-1}) oxygen consumption rates (MO_2), M = wet body mass (kg), *a* and *b* are intercept and slope of least square linear regression after log-transformation of both variables (Clarke and Johnston 1999).

Table 2. Confidence limits of the scaling coefficients relating oxygen consumption rates to body mass. Sample sizes and body mass range are given in Table 1.

	Metabolic scaling exponents (95% CI)	
Species	Mass specific metabolic rate (mg O_2 kg^{-1} h^{-1})	Mass corrected metabolic rate (mg O_2 h^{-1})
Spot prawn	−0.53 to −0.21	0.47 to 0.79
Slender sole	−0.55 to −0.26	0.44 to 0.74
Squat lobster	−0.04 to 0.53	0.79 to 1.40

most organisms. Of the three focal species, only spot prawn followed general scaling patterns. Exponents calculated for mass-specific MO_2 and mass-corrected MO_2 were generally lower in slender sole and higher in squat lobster (mean values in Table 1, 95CI in Table 2). No significant linear relationships were resolved between O_2^{crit} and MO_2 (Fig. 3d) or O_2^{crit} and body mass for any of the three species (all, $p > 0.05$).

Although oxyregulation occurred among species (Fig. 3a) and the metabolic scaling relationships were similar for the three species, hypoxia tolerance and aerobic requirements differed. Mean O_2^{crit} for spot prawn was 1.01 mL L^{-1} or 3.2 kPa ($n = 19$, 95CI = 0.79–1.23 mL L^{-1}), substantially higher than the mean O_2^{crit} of 0.36 mL L^{-1}or 1.1 kPa for slender sole ($n = 34$, 95CI = 0.24–0.47 mL L^{-1}) and 0.21 mL L^{-1} or 0.7 kPa for squat lobster ($n = 25$, 95CI = 0.04–0.39 mL L^{-1}). Because of differences in mean O_2^{crit}, the oxyconformation rate also differed among species. Mass-specific MO_2 declined by 83.9, 115.2, and 537.1 mg O_2 kg^{-1} h^{-1} in spot prawn, slender sole, and squat lobster, respectively, for every mL L^{-1} decrease in $[O_2]_{env}$ until zero (Table 3). Because oxyconformation rates decrease toward zero, larger values are associated with low $[O_2]_{crit}$ and result in greater shifts in MO_2 per unit change in $[O_2]_{env}$. Similarly, SMR was substantially higher in spot prawn (mean effect = 74.7 mg kg^{-1} h^{-1}) compared with slender sole (35.1 mg kg^{-1} h^{-1}) and squat lobster (39.3 mg kg^{-1} h^{-1}).

Metabolic suppression may have partially reduced the overall oxygen requirements of slender sole and squat lobster; both had positive oxyregulation slopes (decreasing MO_2 with decreasing O_2) (Table 3, both 95CI > 0) compared with spot prawn (95CI overlaps with zero). Further evidence of metabolic differences between spot prawn and squat lobster was in their potential to sustain anaerobiosis. All spot prawn died within a few hours when exposed to $[O_2]_{env} < O_2^{crit}$, compared with no mortality occurring in squat lobster even after individuals were exposed to anoxia ($[O_2]_{env}$ = zero), with no measureable MO_2, for up to 36 h (lethal exposure to anoxia was not tested with squat lobster). Prolonged exposure to anoxia was not tested with slender sole.

Changes in field distributions and total aerobic respiration rates

Physiological differences in hypoxia tolerance and oxygen requirements among species corresponded to the in situ response to changing $[O_2]_{env}$ (Fig. 4). Large shifts in the average in situ $[O_2]_{env}$ at which the spot prawn population occurred implies hypoxia avoidance and migration in response to the expanding and contracting hypoxic zone. In May, the lowest $[O_2]_{env}$ at which spot prawn occurred was marked by their O_2^{crit}. During this period, the average in situ $[O_2]_{env}$ of the spot prawn population (total abundance, $n = 670$) was significantly greater than spot prawn O_2^{crit} (difference of + 2.64 mL L^{-1}, $p < 0.05$). This large 'oxygen distance' characterizes the distribution of the population prior to summer deoxygenation. After deoxygenation (September), total abundance of spot prawn decreased ($n = 281$) and the remaining population occurred in $[O_2]_{env}$ that was significantly lower than their O_2^{crit} (difference of −0.10 mL L^{-1}, $p < 0.05$). When reoxygenation occurred in October, spot prawn abundance increased ($n = 684$) and the average in situ $[O_2]_{env}$ of the population was again significantly higher than their species O_2^{crit} (difference of + 0.81 mL L^{-1}, $p < 0.05$). In situ populations of slender sole and squat lobster also occurred in $[O_2]_{env}$ that was significantly higher than their respective species O_2^{crit} (both species, $p < 0.05$ for all periods).

Table 3. Metabolic parameters measured for spot prawn, slender sole, and squat lobster. Metabolic parameters are reported as mean (± 95CI). Slopes for each phase of a species metabolism represent the per unit change of mass-specific metabolic rate (mg kg^{-1} h^{-1}) for every unit of $[O_2]_{env}$ (mL L^{-1}).

	*Metabolic slopes				†SMR		
Species	*n*	O_2^{crit} (mL L^{-1})	conformation (mg kg^{-1} h^{-1} per mL L^{-1})	regulation (mg kg^{-1} h^{-1} per mL L^{-1})	*n*	mass-corrected (mg h^{-1})	mass-specific (mg kg^{-1} h^{-1})
Spot prawn	19	1.01 (0.20)	83.9 (13.9)	−1.5 (3.0)	20	0.41 (0.2)	74.7 (11.2)
Slender sole	34	0.36 (0.11)	115.2 (25.0)	0.9 (0.7)	34	0.23 (0.2)	35.1 (5.3)
Squat lobster	25	0.21 (0.17)	537.1 (313.2)	17.4 (9.3)	32	0.09 (0.1)	39.3 (12.3)

*Determined with closed respirometry.
†Determined with intermittent respirometry.

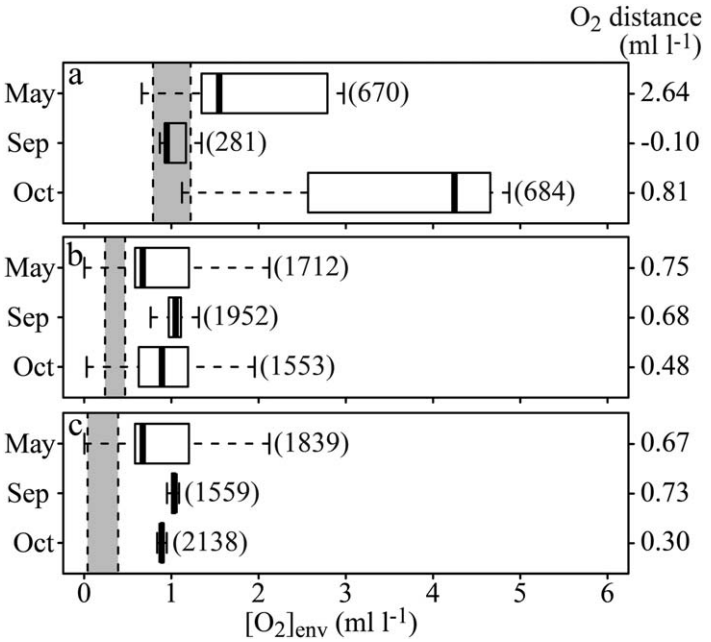

Fig. 4. In situ species distributions relative to species-specific O_2^{crit}. Total in situ $[O_2]_{env}$ occurrence data for (**a**) spot prawn, (**b**) slender sole, and (**c**) squat lobster are summarized for each phase of the 2013 hypoxia cycle. Total species abundances at each time period are in parentheses. Grey bands correspond to the lab-determined O_2^{crit} of each species (95% confidence interval). O_2 distance is the difference between the average $[O_2]_{env}$ at which the population occurred relative to its species-specific O_2^{crit}. In general, in situ populations occurred in higher $[O_2]_{env}$ relative to species-specific O_2^{crit}. For spot prawn, large fluctuations in abundance and O_2 distance implicates hypoxia avoidance in response to the expanding and contracting hypoxia zone. For slender sole and squat lobster, consistently high abundance and smaller O_2 distances with relatively little change between periods indicates a minimal response to the spatially shifting hypoxia interface.

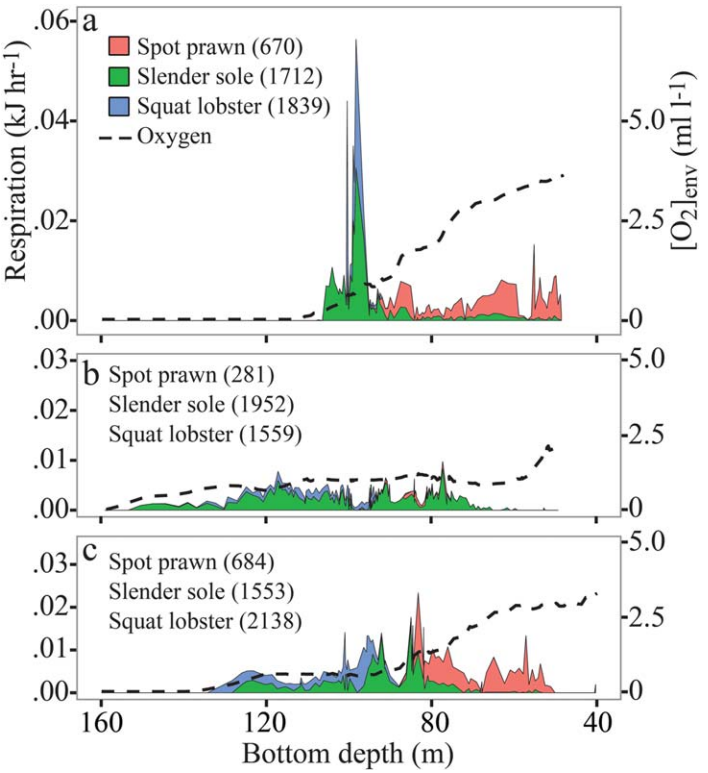

Fig. 5. In situ changes in total aerobic respiration rates in response to seasonally shifting hypoxia. At each phase of the 2013 hypoxia cycle, aerobic respiration rates were calculated for the in situ population of each species and mapped to bottom depth based on the species distributions relative to the $[O_2]_{env}$. Total species abundances are in parentheses. (**a**) In May 2013, before deoxygenation, the three focal species contributed a total aerobic respiration rate of 0.56 kJ m^{-2} h^{-1}. Spot prawn contributed to 34% of the total aerobic respiration rate. (**b**) In September 2013, after deoxygenation, the total aerobic respiration rate decreased to 0.43 kJ m^{-2} h^{-1}. The hypoxia-induced exclusion of spot prawn from the study site resulted in a 23% decrease in the total aerobic respiration rate. (**c**) In October 2013, the total aerobic respiration rate returned to pre-deoxygenation levels (0.55 kJ m^{-2} h^{-1}) when spot prawn returned to the system within 1 month of habitat reoxygenation.

However, the abundances of slender sole ($n = 1712$, 1952, 1553) and squat lobster ($n = 1553$, 1559, 2183) were consistently high in all three phases of the hypoxia cycle (May, Sep, Oct) suggesting minimal migration or hypoxia avoidance occurred for these species. Furthermore, the relative change in the oxygen distance was minimal for slender sole (+0.48 to +0.75 mL L^{-1}) and squat lobster (+0.3 to +0.73 mL L^{-1}) compared with the marked shifts observed for spot prawn (−0.10 to +2.64 mL L^{-1}).

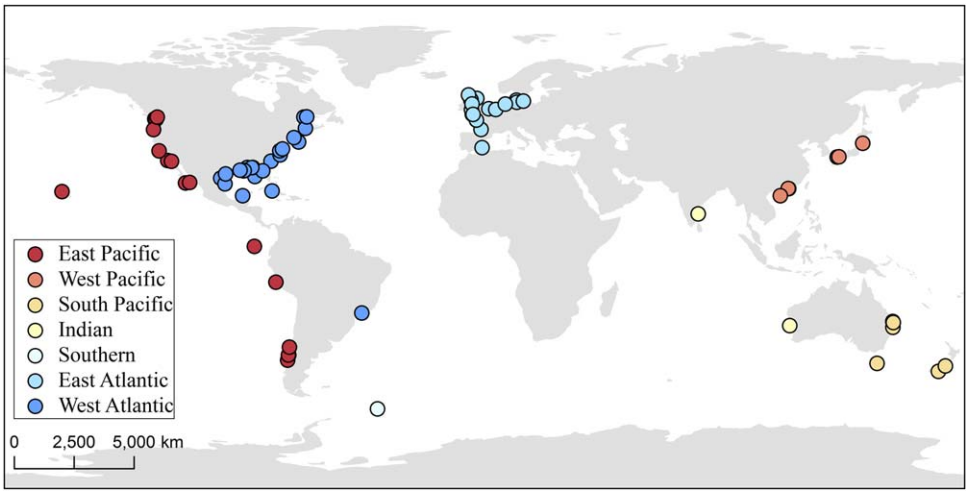

Fig. 6. Global map of O_2^{crit} values reported for crustaceans. Mapped locations represent the collection site of a species that was used in studies where its O_2^{crit} was experimentally determined. General high spatial clustering of study sites prevent all point locations from being visible ($n = 309$). Hypoxia thresholds calculated from regional O_2^{crit} values are presented in Table 4. Species names, locations, and associated references are reported in Supporting Information Table 1.

Shifts in abundance and distribution also changed the amount of in situ aerobic energy sequestered through respiration with respect to location in the habitat (Fig. 5). Before deoxygenation occurred, the three focal species contributed to a total aerobic respiration rate of 0.56 kJ m^{-2} h^{-1}, which is approximately 5% of the microbial respiration rate reported for this study site (Belley *et al.* 2016). Despite representing only 17% of the combined abundance among the three species, spot prawn was responsible for 34% of the total aerobic respiration rate because of their higher metabolic rates (Fig. 5a). Even in severe hypoxia ($[O_2]_{env} < 0.5$ mL L^{-1}), aerobic metabolism was sustained because the O_2^{crit} of resident species (slender sole, squat lobster) are lower than the $[O_2]_{env}$ characterizing most of the study area. After hypoxia expansion, an overall decrease in $[O_2]_{env}$ coincided with the total aerobic respiration rate dropping to 0.43 kJ m^{-2} h^{-1}, an approximately 23% decrease in the rate of energy sequestered. The lower total aerobic respiration rate was primarily driven by the decrease in spot prawn abundance in the study area, with the remaining population being functionally anaerobic (occurring below their species-specific O_2^{crit}). During the period of hypoxia expansion, the abundances of slender sole and squat lobster remained high, thus energy sequestered through respiration became almost entirely coupled to the populations of these two species (93%, Fig. 5b). A pre-deoxygenation level of the total aerobic respiration rate returned (0.55 kJ m^{-2} h^{-1}) when spot prawn migrated back into the system during reoxygenation, which occurred in less than a month (Fig. 5c).

Differences in hypoxia tolerance among oceans

A total of 991 articles were identified and reviewed following the broad search criteria. Of these, 78 articles reported 309 O_2^{crit} values for marine crustaceans (Supporting Information Table 1) from collection sites that generally tracked regional coastlines (Fig. 6). O_2^{crit} values were found for 124 species, of which 55 had multiple O_2^{crit} values reported as some studies experimentally determined O_2^{crit} as a response to other environmental variables such as temperature (e.g., Vargo and Sastry 1977). More than 80% of O_2^{crit} values were for decapods ($n = 254$), although O_2^{crit} values were also reported for amphipods ($n = 21$), euphausiids ($n = 10$), lophogastrids ($n = 8$), mysids ($n = 8$), calanoids ($n = 4$), isopods ($n = 3$), and myodocopids ($n = 1$). A small number of reports ($n = 8$) were associated with no measureable O_2^{crit} (i.e., showed no regulatory ability) and therefore could not be included in the meta-analysis.

Hypoxia thresholds calculated from O_2^{crit} values were significantly different among major ocean basins (Table 4, $p < 0.001$). In general, the lowest hypoxia threshold occurred in the East Pacific Ocean (95 CI, 0.58–0.96 mL L^{-1}), which was 33–39% lower than the hypoxia thresholds calculated for the West Atlantic Ocean (0.99–1.37 mL L^{-1}) and East Atlantic Ocean (1.02–1.77 mL L^{-1}), which more closely followed the general hypoxia threshold of 1.4 mL L^{-1}. Despite the global area covered by polar seas, all O_2^{crit} reported ($n = 20$) from the Southern (Antarctic) Ocean (1.67 ± 0.2 mL L^{-1}) came from a single study (Torres et al. 1994) and O_2^{crit} values have yet to be reported for populations from the Arctic Ocean. Regardless of the oxygen unit used in the regional comparison ($[O_2]^{crit}$ or pO_2^{crit}), a difference in hypoxia tolerance among regions was consistently resolved (Table 4).

Because of the paucity of global coverage, hypoxia thresholds could only be compared among the Atlantic, Pacific, and Antarctic (Southern) Oceans after further subdividing the dataset. In terms of exploitation status, there was a slight bias with proportionally more O_2^{crit} values reported for exploited species in the East Atlantic Ocean (56% of O_2^{crit}

values are from exploited species), West Atlantic Ocean (67%), and West Pacific Ocean (67%) relative to the East Pacific Ocean (20%) (Table 5). Hypoxia thresholds calculated for exploited species were generally higher compared with non-exploited species from the same ocean basin (Table 5). However, there were significant regional differences in O_2^{crit}-constrained hypoxia thresholds regardless of exploitation status. The primary driver of the differences was in the hypoxia thresholds calculated for the East Pacific Ocean (95 CI, exploited: 0.9–1.60 mL L^{-1}, non-exploited: 0.55–93 mL L^{-1}), which were significantly lower than the West Atlantic (exploited: 1.71–2.44 mL L^{-1}, non-exploited: 0.96–1.22 mL L^{-1}) and marginally lower than the East Atlantic (exploited: 1.76–2.62 mL L^{-1}, non-exploited: 0.75–1.86 mL L^{-1}) and Southern Oceans (exploited: 1.73–2.26 mL L^{-1}, non-exploited: 1.60–1.86 mL L^{-1}) (Table 5). Additionally, a comparison of the average O_2^{crit} for spot prawn (*Pandalus platyceros*) and squat lobster (*Munida quadrispina*) to other shrimp species (infraorder Caridea or suborder Dendrobranchiata) and squat lobster species (superfamilies Chirostyloidea or Galathoidea) showed that taxonomically constrained hypoxia thresholds also differ among ocean basins and that the two crustacean species measured in this study were more similar to species from the East Pacific Ocean than those from the Atlantic Ocean (Supporting Information Fig. 1).

Table 4. O_2^{crit}-constrained hypoxia thresholds for major ocean basins. Thresholds were calculated using one O_2^{crit} reported per species in a study ($n_{total} = 171$). Letters indicate significant differences in hypoxia thresholds between ocean basins ($\alpha = 0.05$).

		mL L^{-1}		kPa	
*Region	*n*	Mean (sd)	95% CI	Mean (sd)	95% CI
East Atlantic	28	1.44 (0.9)[a]	1.02–1.77	4.97 (3.1)[a]	3.50–6.24
West Atlantic	62	1.36 (0.9)[a]	0.99–1.37	4.95 (3.4)[a]	3.51–4.90
East Pacific	58	0.88 (0.7)[b]	0.58–0.96	2.74 (2.2)[b]	1.74–2.96
West Pacific	7	1.12 (0.7)[a,b]	0.56–1.79	4.15 (2.8)[a,b]	2.04–6.62
South Pacific	6	1.46 (1.0)[a,b]	0.68–2.36	5.02 (3.3)[a,b]	2.32–8.19
Indian	2	2.73 (1.9)[a]	1.35–2.73	9.90 (7.4)[a]	4.66–9.90
Southern	8	1.67 (0.2)[a]	1.57–1.82	4.33 (0.5)[a,b]	4.05–4.75

*Comparisons between regions (permutation tests) were done separately for $[O_2]_{crit}$ (mL L^{-1}) and equivalent pO_2^{crit} (kPa).

Discussion

Our integrated results illustrate that the in situ biological response to deoxygenation can be quantified by using the metabolic traits of resident epibenthic megafaunal species. Spatially shifting environmental oxygen ($[O_2]_{env}$) induces differential restructuring of the distributions of three co-occurring species because of physiological differences in hypoxia tolerance and oxygen requirements. In general, species-specific critical oxygen levels (O_2^{crit}) are correlated with the lowest $[O_2]_{env}$ at which in situ populations occur (Seibel 2011). During periods of hypoxia expansion, the total aerobic energy sequestered by respiration decreases; overall rates are determined by species-specific ability to regulate oxygen uptake at low $[O_2]_{env}$. By calculating region-specific hypoxia thresholds, constrained to the O_2^{crit} of resident species, we revealed that hypoxia tolerance is different among major ocean basins. Regional differences in physiology-based hypoxia thresholds suggest that the evolutionary history of a system will influence the amount of aerobic habitat and energy sequestration that will be lost to deoxygenation. We suggest integrating metabolism-based traits to calculate hypoxia thresholds when assessing the biological consequences to hypoxia for regions experiencing oxygen loss.

Species-specific traits drive community response

Species-specific metabolic traits determine the extent of community reorganization during periods of hypoxia expansion. Because the abundance and distributions of our focal species strongly influence compositional heterogeneity in the field, the loss of community structure as a result of hypoxia expansion (Chu and Tunnicliffe 2015a) can be linked to the relative metabolic traits of these key species. For example, the lack of a clear scaling relationship between size and

Table 5. O_2^{crit}-constrained hypoxia thresholds calculated for exploited and non-exploited crustacean species for major ocean basins. Letters indicate significant differences in hypoxia thresholds between ocean basins ($\alpha = 0.05$). Thresholds are reported in units of mL L^{-1}.

	Exploited			Non-exploited		
*Region	No. spp.	Mean (sd)	95% CI	No. Spp.	Mean (sd)	95% CI
East Atlantic	10	2.21 (1.1)	1.76–2.62[a]	8	1.27 (0.8)	0.75–1.86[a,b,c]
West Atlantic	16	2.23 (1.3)	1.71–2.44[a]	24	1.14 (0.5)	0.96–1.22[a]
East Pacific	10	1.31 (0.9)	0.91–1.60[b]	40	0.85 (0.6)	0.55–0.93[b]
West Pacific	4	0.98 (0.5)	0.72–1.07[b]	2	0.84 (0.4)	0.56–1.12[b]
Antarctic	2	2.04 (0.4)	1.73–2.26[a,b]	6	1.75 (0.2)	1.60–1.86[c]

*Separate permutation tests were used to compare differences among ocean basins for $[O_2]_{crit}$ (mL L^{-1}) and equivalent pO_2^{crit} (kPa). We report in units of mL L^{-1} because results were the same regardless of the oxygen unit. Equivalent pO_2^{crit} values can be found in Supporting Information Table 1.

oxygen consumption in squat lobster suggests anaerobic processes are important in their metabolism. Squat lobster are naturally found in $[O_2]_{env}$ below their species-specific O_2^{crit} (Chu and Tunnicliffe 2015a) where they aggregate at high densities (>100 individuals m^{-2}, Burd and Brinkhurst 1984; Doya et al. 2016). These dense clusters of squat lobster rapidly migrate into shallower depths to exploit food resources (Burd and Brinkhurst 1984; Anderson and Bell 2014), which is typical of the opportunistic species characterizing seasonally hypoxic systems (Pihl et al. 1992; Diaz and Rosenberg 1995). In general, squat lobsters (superfamilies Chirostyloidea and Galatheoidea) can be characterized with having low O_2^{crit} and metabolic rates, anoxia tolerance, bentho-pelagic switching, and substantial anaerobic capacity (Longhurst 1967; Childress 1975; Quentin and Childress 1976; Zainal et al. 1992). Such physiological and behavioral adaptations likely facilitate rapid utilization of energy in highly variable oxygen conditions and may explain their general abundance in low oxygen systems.

Although slender sole dominate ichthyoplankton and demersal fish biomass throughout the northeast Pacific Ocean (Pearcy 1978; Cross 1987; Auth and Brodeur 2006; Guan 2015) our experiments are the first to highlight their metabolism and hypoxia tolerance. Among major teleost groups, flatfish (order Pleuronectiformes) are not generally considered to be hypoxia tolerant (Hochachka and Somero 2002), which makes the low O_2^{crit} of slender sole (~0.36 mL L^{-1}) particularly unusual. Most pleuronectiforms have $O_2^{crit} > 1.0$ mL L^{-1} (Supporting Information Table 2); only hogchoker *Trinectes maculatus*, which is also known to be abundant in low oxygen systems, has similar hypoxia tolerance (0.28 mL L^{-1}; Pihl et al. 1991). In terms of metabolic rates, meaningful comparisons must be made among species that occupy the same habitat niche. For example, metabolic rates of hogchoker reflect the thermal conditions of their surface water habitat (> 20°C, Pihl et al. 1991), conditions slender sole would never experience nor survive. Aerobic requirements and metabolic scaling coefficients reported for deep-sea fish are scant (Drazen and Seibel 2007) so only broad metabolism comparisons can be made. The ecological role of slender sole is functionally similar to that of the bearded goby *Sufflogobius bibarbatus*, which dominate hypoxic waters in the Benguela upwelling region of the East Atlantic. Although O_2^{crit} are similar between the two hypoxia-tolerant fish (bearded goby $O_2^{crit} \sim 0.3$ mL L^{-1}, Utne-Palm et al. 2010), the goby has a higher metabolic rate (60–80 mg kg^{-1} h^{-1}) that may reflect the energy requirements of its vertical migration behavior (Utne-Palm et al. 2010; Salvanes et al. 2011). Among fish of similar body mass and habitat temperature (adjusted to 9°C using a general Q_{10} of 2.5 for fish, Clarke and Johnston 1999), the metabolic rate of slender sole is similar to that of other deep-sea fish such as fangtooth *Anoplogaster cornuta* (32–45 mg kg^{-1} h^{-1}, Gordon et al. 1976) and hagfish *Eptratretus deani* (~ 24 mg kg^{-1} h^{-1}, Drazen and Yeh 2012).

Although slender sole is not a commercially valuable species (due to their small size), they resuspend large amounts of bottom sediments, which contribute to substantial fluxes in nutrient recycling and transport (Yahel et al. 2008; Katz et al. 2009, 2012). High abundance and fidelity to low $[O_2]_{env}$ (Chu and Tunnicliffe 2015a) also suggest that they could be an important indicator species of hypoxic waters within their habitat range. In the northeast Pacific Ocean, shoaling hypoxia boundaries compress the distribution of hypoxia-sensitive fish into shallower depths but not those of hypoxia-tolerant species (Keller et al. 2010, 2015). Future deoxygenation of surface waters in this region may also shift the distributions of larger, hypoxia-sensitive species poleward (Deutsch et al. 2015). Under future scenarios of oceanic oxygen loss, this potential relaxation of pressure from predation and competition (e.g., Salvanes et al. 2015) might also lead us to predict an expansion in the biogeographic range of slender sole and an increase in their functional contributions to benthic ecosystems in this region.

Deoxygenation-induced shifts in species distributions

A general consequence of hypoxia expansion is the compression of species distributions into shallower depths (Eby and Crowder 2002; Prince and Goodyear 2006; Koslow et al. 2011; Stramma et al. 2012). Among the overlapping species distributions at our study site, only spot prawn were compressed into shallower depths during hypoxia expansion, since lower tolerance and higher oxygen requirements restrict them to more oxygenated waters. Aerobic habitat is spatially constrained to areas where $[O_2]_{env}$ is above metabolic limits and the available extent of aerobic habitat will be smaller for species with relatively high hypoxia sensitivity (high O_2^{crit}) and high oxygen demand (SMR). However, in seasonally hypoxic systems, the realized extent of habitat use will be much smaller for hypoxia-sensitive species (Breitburg 2002) because energy is allocated to migration in response to the spatio-temporal variability of the $[O_2]_{env}$ profile. This is consistent with the relatively large oxygen distance we observed for spot prawn, likely reflecting a balance of maximizing resource exploitation while minimizing energy invested in hypoxia avoidance. In contrast, slender sole and squat lobster consistently occurred much closer to their species-specific O_2^{crit} and persisted in severely hypoxic waters, which are conditions that would also exclude predators (e.g., Altieri 2008). For species adapted to persist in variable hypoxia, energy diverted from hypoxia and predator avoidance can instead be allocated toward growth and reproduction. Because hypoxia sensitivity is not equal among co-occurring species, deoxygenation will differentially affect the component species of a community and the net impact will be largely determined by species-specific metabolic constraints.

Adaptations such as low O_2^{crit}, low oxygen demand, and metabolic suppression underpin the success of many species in a variety of systems influenced by severe hypoxia (Childress and Seibel 1998; Seibel 2011). These traits are advantageous under deoxygenation because they facilitate the ability to regulate oxygen consumption across a wider range of $[O_2]_{env}$. A shift toward smaller individual- and assemblage-level fish sizes is also predicted (Cheung et al. 2013) because of the direct relationship between mass-corrected oxygen demand and body size. However, this relationship was not observed in our study. Inter- and intra-specific measurements of oxygen consumption are typically variable (Clark et al. 2013) because of the compounding effects of life-history strategy, phylogeny, and reproductive condition (Siebenaller et al. 1982; Childress and Somero 1990; Garenc et al. 1999). These factors can mask linear relationships between body size, O_2^{crit}, and metabolism but can be accounted for by measuring oxygen consumption rates of conspecifics with body sizes ranging over four orders of magnitude (Rosa et al. 2009). Thus, unresolved relationships between body size, metabolism, and O_2^{crit} may be due to the small maximum adult sizes characteristic of our focal species.

Deoxygenation-induced shifts in ecosystem function

Species-specific adaptations and evolutionary history strongly reflect the oxygen characteristics of a region. The O_2^{crit} we measured for our focal species, the $[O_2]_{env}$ level at which they respond to 'hypoxia', and the metabolism-based hypoxia thresholds we calculated for the East Pacific Ocean all indicate that species from this region are adapted to much lower $[O_2]_{env}$ (Tunnicliffe 1981; Chu and Tunnicliffe 2015a; Sperling et al. 2016) compared with species from the Atlantic Ocean. The marked difference in metabolic thresholds we report between the East Pacific Ocean and both sides of the Atlantic Ocean follows the $[O_2]_{env}$ minima characterizing these regions (Kamykowski and Zentara 1990; Karstensen et al. 2008). Although common marine hypoxia thresholds (e.g., hypoxia < 1.4 mL L^{-1}) are still used to describe all regions perceived as oxygen deficient, they were originally conceived from observations biased toward systems in the Atlantic Ocean (Chu and Tunnicliffe 2015a). Further evidence that the biological response of communities will be adapted to the natural variability and oxygen exposure in a region comes from analogous studies in a spatio-temporally variable hypoxic system originating from the Black Sea that showed a community threshold response at the general hypoxia threshold of 1.4 mL L^{-1} (Lichtshlag et al. 2015), which is in agreement with our regional threshold for the East Atlantic Ocean. As long-term deoxygenation progresses within a region, extirpation of the more sensitive species will likely lower the overall regional threshold. Empirical knowledge acquired now may not reflect historical conditions (Soulé 2005). The extensive O_2^{crit} data we compiled can be considered baseline thresholds for the most prominently studied taxonomic group among major ocean basins. Limited global coverage of O_2^{crit} reflects the geographic bias of research effort (Richardson et al. 2012) and shows that baselines have yet to be established for most taxa in the global ocean. Thus, an imperative first step for establishing realistic predictions on the biological consequences of deoxygenation will be to assess oxygen requirements and physiological constraints of the local species. This would explain the ocean-scale differences already observed in species responses to deoxygenation (Prince et al. 2010; Sperling et al. 2016) and will ground projections regarding future aerobic habitat loss and reduced ecosystem function.

Studies that make predictions on the biological consequences of marine deoxygenation have mostly projected large-scale shifts in species distributions (Stramma et al. 2012; Deutsch et al. 2015). However, the impacts of deoxygenation on ecosystem function are mostly driven by time-dependent, biological processes such as respiration, which have threshold responses to changes in $[O_2]_{env}$ (Diaz and Rosenberg 1995, 2008). In our system, the seasonal shifts in species distributions, community structure, and energy sequestration highlight the strong coupling of the biological response to the spatial and temporal variability of deoxygenation. The steep oxygen gradients (Chu and Tunnicliffe 2015a) and short-term $[O_2]_{env}$ variability (Matabos et al. 2012) that occur at our study site are typical of poorly-ventilated basins, the upper boundaries of oxygen minimum zones (Brand and Griffiths 2009), and coastal upwelling regions (Booth et al. 2012). In these systems, the depth at which the hypoxia interface occurs is highly variable because the hypoxic volume is controlled by seasonal and interannual variations in hydrography (Rabalais et al. 2002; Astor et al. 2003), wind-driven upwelling (Chan et al. 2008), and primary production (Wang et al. 2015). The amount of local energy displaced from higher trophic levels and diverted toward the microbial community is correlated with the timing and severity of seasonal low oxygen periods, the duration at which a system stays below critical threshold levels, and the population dynamics of the component species (Baird et al. 2004; Diaz and Rosenberg 2008). If there is a long-term increase in the period during which a system remains below critical thresholds, deoxygenation-induced shifts in biological processes such as energy flow, biomass fixation, and nutrient cycling will follow.

Impacts of climate stressors on respiratory physiology

Deoxygenation of the ocean is one of the three main consequences of rising atmospheric CO_2, the others being ocean warming and acidification (Levin and Breitburg 2015). Although the environmental drivers of these three climate-related stressors are different, their influence on biology can be unified by their effect on the aerobic performance and energy turnover of organisms (Pörtner and Farrell 2008; Pörtner 2010, 2012). All three climate-related stressors affect

respiratory physiology by influencing the overall efficiency and capacity of oxygen acquisition, transport, and storage in fish and invertebrates (Hochachka and Somero 2002). Exposure to elevated temperature increases oxygen demand and O_2^{crit} in marine ecotherms (Pörtner and Knust 2007; Pörtner 2010), while exposure to increased pCO_2 can decrease overall aerobic capacity by reducing metabolic and energy turnover rates (Pörtner et al. 2004; Pörtner and Langenbuch 2005; Pörtner 2008). Cumulative exposure to multiple stressors will likely increase the overall magnitude of the response in aerobic capacity, energy allocation, and turnover relative to a single climate-stressor like hypoxia. However, the relative contribution of each climate-related stressor to the overall reduction of aerobic metabolism and biomass fixation remains an open question because there is currently no experimental framework that can accommodate all three environmental variables with a single physiological response measurement. Therefore, unifying the effects of temperature, oxygen, and pH into an integrated, physiological framework (e.g., Del Raye and Weng 2015) will become an important tool in predicting the cumulative impacts of climate-driven change on marine ecosystems and function.

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Conflict of Interest

None declared.

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