Title: Increasing hypoxia on global coral reefs under ocean warming

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Abstract: Ocean deoxygenation is predicted to threaten marine ecosystems globally. However, current and future oxygen concentrations and the occurrence of hypoxic events on coral reefs remain underexplored. Here, using autonomous sensor data to explore oxygen variability and hypoxia exposure at 32 representative reef sites, we reveal that hypoxia is already pervasive on many reefs. 84% of reefs experienced weak to moderate (≤153 to ≤92 μmol O_2 kg^{-1}) hypoxia and 13% experienced severe (≤61 μmol O_2 kg^{-1}) hypoxia. Under different climate change scenarios based on 4 Shared Socioeconomic Pathways (SSPs), we show that projected ocean warming and deoxygenation will increase the duration, intensity, and severity of hypoxia, with more than 94% and 31% of reefs experiencing weak to moderate and severe hypoxia, respectively, by 2100 under SSP5-8.5. This projected oxygen loss could have negative consequences for coral reef taxa due to the key role of oxygen in organism functioning and fitness.

Main Text:

Earth's global ocean has been steadily losing oxygen due to warming-induced decreases in oxygen solubility, accelerated respiration, increases in water column stratification, and coastal eutrophication, commonly referred to as ocean deoxygenation (*1-3*). Since the 1950s, the open ocean has lost more than 2% of its dissolved oxygen, oxygen minimum zones have expanded and shoaled, and hundreds of coastal sites have reported severe hypoxic conditions (i.e., aquatic oxygen levels below a given environmental threshold) (*1-6*). These trends will continue in the future, as ocean surface oxygen concentrations are projected to decrease by an additional 3.2 to 3.7% by 2100, with oxygen loss expected to emerge across 59 to 80% of the ocean by 2050 (*4*). While trends of deoxygenation in the open ocean and the occurrence of temperate hypoxic and anoxic zones (defined as ≤2 and 0 mg O_2 L^{-1}, respectively; *6*) are relatively well-documented (*1-3, 6*), there has been less focus on tropical coastal ecosystems such as coral reefs (*7-9*) despite mounting evidence that modern hypoxic events can lead to mass mortality of coral reef taxa (e.g., *7-10*).

Traditionally, coral reefs have been assumed to be well-oxygenated systems. However, autonomous, high-frequency dissolved oxygen measurements have been historically scarce in reef monitoring efforts (*7-9*). As a result, there is a paucity of high-quality dissolved oxygen measurements from tropical coral reefs and a high likelihood that the occurrence of low oxygen events on tropical coral reefs across the globe has been severely underreported (*7*). Acute, severe hypoxic events can be induced on tropical coral reefs through a variety of physical and biological mechanisms such as warming, restricted water flow, increased biological oxygen demand, nutrient and organic matter loading, and/or an influx of oxygen deficient water (*7-10*). As global temperatures continue to rise and marine heatwaves become more frequent and severe (*11*), low oxygen conditions on coral reefs are likely to become more common as a result of changes in oxygen solubility and biological oxygen demand (*12*). Given the essential role of oxygen in driving aerobic metabolism, hypoxia poses a serious threat to coral reef ecosystems and the humans that depend on them (*3, 8, 13*). Thus, characterizing present-day oxygen concentrations on a variety of reefs across different spatiotemporal scales is imperative for defining "normoxia" on tropical coral reefs, understanding the current extent of hypoxia exposure, and projecting future coral reef oxygen conditions under ocean warming and deoxygenation (*8-9, 13*). To date, a number of studies have expressed grave concerns about the potential consequences of declining available oxygen on coral reefs (*7-9, 13*). However, there are currently no synthesis studies characterizing the range of oxygen conditions experienced on global reefs today and what conditions reefs may experience in the future.

In this study, we leveraged autonomous sensor data from 32 representative reef site deployments at 12 locations around the globe (Fig. 1A, Extended Data Fig. 1, Table S1) to quantify present-day oxygen conditions and hypoxia exposure at a diverse subset of reefs. We also modeled the effect of future warming scenarios on the oxygen solubility and the biological oxygen demand for each site and location to calculate decreases in oxygen availability (i.e., deoxygenation) and hypoxic event frequency, duration, intensity, and severity by the year 2100 (see Methods). The observational data presented here include reef sites between 23 ºS and 32 ºN in the East and South China Sea; North Atlantic; West, Central, and South Pacific; and Caribbean (Fig. 1A). Deployment lengths ranged from 3 to 309 days and occurred between 2013 and 2019 across seasons (see Supplementary Information Table S1 and Extended Methods for detailed site characterization and deployment information). Oxygen data were recorded at sites ranging from 0.7 to 17.1 m in depth from a variety of coral reef habitat types (e.g., reef fronts, terraces, reef flats, reef slopes, lagoons, and patch reefs with different benthic communities; Table S1).

Global variability in dissolved oxygen concentrations

We observed a large range of oxygen conditions among the different reef habitats, with diel oxygen variability, means, and extremes differing between reef habitats at the same location, as well as between study locations in different regions (Fig. 1B-C, Extended Data Fig. 1, Table S2). The mean daily dissolved oxygen concentration across all sites was 173 ± 28 μmol O_2 kg^{-1} (mean ± 1 SD) or 88 ± 13 % expressed as percent saturation and the mean daily range was 81 ± 52 μmol O_2 kg^{-1} (42 ± 28 % saturation). The mean daily minimum oxygen concentration was 136 ± 40 μmol O_2 kg^{-1} (69 ± 20 % saturation) and the mean daily maximum was 217 ± 39 μmol O_2 kg^{-1} (111 ± 20 % saturation), with large variations between reef locations (Fig. 1, 2A, Table S2). The smallest mean daily range in oxygen (23 ± 4 μmol O_2 kg^{-1} and 12 ± 2 %, respectively) was observed at the forereef in Tutuila, which was one of the deeper sites (15.2 m depth) and directly connected to the surrounding open ocean. In contrast, the largest mean daily range (258 ± 11

μmol O_2 kg^{-1} and 139 ± 5 %, respectively) was observed at Taiping 1, which was a shallow (1 m) nearshore reef area dominated by seagrass and scattered coral colonies. At all locations, oxygen was typically lowest in the early morning at all locations and highest in the mid-afternoon as a result of nighttime respiration and daytime photosynthesis, respectively (Fig. 1B). A regression analysis of oxygen variability (mean daily range) as a function of mean depth (Table S3) revealed a moderate, inverse non-linear correlation ($R^2 = 0.3$; Fig. Extended Data Fig. 2A, Table S4). Close to no relationship was detected between oxygen variability and mean flow speed ($R^2 = 0.002$; Extended Data Fig. 2B, Table S4). A positive, non-linear correlation was observed between the mean daily oxygen minimum and mean flow speed ($R^2 = 0.4$; Fig. Extended Data Fig. 2C, Table S4), whereas a weak non-linear correlation was observed as a function of mean depth ($R^2 = 0.1$; Fig. Extended Data Fig. 2D, Table S4). These results (Extended Data Fig. 2, Table S4) are in line with previous studies (e.g., *14*) linking shallower depths to greater variability in seawater chemistry on coral reefs due to a general increase in benthic biomass to water volume ratio. We observed no clear trend in oxygen variability based on the type of reef habitat (e.g., reef fronts, terraces, reef flats, reef slopes, lagoons, and patch reefs with different benthic communities; Table S1).

Pervasive hypoxia under present-day conditions

While many aquatic studies use a threshold of ≤2 mg O_2 L^{-1} (~61 μmol O_2 kg^{-1} depending on seawater density) to define a hypoxic environment, dissolved oxygen thresholds vary as a function of taxa, exposure time, life stage, temperature, and other factors (*8-9, 15-20)*. Evidence from the few experiments conducted on tropical reef organisms suggests that lethal low oxygen thresholds can be as high as 4 mg O_2 L^{-1} (*18*) and sublethal thresholds can be even higher for some species, especially under warming (*17, 19-21*). Thus, a threshold of 2 mg O_2 L^{-1} (61 μmol O_2 kg^{-1}) may not accurately capture the range of all the potential sublethal and lethal impacts of low oxygen for coral reef species. In our analyses, we employed four hypoxia thresholds: "weak hypoxia" of ≤5 mg O_2 L^{-1} (153 μmol O_2 kg^{-1}), a conservative threshold that captures 90% of observed sublethal impacts in temperate benthic marine organisms (*16*), "mild hypoxia" of ≤4 mg O_2 L^{-1} (122 μmol O_2 kg^{-1}), "moderate hypoxia" of ≤3 mg O_2 L^{-1} (92 μmol O_2 kg^{-1}), and "severe hypoxia" as the conventional ≤2 mg O_2 L^{-1} (61 μmol O_2 kg^{-1}) threshold (see Methods).

Based on these thresholds, we found that many reef sites already experience oxygen stress. Nearly all reefs in our study (84 %) experienced weak hypoxia, while 50 %, 34 %, and 13 % experienced mild, moderate, and severe hypoxia, respectively, at some point during the data collection period (Fig. 1B-C, 2A-E). Across all sites, we identified 1,198 weak hypoxic events lasting 0.5 to 64 hours and 229 mild to moderate events lasting up to 18 hours (Fig. 2B-E). Weak to moderate hypoxic events lasting less than 12 hours were most common, whereas those lasting 12 to 24 hours or more than 24 hours were comparatively rarer (Fig. 2B-E). Severe hypoxic events were less common (19 events observed at only 4 sites), with the longest event being 7.5 hours in duration (Fig. 2B-E). The majority of hypoxic observations, regardless of threshold, occurred in the early morning between 2:00 and 7:00 h due to net nighttime respiration (Fig. 3).

Hypoxia projections under warming and deoxygenation by 2100

To project future deoxygenation and resultant hypoxia exposure at each reef site, we employed location-specific projections of ocean warming by the year 2100 to calculate the cumulative effects of warming on oxygen solubility and biological oxygen demand. Warming projections were adopted from the Coupled Model Intercomparison Project 6 Shared Socio-economic Pathways (Extended Data Fig. 3, Table S5) – SSP1-2.6 (+0.3 ºC to +1.1 ºC), SSP2-4.5 (+1.1 ºC to +3.4 ºC), SSP3-7.0 (+1.8 ºC to +3.3 ºC), and SSP5-8.5 (+2.8 ºC to +4.1 ºC) from the Community Earth System Model Whole Atmosphere Community Climate Model (see Methods) – and a severe, acute heatwave scenario of +6 ºC (*22*). The effect on oxygen solubility was calculated based on thermodynamic principles and the effect on biological oxygen demand was approximated from nighttime respiration signals and a temperature coefficient (Q_{10}) (see Methods, Extended Data Fig. 4). These calculations inherently account for site-specific properties that influence seawater oxygen concentrations such as community composition, flow rates and residence time, but do not account for potential future changes to these properties. To verify our approach, we also employed a simple box model to assess the validity of our calculations under a range of temperature and residence time scenarios (see Methods, Fig. Extended Data Fig. 5).

Our results reveal that under the SSP1-2.6 scenario, the number of reef sites assessed in this study experiencing weak hypoxia by 2100 would be similar to present-day observations

(84%), increasing to 94 % under SSP5-8.5 and 97 % during a 6 ºC heatwave event (Fig. 2A, Table S6). The number of sites experiencing mild and moderate hypoxia would increase from 59 % and 34%, respectively, under SSP1-2.6, to 72 % and 44 % of sites under the SSP5-8.5 scenario (Fig. 2A, Table S6) and 75 % and 53 % during a 6 ºC heatwave. Further, under the SSP1-2.6 scenario, 19 % of sites would experience severe hypoxia by the year 2100, increasing to 31 % under the SSP5-8.5 scenario and 34 % during a 6 ºC heatwave event (Fig. 2A, Table S6).

The percent of sites experiencing longer durations of hypoxia will also increase under warming across all of the thresholds considered (Fig. 2B-E, Table S7). More than 28 % of sites would experience mild hypoxic events lasting between 12 and 24 hours under the SSP5-8.5 scenario, increasing to 50 % of sites under a 6 ºC heatwave, compared to 16 % at present-day (Fig. 2C, Table S7). Similarly, the percent of sites experiencing severe hypoxic events of 6 to 12 hours in duration would increase from just 3 % at present-day to 6.3 % under SSP5-8.5 and 19 % under a 6 ºC heatwave (Fig. 2E, Table S7).

Overall, by the year 2100, the total number of hypoxic observations will increase under all warming scenarios, ranging from an increase of 13 % to 42 % under SSP1-2.6 and 97 % to 287 % under SSP-8.5 (Fig. 2F, Extended Data Fig. 6) relative to present-day. As a result, the frequency, duration, intensity (i.e., the difference between a threshold and the measured concentration; *23*), and severity (average intensity multiplied by duration; *23*) of hypoxic events crossing each threshold will also increase (see Methods, Fig. 2, Extended Data Fig. 6-8, Table S6,7). These projections suggest a shift from more acute to more chronic hypoxia exposure under increasing warming, the magnitude of which will depend on future atmospheric CO_2 concentrations and the relevant thresholds of hypoxia tolerance for reef taxa (Fig. 2, Extended Data Fig. 6-8, Table S6,7).

Implications of increasing hypoxia

A better understanding of what changing oxygen dynamics on coral reefs means for corals and reef ecosystems is needed. Field data from severe hypoxic events on coral reefs report extremely variable responses of different coral genera (*8*), revealing both sensitive (e.g., *Acropora* and *Pocillopora* spp.) and tolerant (e.g., *Porites* spp.) groups (*7, 24-26*). Similarly, data from the relatively few laboratory low oxygen experiments we could find in the literature reveal a wide range of species-specific tolerances to low oxygen intensity and duration under both constant and nightly low oxygen exposure regimes (for a literature review, see Table S8). For example, under constant exposure to severe hypoxia of 1 mg O_2 L^{-1} (~31 μmol O_2 kg^{-1}), *Acropora cervicornis* experienced tissue loss, bleaching, and mortality after just 2 days, whereas *Orbicella faveolata* survived more than 11 days under the same conditions (*19*). In another study, *Agaricia lamarcki* survived 7 days of exposure to hypoxic conditions of 0.5 mg O_2 L^{-1} (~15 μmol O_2 kg^{-1}) whereas all *Stephanocoenia intersepta* colonies experienced complete mortality (*7*), suggesting some species or populations may be particularly resilient (or susceptible) to low oxygen stress. Based on the results of the present study, none of our reef sites are projected to experience multi-day severe hypoxia under the warming scenarios used in our analyses. However, these conditions may still occur on these reefs in the future. Data from field observations demonstrate that additional drivers, such as reduced winds, slow flow, stratification, reduced mixing, or other unique meteorological or oceanographic conditions can and will interact to lead to acute, severe hypoxic events of comparable intensity and duration on reefs (*7-8*, *10*, *24-27*), which will be further exacerbated by warming (*28*).

Importantly, exposure to nighttime (<12 hours) low oxygen conditions alone with reoxygenation during daytime has been shown to cause both sublethal and lethal impacts in tropical corals under a range of oxygen concentrations (Table S8). *Acropora yongeii* exposed to nightly mild to moderate hypoxia of 2-4 mg O_2 L^{-1} (61-122 μmol O_2 kg^{-1}) experienced partial to full mortality and significant tissue loss after just 3 days (*18*). Similarly, the majority of *Montipora capitata* corals exposed to nightly anoxia (0 mg O_2 L^{-1}) experienced bleaching after just 2 days and full mortality within 5 days (*29*). At the sublethal level, bleaching (*29-30*), tissue loss (*18, 29*), reductions in calcification rates (*31-33*), DNA damage (*34*), changes in gene expression (*30, 35*), shifts in metabolism (*29*), and reductions in photosynthetic capacity (*18*) have all been observed in a variety of coral species exposed to only nighttime hypoxia (<12 hours) of varying intensity (see Table S8), highlighting the potential consequences of even short-term exposure to low oxygen conditions. For the reef habitats surveyed in the present study, we project an increase in the number of sites experiencing hypoxic events lasting between 12 and 24 hours under increasing warming across all thresholds (Fig. 2B-E, Table S7). For example, the percent of sites experiencing mild hypoxic events (≤4 mg O_2 L^{-1} or 122 μmol O_2 kg^{-1}) lasting 12-24 hours would nearly double under an SSP5-8.5 warming scenario (increasing from 16 to 28 %)

and more than triple under an acute 6ºC heatwave event (50 % of sites), posing a potential threat to the more sensitive corals at these sites (Fig. 2C, Table S7). While reef habitats tend to experience low oxygen conditions at night regularly under present-day conditions (Fig. 3), increased intensity and/or duration of nighttime hypoxic exposure may have significant sublethal to lethal effects on corals, as accumulated oxygen produced through light-driven photosynthesis in the daytime may not be enough to effectively buffer against lower nighttime oxygen conditions (*31-33*).

Physiologically, some coral species may be able to cope with varying degrees of hypoxia (here, insufficient supply of O_2 to tissues to maintain normal functioning) by increasing anaerobic respiration (*29*) and engaging transcriptional hypoxia-response systems (*30, 36*; Table S8). However, these strategies may not be equally effective for all corals or sustainable under repeated stress or longer hypoxic events. Studies of coral larvae and recruits demonstrate that hypoxic conditions can impair coral settlement (*37*), reduce survivorship of coral recruits (*38*), and hinder the expression of key genes associated with early development regulation (*35*), further limiting ecosystem recovery under repeated or long-term hypoxic conditions.

Low oxygen tolerance also varies between reef-associated organisms by orders of magnitude, with some thresholds well above the generalized environmental hypoxia threshold of 2 mg O_2 L^{-1} for aquatic organisms. A 2008 meta-analysis of temperate species found bivalves and gastropods were the most tolerant to low oxygen whereas crustaceans and fishes were the most sensitive in terms of mortality (*16*). Median lethal time also varied significantly both between and within taxonomic groups, ranging from 23 minutes for a species of flounder to 32 weeks for a species of bivalve (*16*). Aside from direct mortality, organisms experiencing intratissue hypoxia can experience changes in behavior, feeding, respiration, reproduction, and/or general performance, which can scale up to impair ecosystem function through loss or migration of key species (*6, 8*). It is also important to understand the tolerance of photosynthetic organisms to low oxygen, as a reduction in photosynthetic activity during the day will have implications for the mean and extreme oxygen conditions on a reef (*8*).

Notably, oxygen loss and hypoxic events are not occurring in isolation from other stressors. Oxygen and temperature are tightly linked in terms of organism metabolism and together may severely limit species performance and restrict the availability of habitats that are metabolically viable (*17, 28, 39-40*). For tropical corals, there is evidence that the ability to effectively respond to low oxygen conditions and overcome a metabolic crisis is a key factor in determining bleaching tolerance versus susceptibility (*30, 41*). In addition, low oxygen conditions typically co-occur with acidification, as increased respiration decreases both pH and dissolved oxygen concentrations (*28*). The combination of low oxygen and acidification stress has been shown to be mainly additive, with negative impacts across a wide range of taxa (*42*). Coastal eutrophication, which drives increased respiration, therefore has the capacity to intensify local hypoxia and acidification, suggesting a reduction of nutrient inputs may improve projected conditions at local scales under ongoing global change (*43-44*).

Here, we provide the first comprehensive synthesis of oxygen concentrations and variability as well as hypoxia frequency, intensity, severity, and duration on tropical coral reefs. Our findings suggest hypoxia is already pervasive in coral reef habitats around the world and will become more common and severe as ocean temperatures increase. While these projections are specific to the reefs and locations included in this study, and our calculations are limited by the available environmental and physical data for each reef, the observations presented here provide broad representation of different reef systems and environments found around the world. Continued and additional high-frequency oxygen data measurements on coral reefs over different seasons and longer time scales will be imperative for establishing baseline conditions, tracking potential hypoxic events, expanding the applicability of these predictions, and characterizing impacts on reef communities in the future. Further, depositing data in public repositories can help to ensure data transparency and encourage data sharing (e.g., GO2DAT, *45*; or other commonly used and open-access databases). At the same time, field and laboratory experiments must aim to further refine accurate and realistic thresholds and durations of exposure to low oxygen for different coral reef organisms to better predict future impacts on reef ecology, health, and function.

Data Availability:

All data included in this study (for all figures and statistics; *56*) are freely available on Dryad (https://doi.org/10.5061/dryad.41ns1rnj7). Data may be used if cited appropriately.

Code Availability:

All code files written and used for analyses in this study (*57*) are freely available on GitHub (https://github.com/apezner/GlobalReefOxygen). Code may be used if cited appropriately.

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Author Contributions:

AKP, TAC, and AJA conceptualized the manuscript and methodology, with contributions from MSR to methodology. AKP performed the formal analysis and visualization AKP, under supervision of TAC and AJA. AKP and AJA wrote the original draft of the manuscript. All authors (AKP, TAC, HCB, WCC, HCC, SMC, TC, MDD, SAHK, DIK, YBL, TRM, SM, HNP, MSR, JES, KS, YT, MT, YW, KKY, and AJA) contributed to investigation as well as review and editing of the manuscript.

Competing Interests Statement:

Authors declare that they have no competing interests.

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Methods:

Sensor and deployment information

The majority of dissolved oxygen data presented in the current study (25 of 32 sites) were recorded by SeapHOx or Sea-Bird Scientific CTD sensor packages with Aanderaa oxygen optodes (Table S1). The remaining oxygen datasets were recorded by Idronaut CTD and oxygen sensor packages (Dongsha 1 and Dongsha 2), Sea-Bird SBE19 Plus CTD and SBE 43 oxygen sensor packages (Baker, Jarvis, Palmyra 3, and Tutuila), or Sea-Bird Scientific CTD and PME miniDOT sensor packages (Taiping 1). Detailed site and deployment information can be found in the Supplementary Information Extended Methods section. For each location, different instrument deployment sites are represented by numbers (e.g., Dongsha 1 and Dongsha 2), or a combination of letters and numbers where letters represent either different depths at the same site (e.g., Bocas 1a, 1b, 1c, and 1d) or different deployments at the same site over time (e.g., Crocker 1a, 1b, and 1c).

Calibrations and conversions of datasets

All sensors were calibrated by the manufacturer or according to manufacturer's instructions by the user as noted in previous publications *(46-53)*. If applicable, salinity corrections were implemented according to manufacturer's specifications and analog measurements were converted from voltages to concentrations. Data were assessed for quality and erroneous data points (defined as missing values or values that exceeded the measurement range of the instrument), which were flagged and excluded from any subsequent analyses. Deployment data were restricted to measurements in seawater based on salinity values to exclude extraneous data points collected during instrument transport, initial deployment, or recovery (exposure to air). Density calculations using the Gibbs Seawater Toolbox functions *(54)* in RStudio *(55)* were used to convert all oxygen concentration units to μmol O_2 kg^{-1}. See Supplementary Information Extended Methods (and Table S9) for an assessment and discussion on the potential errors and uncertainty of the oxygen measurements. All data (*56*) and relevant code (*57*) files are available for download online and may be used with proper attribution.

Literature review of tropical coral low oxygen experiments

In order to place our results into context of reported tropical coral responses to low oxygen conditions, we conducted a literature review of published, peer-reviewed studies that tested the effects of low oxygen conditions on coral responses (Table S8). The review was conducted using references cited in previous review papers (*8-9*) as well as searches on Google Scholar of "coral hypoxia experiment", "coral oxygen experiment", and "coral anoxia experiment" and references of papers found via these searches. Experiments testing oxygen alone or in combination with other stressors were included. In total, 16 studies were identified testing 19 different species of tropical corals (Table S8).

Calculations of daily statistics

The mean and absolute daily minimum and maximum (Fig. 2A, Table S2) as well as the mean daily range (Table S2) were calculated for each site. These calculations excluded partial days of data (i.e., the first and last days of the deployment were excluded to avoid bias) to ensure means and extremes were calculated over full 24-hour cycles.

Depth, flow speed, and reef type analyses

To test the influence of depth, flow speed, and reef type on oxygen variability, we performed regression analyses to assess the relationship between: (1) oxygen variability, depth, and reef type; (2) oxygen variability, flow speed, and reef type; (3) oxygen minimum, depth, and reef type; and (4) oxygen minimum, flow speed, and reef type. Oxygen variability was defined as the mean daily range in dissolved oxygen for each site and oxygen minimum was defined as the mean daily minimum dissolved oxygen for each site (both in μmol O_2 kg^{-1}). Depth used was either the depth provided by the data owners and reported in the relevant studies (see Table S1) or as the mean ± 1 standard deviation as recorded by current meters deployed alongside the oxygen sensors at select sites. Mean flow speed was calculated as the mean, depth-integrated flow speed from current meters that were co-deployed with a subset of the oxygen sensors used in this study. The analyses using depth and oxygen variability or oxygen minimum were performed for all sites, excluding Hog 1a, as this sensor was not deployed on the benthos. The analyses using flow speed were only performed for a subset of sites where flow meters were deployed at the same time and in the same location as the oxygen sensor (Table S3). Reef type was defined for each site using a published guide of reef cover classifications (*58*, Table S1). Regression coefficients were determined using the MATLAB Curve Fitting Tool using a Power fit type (as in *14*; see Table S4).

Calculations of intensity, duration, and severity

The intensity (*I*), duration (*D*), and severity (*S*) of hypoxic observations and events were calculated by modifying a methodology applied to seawater aragonite saturation states by Hauri et al. (*23*) according to Equations 1-3 below. Prior to calculations, datasets that were not at a 30-minute sampling frequency were either subsampled (Dongsha 1, Dongsha 2, Hog 1a, Hog 1b, Dongsha 3, Okinawa 2, Okinawa 3, Taiping 1, Taiping 2, Tutuila, Baker, Jarvis, Palmyra 3) or interpolated (Crocker 1a, 1b, 1c; Palmyra 1b) to a 30-minute sampling frequency to standardize comparisons across datasets. Linear interpolations were performed using the approx() function in RStudio (*55*).

For individual hypoxic observations, the intensity (I_{obs}; μmol O_2 kg^{-1}) was calculated as the difference between the observed oxygen concentration (DO_{obs}; μmol O_2 kg^{-1}) and the threshold of hypoxia (T; μmol O_2 kg^{-1}):

$$I_{obs} = T - DO_{obs} \qquad \text{(Equation 1)}$$

For hypoxic events, consecutive observations below a given oxygen threshold were identified using the rleid() function of the data.table package (*59*) in RStudio (*55*, *57*). Intensity of the event (I_{event}; μmol O_2 kg^{-1}) was calculated as the difference between the threshold (T) and the mean oxygen concentration during the event ($\overline{DO_{event}}$):

$$I_{event} = T - \overline{DO_{event}} \qquad \text{(Equation 2)}$$

Severity of the event (S; μmol O_2 kg^{-1} hr) was calculated as the product of the event intensity (I_{event}) and duration (D; hours) (*23*):

$$S = I_{event} * D \qquad \text{(Equation 3)}$$

For these calculations, we used four hypoxia thresholds: 153 μmol O_2 kg^{-1} (~5 mg O_2 L^{-1}), 122 μmol O_2 kg^{-1} (~4 mg O_2 L^{-1}), 92 μmol O_2 kg^{-1} (~3 mg O_2 L^{-1}), and 61 μmol O_2 kg^{-1} (~2 mg O_2 L^{-1}). While many aquatic studies use the threshold of ≤2 mg O_2 L^{-1} (~61 μmol O_2 kg^{-1}) to define environmental dissolved oxygen levels as hypoxic, it has been shown that this threshold, originally identified as the level at which great reductions in benthic macrofauna would be observed in Northern European fjords (*60*), is inadequate as a threshold for all marine species (*15-16, 61*). We provide the three additional thresholds to better capture a range of organism sensitivities to both lethal and sublethal impacts. Based on Vaquer-Sunyer and Duarte (*16*), we chose a "weak" hypoxia threshold of 153 μmol O_2 kg^{-1} (~5 mg O_2 L^{-1}) as the upper bound of our thresholds, as it is the oxygen concentration that captured 90% of sublethal impacts in temperate benthic marine organisms. We then added thresholds at regular intervals between the severe and weak thresholds, with a "mild" hypoxia threshold of 122 μmol O_2 kg^{-1} (~4 mg O_2 L^{-1}; an upper bound of lethal oxygen levels determined for the tropical coral *Acropora yongeii*; *18*) and a "moderate" hypoxia threshold of 92 μmol O_2 kg^{-1} (~3 mg O_2 L^{-1}). The terminology of "deoxygenation" was not used in this context, as "ocean deoxygenation" has been previously defined as "the global process of declining O_2 concentrations projected to occur over an extended period, decades or longer, caused predominantly by processes resulting from climate change," (*62*) and thus is a process occurring on a much greater time and space scale than the individual reef habitats we surveyed here. Calculations of intensity (for events and observations), duration of events, and severity of events were performed for each threshold (Fig. 2B-F, Extended Data Fig. 6-8).

Temperature projection data

We extracted predicted sea surface temperature (SST) rise values for each location (Extended Data Fig. 3) from the Coupled Model Intercomparison Project 6 (CMIP6) ensemble member Community Earth System Model Whole Atmosphere Community Climate Model (CESM2-WACCM) (*63-64*). The model was run by the National Center for Atmospheric Research (NCAR) in 2018, with a 0.9° × 1.25° finite volume grid atmosphere with 70 levels coupled with 320 × 384 longitude/latitude ocean with 60 levels (*63-64*). The model used the Historical, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 simulations (*63-64*). Monthly SST data from the closest grid cell to each location's latitude and longitude were averaged and compared between present-day (mean of the 2015–2020 annual SST) and end of century (mean of 2090–2100 annual SST) to calculate anticipated increase in temperature by 2100 (Table S5). This methodology was used so that the warming estimates would be less dependent on year-to-year climate variability events.

Predicting changes in dissolved oxygen due to warming

We calculated changes in DO concentrations as a result of the physical and biological effects of temperature rise on DO solubility and biological oxygen demand (i.e., total respiration rates), respectively, based on measured DO at each reef site and the projected CMIP6 temperature rise for each location. A simple box model was also used to validate the methodology and calculations used to approximate changes in DO solubility and biological oxygen demand (see Supplementary Material Extended Methods and Extended Data Fig. 5).

Calculating the impact of warming on solubility

Changes in DO solubility were calculated for each site under each climate projection (DO_{sol_SSP126}, DO_{sol_SSP245}, DO_{sol_SSP370}, DO_{sol_SSP585}) and a 6 ºC heatwave scenario ($DO_{sol\_heatwave}$) using Equations 4–5 (*65*) assuming only changes in temperature:

$$T_s = \log\left(\frac{(298.15 - t)}{(273.15 + t)}\right) \qquad \text{(Equation 4)}$$

$$\ln(DO_{sol}) = A_0 + A_1T_s + A_2T_s^2 + A_3T_s^3 + A_4T_s^4 + A_5T_s^5 + S(B_0 + B_1T_s + B_2T_s^2 + B_3T_s^3) + C_0S^2 \qquad \text{(Equation 5)}$$

where t is temperature (ºC), T_s is the scaled temperature, DO_{sol} is the solubility (μmol O_2 kg^{-1}), A_0 is 5.80818, A_1 is 3.20684, A_2 is 4.11890, A_3 is 4.93845, A_4 is 1.01567, A_5 is 1.41575, B_0 is -7.01211e-03, B_1 is -7.25958e-03, B_2 is -7.93334e-03, B_3 is -5.54491e-03, C_0 is -1.32412e-07, and S is salinity (PSU) (constants provided in *65*).

Changes in DO concentration as a result of changes in solubility (ΔDO_{sol}) due to warming from present-day were then calculated for each site and projection:

$$\Delta DO_{sol} = DO_{sol\,present} - DO_{sol\,proj} \qquad \text{(Equation 6)}$$

where $DO_{sol\_present}$ is the solubility of DO under present-day measured temperature and salinity conditions (μmol O_2 kg^{-1}) and DO_{sol_proj} is the solubility of DO for a given temperature rise projection or scenario, calculated from Equations 4–5 (μmol O_2 kg^{-1}).

Calculating the impact of warming on respiration

The respiration signal of each reef at present-day was approximated from the difference between the mean dissolved oxygen ($\overline{DO}$; μmol O_2 kg^{-1}) across the entire deployment and the mean daily minimum dissolved oxygen concentration ($\overline{DO_{min}}$; μmol O_2 kg^{-1}), according to Equation 7:

$$DO_{offset} = \overline{DO} - \overline{DO_{min}} \quad \text{(Equation 7)}$$

Thus, DO_{offset} (μmol O_2 kg^{-1}) reflects the observed changes in DO owing to the net effect of nighttime respiration, air-sea gas exchange, and physical transport processes, assuming that, on average, the daily mean DO at each location is close to 100% saturation. However, since air-sea gas exchange is quantitatively small relative to respiration rates on coral reefs and the flow is from air to sea at night, gas exchange was assumed to be negligible although it leads to a slight underestimation of the respiration signal. Similarly, day-to-day changes in water transport, current speed, trajectory, and residence time could also influence the observed DO loss, but on average each site is characterized by a set of baseline conditions constrained by the tidal cycle, depth, geomorphology, wind and swell conditions, which favors the application of DO_{offset} as an approximation of the respiration signal at each location. The daily statistics of DO_{offset} were calculated excluding the first and last days of the deployment in order to exclude partial days (less than full 24-hour periods) from the mean.

To assess the biological impacts of each temperature rise scenario on biological oxygen demand, the change in respiration rate was calculated using a Q_{10} relationship according to Equations 8–9 for each site and temperature scenario:

$$T_{rise} = T_2 - T_1 \quad \text{(Equation 8)}$$

$$R_2 = R_1 * Q_{10}^{\left(\frac{T_{rise}}{10}\right)} \quad \text{(Equation 9)}$$

where T_{rise} is the difference between baseline T_1 and projected T_2, R_2 is the respiration rate under increased temperature T_2, R_1 is the respiration rate at present temperature (T_1), and Q_{10} is the unitless metabolic quotient (*66-67*). In the present study, we assumed a Q_{10} of 2 (i.e., metabolic rate, in this case respiration, doubles for every temperature increase of 10 ºC), based on the literature for coral metabolism (*68-72*). However, because absolute respiration rates were unknown (i.e., R_1), the reduction in DO concentrations due to increased respiration under different warming scenarios was calculated based on the ratio of R_2 and R_1 and the estimated respiration signal, DO_{offset}, according to Equations 10–11 (Extended Data Fig. 4):

$$DO_{offset_{Q10}} = DO_{offset} * \left(\frac{R_2}{R_1}\right) \qquad \text{(Equation 10)}$$

$$\Delta \mathrm{DO}_{Q10} = DO_{offset_{Q10}} - DO_{offset} \qquad \text{(Equation 11)}$$

where DO_{offset_Q10} (μmol O_2 kg^{-1}) is the expected change in DO_{offset} (change in DO due to respiration at present) as a result of increased respiration and ΔDO_{Q10} is the decrease in DO concentration, accounting for present-day respiration rates.

Combined impacts of warming on solubility and respiration

Combining the physical (changes in solubility) and biological (changes in respiration rate) effects of temperature rise, expected net reduction in DO concentration for each reef site and under each scenario was calculated using Equations 12-13 (Extended Data Fig. 4):

$$\Delta DO = \Delta DO_{Q10} + \Delta DO_{sol} \qquad \text{(Equation 12)}$$

$$DO_{proj} = DO - \Delta DO \qquad \text{(Equation 13)}$$

where ΔDO (μmol O_2 kg^{-1}) is the total combined decrease in DO concentration, DO_{proj} is the projected DO concentration (μmol O_2 kg^{-1}) for each site and under each warming scenario, and DO is the present-day measured DO concentration at each site (μmol O_2 kg^{-1}).

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Figure Legends/Captions:

Fig. 1. Oxygen sensor deployment sites and locations, hourly oxygen climatologies, and oxygen distributions on global coral reefs. (**A**) Map and satellite images (Google Earth) of the study locations including specific instrument deployment sites (symbols) at each location. Reef type is indicated by the shape of the symbols according to the legend below the images. Some sites had instruments deployed at multiple depths or over multiple years and seasons (Table S1). Map Images and Data: Google, Maxar Technologies, CNES/Airbus, SIO, NOAA, U.S. Navy, NGA, GEBCO. (**B**) Mean ± shaded lower and upper 95 % confidence interval of the hourly climatology of dissolved oxygen (DO) concentrations for all sites (n varies by site, see Table S2). The grey dashed lines indicate the four hypoxia thresholds: 153, 122, 92, and 61 μmol O_2 kg^{-1}. (**C**) Ridgeline distributions of DO concentration and percent saturation grouped by location. Vertical grey dashed lines indicate four hypoxia concentration thresholds as in **B**. In all panels, the color scheme follows the location colors used in **A**.

Fig. 2. Shifts in dissolved oxygen concentration, hypoxic event duration, and occurrence of hypoxia exposure under warming on global coral reef sites. (**A**) Dissolved oxygen (DO; μmol O_2 kg^{-1}) at present-day and under 5 different warming projections (including 4 Shared Socioeconomic Pathways (SSPs) and a heatwave scenario; blue to red). Vertical dark shaded bars represent the mean daily range of DO for each reef site (n varies by site, see Table S2) (Table S5). The lower and upper bounds of the vertical light shaded bars represent the lowest daily minimum oxygen and highest daily maximum oxygen concentration, respectively (n varies by site, see Table S2). The grey dashed lines indicate the hypoxia thresholds: 153 μmol O_2 kg^{-1} (weak), 122 μmol O_2 kg^{-1} (mild), 92 μmol O_2 kg^{-1} (moderate), and 61 μmol O_2 kg^{-1} (severe). Within each location, different instrument deployment sites are represented by numbers (e.g., Dongsha 1 and Dongsha 2), or a combination of letters and numbers where letters represent either different depths at the same site (e.g., Bocas 1a and 1b) or different deployments at the same site over time (e.g., Crocker 1a, 1b, and 1c) (see Table S1 for specific site information). (**B-E**) Percent of sites (n = 32) that experience hypoxic events lasting within different categories of duration (x-axis; hours) at present-day and for each warming projection (blue to red) for each hypoxia threshold (153, 122, 92, or 61 μmol O_2 kg^{-1}; **B-E**, respectively). (**F**) Percent increase in

the total number of observations below each hypoxia threshold (153, 122, 92, and 61 μmol O_2 kg^{-1}) across all sites for each warming projection relative to present-day.

Fig. 3. Timing of present-day hypoxic observations across global coral reef sites. Percent of recorded dissolved oxygen observations below each hypoxia threshold (153, 122, 92, and 61 μmol O_2 kg^{-1}; light to dark blue) occurring at each hour of the day for all global coral reef sites and deployments. Daylight hours denoted by orange shaded box (local time).