



Tropical dead zones and mass mortalities on coral reefs

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Degradation of coastal water quality in the form of low dissolved oxygen levels (hypoxia) can harm biodiversity, ecosystem function, and human wellbeing. Extreme hypoxic conditions along the coast, leading to what are often referred to as “dead zones,” are known primarily from temperate regions. However, little is known about the potential threat of hypoxia in the tropics, even though the known risk factors, including eutrophication and elevated temperatures, are common. Here we document an unprecedented hypoxic event on the Caribbean coast of Panama and assess the risk of dead zones to coral reefs worldwide. The event caused coral bleaching and massive mortality of corals and other reef-associated organisms, but observed shifts in community structure combined with laboratory experiments revealed that not all coral species are equally sensitive to hypoxia. Analyses of global databases showed that coral reefs are associated with more than half of the known tropical dead zones worldwide, with >10% of all coral reefs at elevated risk for hypoxia based on local and global risk factors. Hypoxic events in the tropics and associated mortality events have likely been underreported, perhaps by an order of magnitude, because of the lack of local scientific capacity for their detection. Monitoring and management plans for coral reef resilience should incorporate the growing threat of coastal hypoxia and include support for increased detection and research capacity.

biodiversity | coral bleaching | dissolved oxygen | hypoxia | water quality

The decades-long decline of coral reefs and the roles of overfishing, pollution, and climate change in this decline have been documented extensively (1–6). Although hypoxia and the associated phenomenon of “dead zones” have gained increasing attention of late (7, 8), the threat posed by hypoxia to coral reefs is rarely mentioned. For example, hypoxia is not discussed in several of the most influential reviews of threats to coral (4, 9, 10) and was mentioned in only 0.2% of the abstracts from the 2016 International Coral Reef Symposium (Table S1). Here we describe a massive coral-mortality event caused by hypoxia and document how such events may be underreported globally because of the lack of scientific capacity in regions where coral reefs are found.

Bahía Almirante in the Bocas del Toro region of Panama is a large, semienclosed basin of 450 km². It displays many characteristics common to temperate estuaries that suffer from episodic or seasonal anthropogenic hypoxia, including restricted exchange with the open ocean, seasonal periods of low winds and high temperatures, and a watershed delivering increasing amounts of nutrients from agricultural run-off and untreated sewage (11, 12). Although the reefs in the bay showed some signs of human impacts before the hypoxic event, they were relatively healthy for the region, averaging 25–30% cover of live coral (6, 13). The dominant corals were *Porites* spp. in shallow water and a mixture of *Agaricia* spp. and mounding corals at greater depths (13).

In late September 2010, reefs within Bahía Almirante exhibited widespread coral bleaching and some mortality (Fig. 1*A–D*). Some of those reefs showed additional signs of severe stress not typically associated with coral bleaching: Sponges exhibited extensive necrosis; recruitment tiles retrieved after 1 y had an atypical lack of successful recruitment by fouling organisms; mobile organisms displayed

unusual behaviors such as migration out of crevices; dead bodies of crustaceans, gastropods, and echinoderms littered the bottom (Fig. 1*E*); and thick mats of *Beggiatoa* bacteria covered the surface of sediments. The presence of dead but intact bodies of sponges, crustaceans, and echinoderms suggested that the extreme stress leading to mortality had occurred relatively recently and was possibly ongoing, and that hypoxia likely excluded consumers that otherwise would have targeted dead and moribund prey (14). Most notably on these reefs, signs of mortality and stress occurred below a clearly demarcated depth horizon. This line was sufficiently distinct that sponges and mounding coral colonies that straddled the line initially suffered mortality at the bottom but not at the tops of their structures (Fig. 1*F*). Together these observations were highly suggestive of hypoxic stress caused by benthic microbial activity whose effects were isolated from shallower waters by stratification of the water column (15). Initial measurements confirmed this hypothesis, with extremely low oxygen levels (<0.5 mg/L) near the bottom at some sites, a phenomenon that had not been recorded previously in the lagoon (16).

We therefore initiated a widespread survey of water-column conditions across Bahía Almirante on October 1, 2010. The 19 survey sites spanned from the more impacted inner bay, where biological evidence of stressful conditions was most marked, to the outer bay near passages that promote exchange with the open ocean. We found that oxygen concentrations varied widely along this spatial gradient, with very low concentrations (<0.5 mg/L) of dissolved oxygen near the bottom (at a depth >10 m) at several sites (Fig. 2*A*). Consistent with biological observations, dissolved oxygen levels were always high at shallow depths, with concentrations >4.8 mg/L at 3–4 m at all sites. Notably, the most hypoxic deeper waters were those closest to the mainland, where terrestrial inputs are expected to be greatest and exchange with the open ocean lowest, and near settlements that discharge untreated sewage.

Significance

Oxygen-starved coastal waters are rapidly increasing in prevalence worldwide. However, little is known about the impacts of these “dead zones” in tropical ecosystems or their potential threat to coral reefs. We document the deleterious effects of such an anoxic event on coral habitat and biodiversity, and show that the risk of dead-zone events to reefs worldwide likely has been seriously underestimated. Awareness of, and research on, reef hypoxia is needed to address the threat posed by dead zones to coral reefs.

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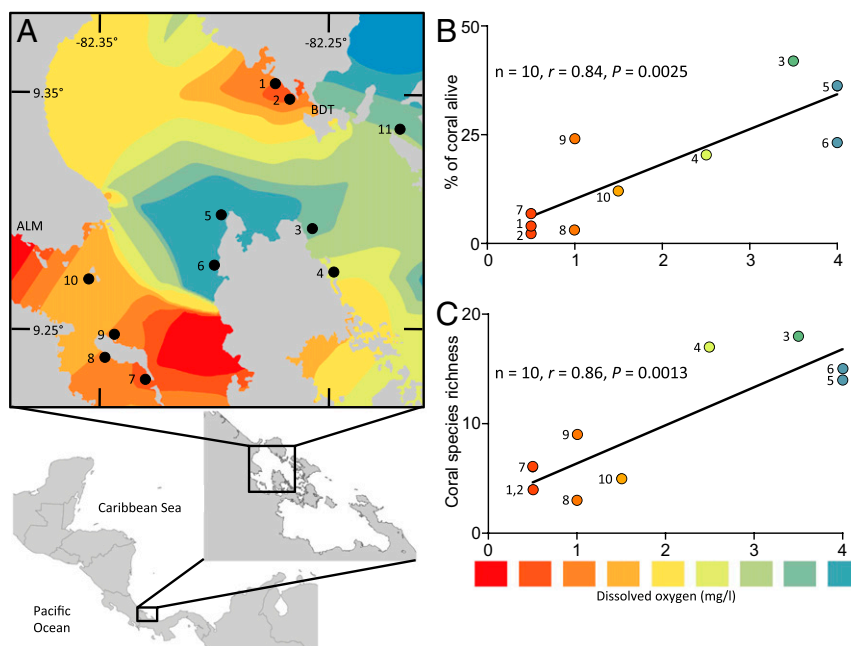


Fig. 2. Spatial distribution of hypoxia at 10–12 m depth (October 2010) and its consequences. (A) There were two distinct pockets of hypoxia, one near the mainland with terrestrial inputs [lower left, near Almirante town (ALM)], and the other near dense settlements of Bocas del Toro (BDT) where the Bocas del Toro Research Station is located. Land is shown in gray. Color indicates the intensity of hypoxia as shown in the scale in the figure. Sites 1 and 11 were initial reef-assessment sites (2010–2011); sites 1–10 were 10 subsequent coral-survey sites (2012). (B and C) Dissolved oxygen during the hypoxic period in 2010 was correlated with both the percent of coral cover at a site that was alive (B) and species richness of coral remaining alive in 2012 (C). Data were analyzed by Pearson's correlation. Note that dissolved oxygen levels were always >4.8 mg/L at the shallow depth (3–4 m) (Fig. S1A).

tolerance. We tested this hypothesis (and the alternative that thermal stress was the cause of mortality) by conducting multifactorial laboratory experiments in which we challenged *Agaricia lamarcki* and *S. intersepta* with the oxygen and temperature conditions that occurred during the hypoxic event. We found that the two species were similarly able to tolerate thermal stress but varied greatly in their hypoxia tolerance, with *S. intersepta* exhibiting a threefold greater hypoxia tolerance than *A. lamarcki* (Fig. 3 C and D).

To examine whether comparable hypoxic events had occurred in the recent past in Bocas del Toro, we compared the death assemblage at impacted sites with the living assemblage at unimpacted sites by measuring the size of the largest colonies of *A. lamarcki* (living or dead) in randomly selected plots at the sites that were most (sites 1 and 2) and least (sites 3 and 5) impacted by hypoxic mortality. We assumed that large colony size is indicative of colony longevity and that previous hypoxic events that caused coral mortality would have truncated colony size. We found no difference in average colony size across sites ($F_{3,77} = 0.64$, $P = 0.59$), suggesting that other major hypoxia-associated mortality events had not occurred recently.

To determine the likelihood of similar hypoxic events occurring on coral reefs elsewhere, we compiled and analyzed several global databases. First, we assessed a global database of all known dead zones and found that coral reefs are located in approximately half (22/43) of the tropical bays or estuaries where dead zones have been reported (Fig. 4A). Second, we randomly selected 100 reefs from each of the six global coral regions and found that an average of 13% of coral reefs worldwide are at an increased risk of hypoxia, both because of their elevated score on an index of exposure to anthropogenic impacts that contribute to low oxygen conditions (e.g., eutrophication and climate change) and because of their occurrence in semienclosed bays that can support the formation of dead zones (Fig. 4B). Third, we conducted a thorough review of the literature and identified 20 instances in which hypoxia was implicated in the mass mortality of coral reef organisms (Fig. 4A and Table S2).

These analyses also suggest that dead zones on coral reefs are likely severely underreported, perhaps by an order of magnitude. The number of documented dead zones is higher in temperate regions than in the tropics by a factor of 10 (Fig. 4A and C), a trend that persists even after correcting for the length of coastline in each region and even though higher temperatures increase the severity of dead zones and the sensitivity of organisms to hypoxia (24). If the density of dead zones scales from temperate to tropical regions as a function of shoreline length, then at least 370 dead zones are yet to be described, half of which could be expected to affect coral reefs based on the assessment above. Although the historically greater intensity of agricultural fertilizer use in developed countries may have contributed to the relatively higher number of documented hypoxic ecosystems in temperate regions (7), the widespread evidence for eutrophication effects on coral reefs associated with run-off from intensifying agricultural practices, poorly regulated sewage discharge, and rapidly growing coastal populations suggests that tropical ecosystems are highly susceptible to the localized effects of anthropogenic nutrient inputs (25).

Many factors likely contribute to the underreporting of dead zones affecting tropical ecosystems and the lack of recognition of dead zones as a threat to coral reefs (4, 9, 26). In the case of the Bocas del Toro event, documentation of hypoxia and associated coral reef mortality in the present study was largely a serendipitous result of having an active international research station near one of the most impacted reefs (Fig. 2A); had observers not been on hand, attributing the cause of mortality to low oxygen even a few months later would have been extremely difficult. In addition, as is generally the case, scientific research on dead zones is dominated by investigators from temperate zone countries or other countries with strong research investment (Fig. 4C); 37% of the 43 known tropical dead zones were first described by research teams led by principal investigators based in the United States or Europe, and another 28% were described by teams with principal investigators from Brazil, India, or China—countries with

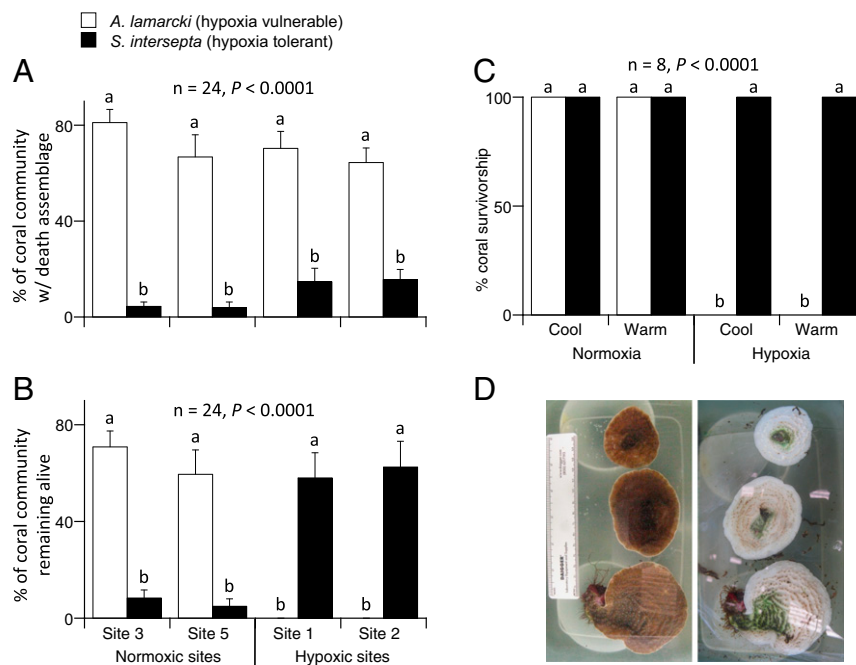


Fig. 3. Shifts in community structure toward hypoxia-tolerant coral species. (A) Before the hypoxic event, using the record of all corals both alive and dead as a proxy for relative abundance, the cover of *Agaricia* spp. was consistently higher than *S. intersepta* across all four sites, and there was no difference among sites in the cover of either taxon. (B) Following the hypoxic event, *S. intersepta* emerged as the dominant species among the corals remaining alive at the two sites that experienced hypoxia, whereas *Agaricia* spp. persisted as the dominant living coral at the two sites that did not experience hypoxia. (C) Subsequent laboratory tolerance experiments suggested that hypoxia, not thermal stress, was the primary driver of the mortality patterns in the field because *S. intersepta* had high survivorship across all treatments, and *A. lamarcki* (92% of *Agaricia* spp. at study sites) survivorship was affected by hypoxia but not by temperature treatment. Cool = 28 °C; warm = 32 °C; normoxic = >5 mg/L dissolved oxygen; hypoxic = 0.5 mg/L dissolved oxygen. (D) Photos of *A. lamarcki* on day 0 (Left) and day 7 (Right) of the cool, hypoxic treatment. Note green algae colonizing dead colonies on day 7. Data in A and B are mean (\pm SE) percent cover analyzed by ANOVA. Data in C are the proportion of replicate containers with surviving corals analyzed by Kaplan–Meier survivorship analysis. Different letters above bars indicate significant differences in percent cover and survivorship, respectively.

advanced research infrastructure. These findings suggest that the skewed distribution of research capacity contributes to the apparent deficit of documented dead zones in tropical ecosystems, and that further economic development may increase the detection of those hypoxic ecosystems.

Other aspects of coral reef research traditions probably contribute to the lack of recognition of hypoxia on coral reefs as well. Monitoring protocols for coral reefs typically do not call for measurements of oxygen concentrations (27), making it difficult to identify hypoxia-driven mortality after it has occurred. In fact, of the 20 instances that we uncovered in which coral reef mortality was attributed to hypoxia, only four studies in addition to ours collected both biological and oxygen data, and only one included data on corals (Table S2). Moreover, investigators often focus their studies on relatively healthy coral communities and avoid those near shoreline development and terrestrial inputs (28). Hence, hypoxia may cause a shift toward tolerant species or the elimination of entire reefs before scientific documentation, resulting in a shifted baseline (29).

How coral reefs recover from hypoxia is even less understood. In the case of reefs in Bocas del Toro, it remains to be seen what factors will control recovery, whether phase shifts will occur, and how ecosystem functions will be affected. Changes in coral community structure were still evident nearly 4 y after the hypoxic event, with no apparent recovery in the cover of live coral ($P > 0.10$). Moreover, these changes occurred in an ecosystem where the coral community had already shifted toward more stress-tolerant species in recent centuries in association with human impacts, including fisheries exploitation and land-use change (30–32). The long-term effects of hypoxia are potentially different from, and more substantial than, those of other disturbances on coral reefs because hypoxia affects a broad range of taxa including consumers, habitat

formers, and pathogens. However, at least some functional groups show high resilience, because several years after the event the diversity and abundance of mobile invertebrates on previously hypoxic reefs was found to be the same as, or higher than, the diversity and abundance on unaffected reefs (33), and grazing pressure has been sufficient to preempt overgrowth of dead coral by algae (34).

Although death by hypoxia can be widespread and swift, local management of terrestrial inputs (e.g., nutrients and organic carbon loading from run-off and sewage) within a watershed can be effective in reducing the probability that hypoxic events will occur (7). Indeed 494 coastal dead zones are currently listed, but 55 are recorded as having improved water quality (35). Thus, enhanced research capacity, particularly in developing countries, and awareness of hypoxia's potential impacts on coral reefs could form the basis for targeted efforts to manage tropical shorelines to protect them from the threat of coral reef mortality associated with dead zones.

Materials and Methods

To rank the research attention that hypoxia receives relative to other threats to coral reefs, we quantified the number of ICRS 2016 abstracts that examined the effects of climate/thermal stress, fishing, disease/invasive species, sedimentation/land use, ocean acidification, and hypoxia. We assessed dissolved oxygen, salinity, and temperature conditions at shallow (3–4 m) and deep (10–12 m) depths at 19 sites in Bahia Almirante in October 2010, and maps of variation in each parameter across the study area (at 10–12 m depth) were created in ArcGIS (Fig. 2 and Fig. S1). To assess the initial response of coral reefs to hypoxia, we sampled the cover of live, dead, and bleached coral from representative reefs inside (site 1) and outside (site 11) the hypoxic area (Fig. 2A) on November 2010, January 2011, and July 2011. We then conducted a more detailed survey of coral cover and species richness at both shallow and deep depths at 10 sites that spanned the hypoxia gradient in April 2012 (Fig. 2) and again in April 2014. To test for evidence of prior mass-mortality events that would truncate the size distribution of corals, we quantified colony size at two dead

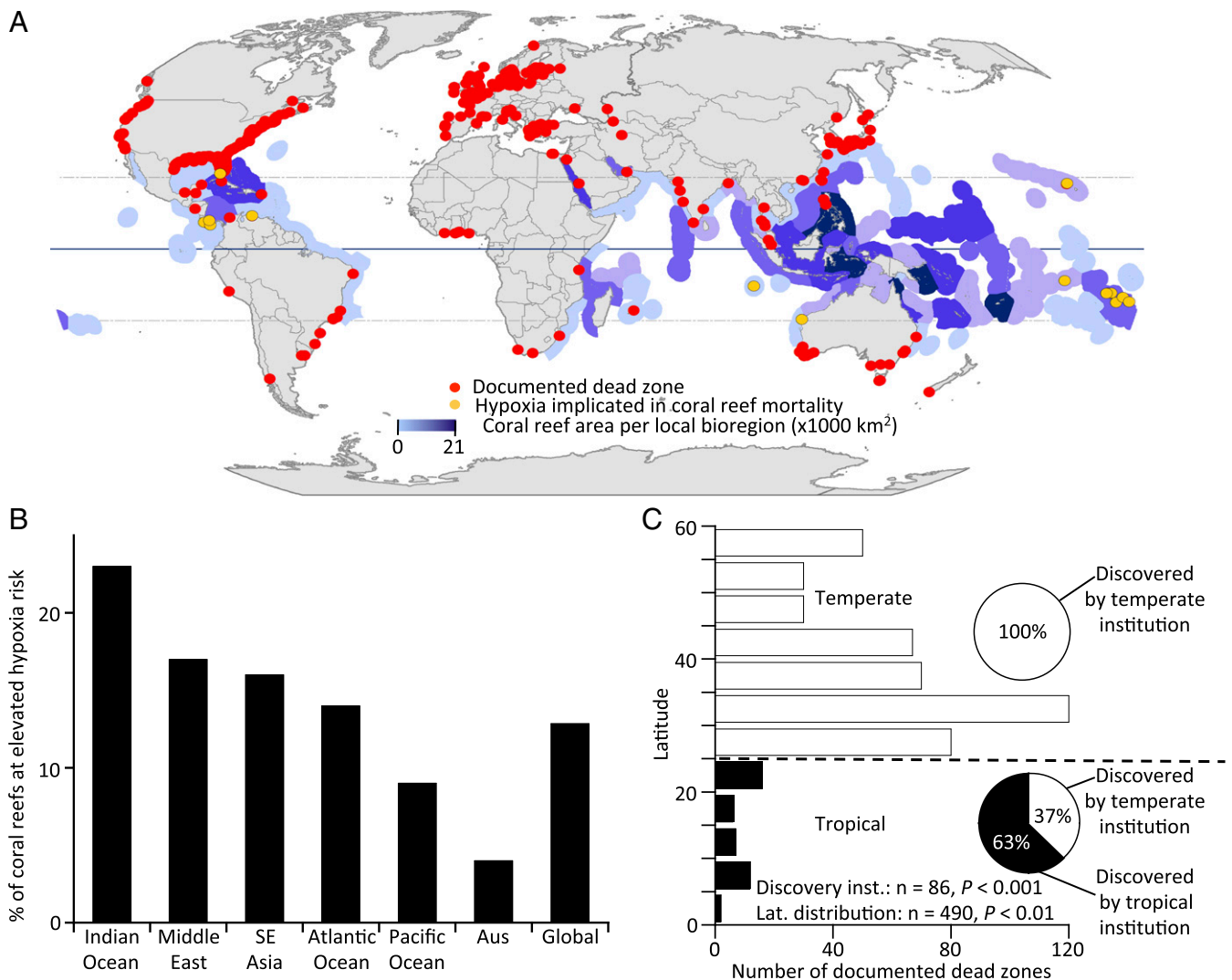


Fig. 4. Worldwide distribution of dead zones and coral reefs. (A) Global map with all known dead zones (red dots) and coral reefs where hypoxia has been implicated in mass mortality of reef organisms (gold dots). Documented dead zones are notably concentrated in temperate regions in areas with relatively greater research capacity, whereas coral reefs are found primarily in the tropics. The solid horizontal line represents the equator, and the upper and lower dashed lines represent the Tropics of Cancer and Capricorn respectively. Intensity of purple color indicates densities of coral reef area per ecoregion, from lightest to darkest: 0, 1–1,000, 1,001–2,500, 2,501–5,000, 5,001–10,000, and 10,001–21,000 km². (B) The proportion of coral reefs at elevated risk of hypoxia, for each major coral region and a global average weighted by relative coral area in each region, based on coastal geomorphology and anthropogenic drivers of low oxygen. (C) The distribution of dead zones by latitude. Dead zones are relatively underrepresented in tropical regions and are overrepresented in temperate areas given the length of the coastline in each region (analysis by Kolmogorov–Smirnov test). Degrees of latitude are absolute values, so northern and southern hemisphere latitudes are pooled. (Insets) Circle graphs show that tropical dead zones were likely to be first identified by research teams from temperate institutions, whereas temperate dead zones were never identified by teams from tropical institutions (analysis by χ^2 test).

zone sites and two unimpacted sites. We conducted a laboratory experiment to examine the relative tolerance of *A. lamarcki* and *S. intersepta* to temperature and hypoxia conditions associated with the dead-zone event at the Bocas del Toro Research Station and to test whether levels of those factors during the event were sufficient to cause mortality in either species (Fig. 3). We updated the global database of hypoxic sites (7, 35) by conducting a literature search and then examined geographic trends in the risk of dead zones to coral reefs in three ways (Table S3). First, we quantified the proportion of coral reefs worldwide that are at elevated risk of exposure to hypoxia based on geomorphological setting and an index of exposure to anthropogenic factors (Fig. 4 A and B) (27). Second, we examined the proportion of known tropical hypoxic ecosystems in our global hypoxia database that contain coral reefs according to reef locations documented in the databases (e.g., ref. 27) and the literature. Third, we searched the literature for all studies that associated hypoxia with the death of corals or other reef organisms (Table S2). We tested whether the distribution of known dead zones was disproportionately skewed away from the tropics and toward temperate regions by comparing the

distribution of dead zones in our database with the distribution of relative coastline length across 5° latitude bins (Fig. 4C). To examine whether research capacity could explain this skewness, we tested whether dead zones in tropical and temperate regions were more likely to have been first described by investigators from the other region (Fig. 4C). Extended materials and methods that detail procedures and analyses are available in *SI Materials and Methods*.

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