



W&M ScholarWorks

VIMS Articles

2017

Tropical dead zones and mass mortalities on coral reefs

AH Altieri

SB Harrison

J Seemann

R Collin

RJ Diaz

Virginia Institute of Marine Science

See next page for additional authors

Follow this and additional works at: <https://scholarworks.wm.edu/vimsarticles>



Part of the [Aquaculture and Fisheries Commons](#)

Recommended Citation

Altieri, AH; Harrison, SB; Seemann, J; Collin, R; Diaz, RJ; and Knowlton, N, "Tropical dead zones and mass mortalities on coral reefs" (2017). *VIMS Articles*. 770.

<https://scholarworks.wm.edu/vimsarticles/770>

This Article is brought to you for free and open access by W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.

Authors

AH Altieri, SB Harrison, J Seemann, R Collin, RJ Diaz, and N Knowlton



Tropical dead zones and mass mortalities on coral reefs

Andrew H. Altieri^{a,1}, Seamus B. Harrison^a, Janina Seemann^{a,b}, Rachel Collin^a, Robert J. Diaz^c, and Nancy Knowlton^{d,1}

^aSmithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama; ^bFreie Universität Berlin, 12249 Berlin, Germany; ^cVirginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062; and ^dDepartment of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013

Contributed by Nancy Knowlton, January 30, 2017 (sent for review December 11, 2015; reviewed by Nancy N. Rabalais and Robert S. Steneck)

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.

Author contributions: A.H.A. and N.K. designed research; A.H.A., S.B.H., J.S., R.C., R.J.D., and N.K. performed research; A.H.A. analyzed data; and A.H.A. and N.K. wrote the paper.

Reviewers: N.N.R., Louisiana Universities Marine Consortium; and R.S.S., University of Maine.

The authors declare no conflict of interest.

Freely available online through the PNAS open access option.

¹To whom correspondence may be addressed. Email: AltieriA@si.edu or knowlton@si.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1621517114/-DCSupplemental.

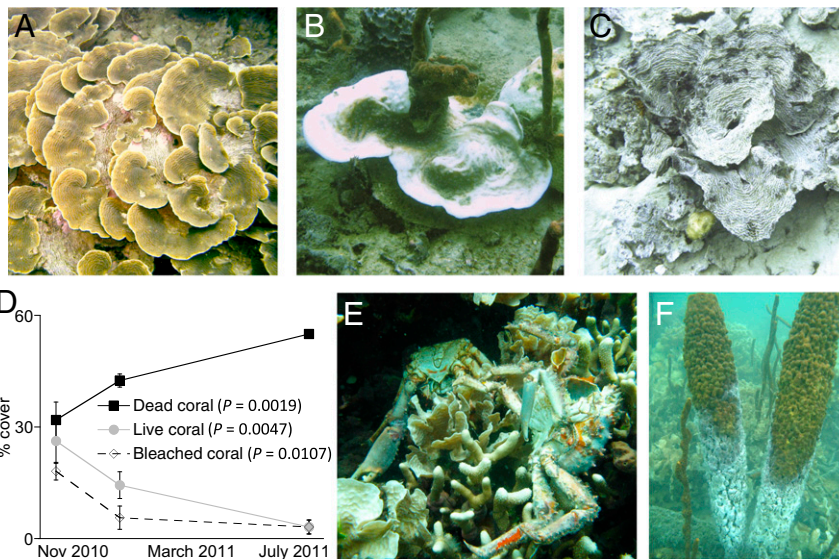


Fig. 1. Immediate effects of the hypoxic event. (A–C) Photographs of the dominant reef-building coral *A. lamarcki* found alive in normoxic sites (A), bleached during a hypoxic event (B), and dead following hypoxia (C). (D) Sampling initiated in the hypoxic area tracked initially high coral bleaching that declined in association with an increase in the prevalence of dead coral and a reduction in cover by living coral. There was no change in cover of living, dead, or bleached coral during the same period at a nearby site without hypoxia ($P > 0.38$ all analyses). Total values for a given date are $<100\%$ because of noncoral habitat within the survey area. Data are the mean (\pm SE) of the percent cover of coral category and were analyzed by ANOVA ($n = 4$ transects with 40 points per time point per site) where P values indicate change through time within a given coral category. (E and F) As is typical of hypoxic events, mortality affected a broad taxonomic cross-section of the community including reef crabs (E) and sponges (F), the latter showing gray, dead portions below the distinct depth horizon of the oxycline. A–C courtesy of Cindy T. Gonzalez (Universidad de los Andes, Bogotá, Colombia). E–F courtesy of Arcadio Castillo (Smithsonian Tropical Research Institute, Balboa, Panama).

To document the effect of this hypoxia on corals further, we quantified coral bleaching and mortality at a pair of sites near the Smithsonian's Bocas del Toro Research Station: one located within, and the other located outside of, the hypoxic area (Fig. 2A). At a depth of 10–12 m, both sites had $>25\%$ cover of live coral in November 2010. However, $76 \pm 11\%$ (mean \pm SE) of the corals were bleached at the hypoxic site, whereas only $3 \pm 2\%$ of corals were bleached at the normoxic site. By July 2011, many of the bleached corals at the hypoxic site had died, and the cover of live coral was reduced by an order of magnitude, whereas the normoxic site saw no change in the cover of live coral (Fig. 1D). These field patterns were in agreement with subsequent observations in our laboratory experiment (described below) in which hypoxic stress alone was sufficient to induce bleaching followed by death at nonstressful temperatures.

We returned to Bahía Almirante in April 2012 to conduct a more thorough and widespread survey of 10 sites for the imprint of hypoxic stress on patterns of coral community structure (Fig. 2A). At depths of 10–12 m, all sites had $>45\%$ of space occupied by coral skeletons (indicative of their potential for coral occupancy), but the proportion of coral that remained alive varied widely (2–42%). That variation was correlated with dissolved oxygen levels surveyed during the hypoxic episode (Fig. 2B). Notably, the site where widespread bleaching was documented during our earlier assessments suffered severe coral mortality, with only 4% cover of live coral remaining. There was also a spatial relationship between previous oxygen levels and live coral diversity, with the lowest diversity at the most hypoxic sites (Fig. 2C).

We detected no evidence for strong differences in water quality among the sites that could explain patterns in coral cover and richness at depth apart from the differences in observed oxygen concentration. Temperature varied by 1.5 °C, and salinity varied by one part per thousand (ppt) across our study area at the depth of the coral mortality (Fig. S1); however, we detected no influence of temperature or salinity variation on patterns of coral cover and richness among sites when considering their effects separately or their potential interactions with dissolved oxygen ($P > 0.12$ all

analyses). Nevertheless, overall elevated temperatures in the region during the hypoxic period may have increased background stress levels and the susceptibility of the coral community to hypoxia (17, 18), as is known to occur in other taxa (19). Lowered pH, which can co-occur with hypoxic conditions (20), is unlikely to have played a primary role in the mortality event we observed because coral survivorship is relatively unaffected by acidified conditions (21, 22), and coral reefs commonly tolerate wide fluctuations in pH (23).

We collected analogous community and water-quality data at shallower depths that substantiated our initial observations that the mortality event primarily impacted deeper portions of reefs and was driven by hypoxia. We found no change in cover of live coral at either of the initially surveyed sites at the 3–4 m depth ($F < 4.20$, $P > 0.05$ for all analyses) spanning the period in which we documented decline at deeper depths at the hypoxic site. At the two sites that were found in the later survey to be most impacted by hypoxia (sites 1 and 2), the percent of living coral was substantially greater in shallow water than in deep water, by a factor of three at one site and by more than an order of magnitude at the other. Thus, mortality patterns were decoupled across depths, with overall higher survivorship at shallow depths. Stratification of the water column explains this pattern; dissolved oxygen concentrations at a given site were consistently higher at a depth of 3–4 m than at a depth of 10–12 m ($t_{1,18} = 7.56$, $P < 0.0001$) and were normoxic at 3–4 m at all sites (>4.8 mg/L), including sites that were hypoxic at deeper depths (Fig. S1A). Stratification was driven primarily by variation in salinity, which was slightly (1.55 ± 0.13 ppt) but consistently ($t_{1,18} = 11.54$, $P < 0.0001$) higher at a depth of 10–12 m than at a depth of 3–4 m (Fig. S1B). Temperature did not differ between shallow and deep depths across our study area ($t_{1,18} = 0.69$, $P = 0.50$) and so cannot explain the difference in coral mortality across depths or the stratification of the water column (Fig. S1C).

Although the overall effects on coral cover were strong, not all species were equally affected by the hypoxic event. In particular, the relative abundance of live corals at the most hypoxic sites shifted from *Agaricia* spp. to *Stephanocoenia intersepta* (Fig. 3A and B), suggesting that selective mortality was caused by variation in hypoxia

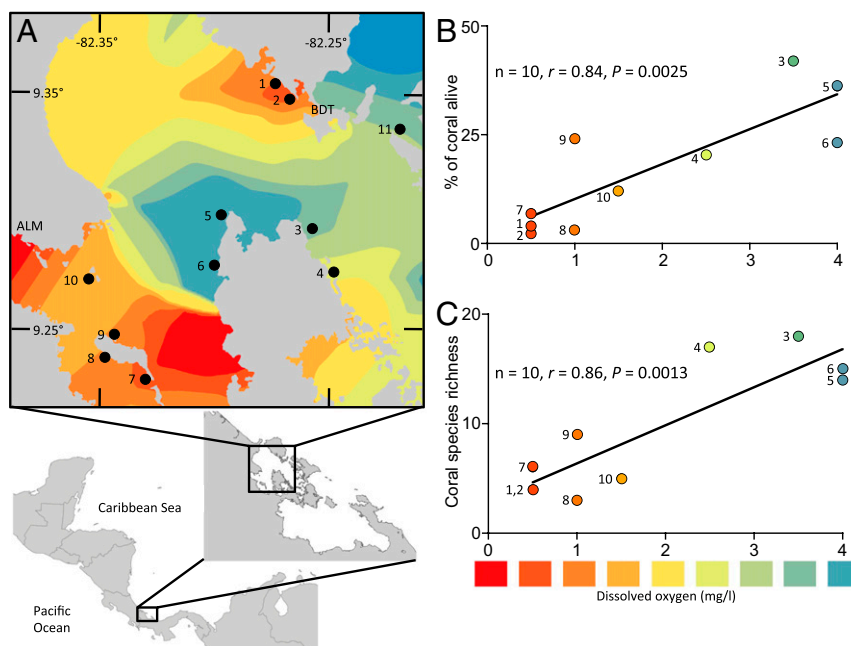


Fig. 2. Spatial distribution of hypoxia at 10–12 m depth (October 2010) and its consequences. (A) There were two distinct pockets of hypoxia, one near the mainland with terrestrial inputs [lower left, near Almirante town (ALM)], and the other near dense settlements of Bocas del Toro (BDT) where the Bocas 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

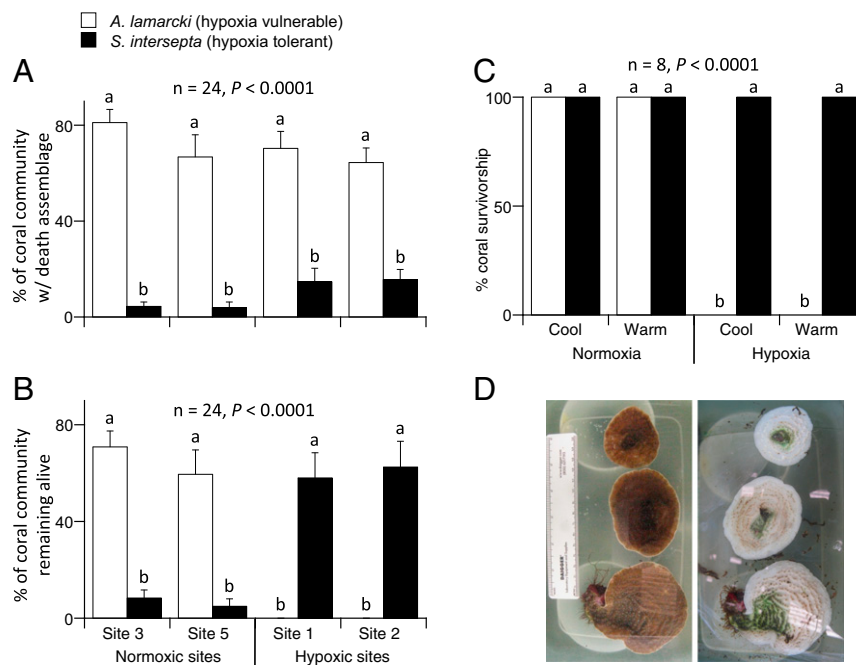


Fig. 3. Shifts in community structure toward hypoxia-tolerant coral species. (A) Before the hypoxic event, using the record of all corals both alive and dead as a proxy for relative abundance, the cover of *Agaricia* spp. was consistently higher than *S. intersepta* across all four sites, and there was 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

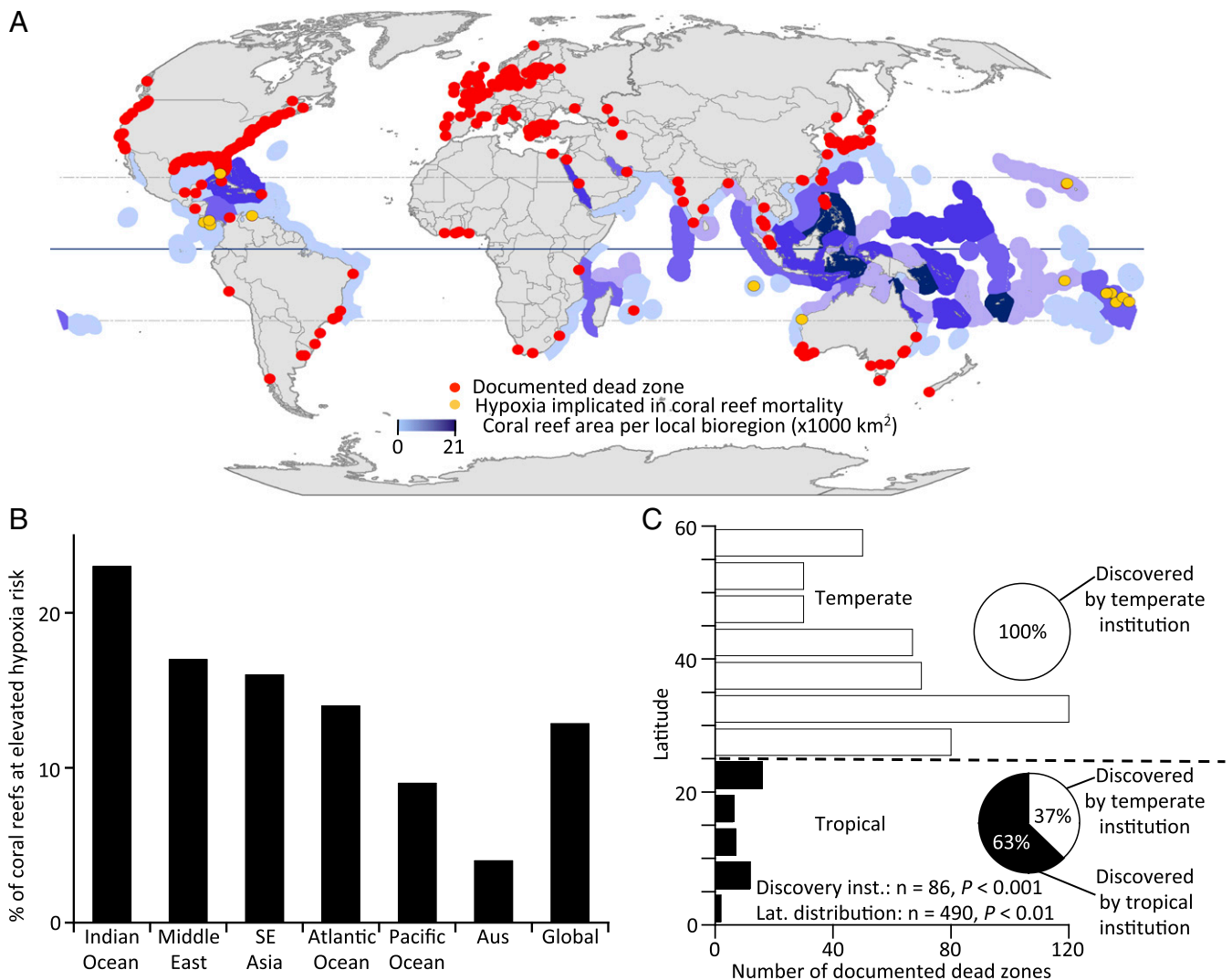


Fig. 4. Worldwide distribution of dead zones and coral reefs. (A) Global map with all known dead zones (red dots) and coral reefs where hypoxia has been implicated in mass mortality of reef organisms (gold dots). Documented dead zones are notably concentrated in temperate regions in areas with relatively 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*.

ACKNOWLEDGMENTS. We thank B. Silliman for comments on earlier versions of this paper; P. Gondola, C. Gonzalez, S. Loranger, and A. Castillo for assistance in the field; and M. Solano for assistance with Geographical Information System maps. This research was supported by the Smithsonian Tropical Research Institute, a grant from Deutscher Akademischer Austauschdienst-The German Academic Exchange Service and the Pawel-Ramminger Foundation, the Sant Chair for Marine Science, and the Hunterdon and Johnson Oceanographic Research Endowment. Research permits were provided by the Autoridad de Recursos Acuático de Panamá and the Autoridad Nacional del Ambiente de Panamá. This paper is contribution number 8 from the Marine Global Earth Observatory (MarineGEO) and the Smithsonian's Tennenbaum Marine Observatories Network.

1. Hoegh-Guldberg O, et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318(5857):1737–1742.
2. Pandolfi JM, et al. (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301(5635):955–958.
3. Bruno JF, et al. (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biol* 5(6):e124.
4. Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol Evol* 23(10):555–563.
5. McCauley DJ, et al. (2015) Marine defaunation: Animal loss in the global ocean. *Science* 347(6219):1255641.
6. Jackson JBC, Donovan MK, Cramer KL, Lam W (2014) *Status and Trends of Caribbean Coral Reefs: 1970–2012. Global Coral Reef Monitoring Network* (International Union for the Conservation of Nature, Gland, Switzerland).
7. Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321(5891):926–929.
8. Vaquer-Sunyer R, Duarte CM (2008) Thresholds of hypoxia for marine biodiversity. *Proc Natl Acad Sci USA* 105(40):15452–15457.
9. Côté IM, Knowlton N (2013) Coral reef ecosystems: A decade of discoveries. *Marine Community Ecology and Conservation*, eds Bertness MD, Bruno JF, Silliman BR, Stachowicz JJ (Sinauer Associates, Sunderland, MA), pp 299–314.
10. Jackson JBC, et al. (1989) Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science* 243(4887):37–44.
11. Cramer KL (2013) History of human occupation and environmental change in western and central Caribbean Panama. *Bull Mar Sci* 89(4):955–982.
12. Guzmán HM, Barnes PAG, Lovelock CE, Feller IC (2005) A site description of the CARICOMP mangrove, seagrass and coral reef sites in Bocas del Toro, Panama. *Caribb J Sci* 41(3):430–440.
13. Guzmán HM (2003) Caribbean coral reefs of Panama: Present status and future perspectives. *Latin American Coral Reefs*, ed Cortés J (Elsevier Science, Amsterdam), pp 241–274.
14. Altieri AH (2008) Dead zones enhance key fisheries species by providing predation refuge. *Ecology* 89(10):2808–2818.
15. Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr Mar Biol Annu Rev* 33:245–303.
16. Collin R, D’Croz L, Gondola P, Del Rosario JB (2009) Climate and hydrological factors affecting variation in chlorophyll concentration and water clarity in the Bahía Almirante, Panama. *Smithson Contrib Mar Sci* 38:323–334.
17. Neal BP, et al. (2014) When depth is no refuge: Cumulative thermal stress increases with depth in Bocas del Toro, Panama. *Coral Reefs* 33(1):193–205.
18. Levitan DR, Boudreau W, Jara J, Knowlton N (2014) Long-term reduced spawning in *Orbicella* coral species due to temperature stress. *Mar Ecol Prog Ser* 515:1–10.
19. Vaquer-Sunyer R, Duarte CM (2011) Temperature effects on oxygen thresholds for hypoxia in marine benthic organisms. *Glob Change Biol* 17(5):1788–1797.
20. Wallace RB, Baumann H, Grear JS, Aller RC, Gobler JC (2014) Coastal ocean acidification: The other eutrophication problem. *Estuar Coast Shelf Sci* 148:1–13.
21. Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proc Natl Acad Sci USA* 105(45):17442–17446.
22. Stubler AD, Furman BT, Peterson BJ (2015) Sponge erosion under acidification and warming scenarios: Differential impacts on living and dead coral. *Glob Change Biol* 21(11):4006–4020.
23. Duarte CM, et al. (2013) Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. *Estuaries Coasts* 36(2):221–236.
24. Altieri AH, Gedan KB (2015) Climate change and dead zones. *Glob Change Biol* 21(4):1395–1406.
25. Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Mar Pollut Bull* 50(2):125–146.
26. Pandolfi JM, et al. (2005) Ecology. Are U.S. coral reefs on the slippery slope to slime? *Science* 307(5716):1725–1726.
27. Burke L, Reyta R, Spalding M, Perry A (2011) *Reefs at Risk Revisited* (World Resources Institute, Washington, DC), p 130.
28. Sandin SA, et al. (2008) Baselines and degradation of coral reefs in the Northern Line Islands. *PLoS One* 3(2):e1548.
29. Knowlton N, Jackson JBC (2008) Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biol* 6(2):e54.
30. Aronson RB, MacIntyre IG, Wapnick CM, O’Neill MW (2004) Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* 85(7):1876–1891.
31. Cramer KL, Jackson JBC, Angioletti CV, Leonard-Pingel J, Guilderson TP (2012) Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching. *Ecol Lett* 15(6):561–567.
32. Aronson RB, Hilbun NL, Bianchi TS, Filley TR, McKee BA (2014) Land use, water quality, and the history of coral assemblages at Bocas del Toro, Panama. *Mar Ecol Prog Ser* 504:159–170.
33. Nelson HR, Kuempel CD, Altieri AH (2016) The resilience of reef invertebrate biodiversity to coral mortality. *Ecosphere* 7(7):e1399.
34. Kuempel CD, Altieri AH (2017) The emergent role of small-bodied herbivores in pre-empting phase shifts on degraded coral reefs. *Sci Rep* 7:39670.
35. Diaz RJ, Selman M, Chique C (2011) *Global Eutrophic and Hypoxic Coastal Systems* (World Resources Institute, Washington, DC).
36. Hodgson G, Maun L, Shuman C (2004) *Reef Check Survey Manual. Reef Check* (Institute of the Environment, University of California, Los Angeles, CA).
37. Diaz RJ (2001) Overview of hypoxia around the world. *J Environ Qual* 30(2):275–281.
38. Levin LA, et al. (2009) Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6(10):2063–2098.
39. Rabalais NN, et al. (2010) Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7(2):585–619.
40. Laboy-Nieves EN, et al. (2001) Mass mortality of tropical marine communities in Morocco, Venezuela. *Bull Mar Sci* 68(2):163–179.
41. Simpson CJ, Cary JL, Masini RJ (1993) Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs* 12(3–4):185–191.
42. Hobbs J-PA, McDonald CA (2010) Increased seawater temperature and decreased dissolved oxygen triggers fish kill at the Cocos (Keeling) Islands, Indian Ocean. *J Fish Biol* 77(6):1219–1229.
43. Hobbs J-PA, Macrae H (2012) Unusual weather and trapped coral spawn lead to fish kill at a remote coral atoll. *Coral Reefs* 31(4):961.
44. Andréfouët S, Duthéil C, Menkes CE, Bador M, Lengaigne M (2015) Mass mortality events in atoll lagoons: Environmental control and increased future vulnerability. *Glob Change Biol* 21(1):195–205.
45. Guzman HM, Cortes J, Glynn PW, Richmond RH (1990) Coral mortality associated with dinoflagellate blooms in the eastern Pacific (Costa Rica and Panama). *Mar Ecol Prog Ser* 60(3):299–303.
46. Jokiel PL, Hunter CL, Taguchi S, Watarai I (1993) Ecological impact of a fresh-water reef kill in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs* 12(3–4):177–184.
47. Lapointe BE, Matzie WR (1996) Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. *Estuaries* 19(2B):422–435.
48. Roberts KL, Eate VM, Eyre BD, Holland DP, Cook PLM (2012) Hypoxic events stimulate nitrogen recycling in a shallow salt-wedge estuary: The Yarra River estuary, Australia. *Limnol Oceanogr* 57(5):1427–1442.
49. Conley DJ, et al. (2011) Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environ Sci Technol* 45(16):6777–6783.
50. Chantraine J-M (1980) La Lagune Abe (Cote D’Ivoire) morphologie, hydrologie, paramètres physico-chimiques. *Documents Scientifique de Centre de recherches oceanographiques Abidjan* 11:39–77.
51. Seisdedo Losa M (2006) Variaciones espaciales y temporales en indicadores de la calidad ambiental de las aguas de la Bahía de Cienfuegos, Cuba. *Rev Investig Mar* 27(2):159–164.
52. Lanoux A, et al. (2013) Factors contributing to hypoxia in a highly turbid, macrotidal estuary (the Gironde, France). *Environ Sci Process Impacts* 15(3):585–595.
53. Gianni A, Kehayias G, Zacharias I (2011) Geomorphology modification and its impact to anoxic lagoons. *Ecol Eng* 37(11):1869–1877.
54. Ferentinos G, et al. (2010) Fjord water circulation patterns and dysoxic/anoxic conditions in a Mediterranean semi-enclosed embayment in the Amvrakikos Gulf, Greece. *Estuar Coast Shelf Sci* 88(4):473–481.
55. Shanmugam P, Neelamani S, Ahn YH, Philip L, Hong GH (2007) Assessment of the levels of coastal marine pollution of Chennai city, Southern India. *Water Resour Manage* 21(7):1187–1206.
56. Vijay R, Sardar VK, Dhage SS, Kelkar PS, Gupta A (2010) Hydrodynamic assessment of sewage impact on water quality of Malad Creek, Mumbai, India. *Environ Monit Assess* 165(1–4):559–571.
57. Deshkar S, Lakhmapurkar J, Gavali D (2012) State of three estuaries of Gulf of Khambhat. *Indian J Mar Sci* 41(1):70–75.
58. Rixen T, et al. (2008) The Siak, a tropical black water river in central Sumatra on the verge of anoxia. *Biogeochemistry* 90(2):129–140.
59. Henry LM, Kennedy R, Keegan BF (2008) An investigation of periodic hypoxia at Ardbear Salt Lake. *J Mar Biol Assoc U K* 88(7):1297–1307.
60. Haraguchi K, Yamamoto T, Chiba S, Shimizu Y, Nagao M (2010) Effects of phytoplankton vertical migration on the formation of oxygen depleted water in a shallow coastal sea. *Estuar Coast Shelf Sci* 86(3):441–449.
61. Ichikawa T, Aizaki M, Takeshita M (2007) Numerical study on amelioration of water quality in Lakes Shinji and Nakaumi: A coastal brackish lagoon system. *Limnology* 8(3):281–294.
62. Okada T, Nakayama K (2007) Density intrusion and variation in dissolved oxygen concentrations in a bay with a sill at its mouth. *J Environ Eng* 133(4):447–453.
63. Jang PG, Shin K, Chang M, Kim D (2011) Spatial and temporal trends in water quality in response to sewage discharge in Masan and Hangam Bays, Korea. *J Coast Res* 27(6A):144–155.
64. Bouchet VMP, Alve E, Rygg B, Telford RJ (2012) Benthic foraminifera provide a promising tool for ecological quality assessment of marine waters. *Ecol Indic* 23:66–75.
65. San Diego-McGlone ML, Azanza RV, Villanoy CL, Jacinto GS (2008) Eutrophic waters, algal bloom and fish kill in fish farming areas in Bolinao, Pangasinan, Philippines. *Mar Pollut Bull* 57(6–12):295–301.
66. Mikhailik TA, Tishchenko PY, Koltunov AM, Tishchenko PP, Shvetsova MG (2011) The effect of Razdol’naya River on the environmental state of Amur Bay (The Sea of Japan). *Water Resour* 38(4):512–521.
67. Kaselowski T, Adams JB (2013) Not so pristine - characterising the physico-chemical conditions of an undescribed temporarily open/closed estuary. *Water SA* 39(5):627–635.
68. Canedo-Arguelles M, Rieradevall M, Farres-Correll R, Newton A (2012) Annual characterisation of four Mediterranean coastal lagoons subjected to intense human activity. *Estuar Coast Shelf Sci* 114:59–69.
69. Hsieh WC, et al. (2012) Community metabolism in a tropical lagoon: Carbon cycling and autotrophic ecosystem induced by a natural nutrient pulse. *Environ Eng Sci* 29(8):776–782.
70. Weston K, et al. (2008) Sedimentary and water column processes in the Oyster Grounds: A potentially hypoxic region of the North Sea. *Mar Environ Res* 65(3):235–249.
71. Tyler RM, Brady DC, Targett TE (2009) Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. *Estuaries Coasts* 32(1):123–145.