RESEARCH REVIEW

Climate change and dead zones

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Abstract

Estuaries and coastal seas provide valuable ecosystem services but are particularly vulnerable to the co-occurring threats of climate change and oxygen-depleted dead zones. We analyzed the severity of climate change predicted for existing dead zones, and found that 94% of dead zones are in regions that will experience at least a 2 °C temperature increase by the end of the century. We then reviewed how climate change will exacerbate hypoxic conditions through oceanographic, ecological, and physiological processes. We found evidence that suggests numerous climate variables including temperature, ocean acidification, sea-level rise, precipitation, wind, and storm patterns will affect dead zones, and that each of those factors has the potential to act through multiple pathways on both oxygen availability and ecological responses to hypoxia. Given the variety and strength of the mechanisms by which climate change exacerbates hypoxia, and the rates at which climate is changing, we posit that climate change variables are contributing to the dead zone epidemic by acting synergistically with one another and with recognized anthropogenic triggers of hypoxia including eutrophication. This suggests that a multidisciplinary, integrated approach that considers the full range of climate variables is needed to track and potentially reverse the spread of dead zones.

Introduction

Dead zones created by the depletion of dissolved oxygen in coastal waters are one of the most widespread and detrimental anthropogenic threats to marine ecosystems worldwide and have been doubling in occurrence each decade since the mid-1900s (Diaz, 2001; Diaz & Rosenberg, 2008; Vaquer-Sunyer & Duarte, 2008; Gooday *et al.*, 2009; Rabalais *et al.*, 2010). Dead zones have significant consequences for the biodiversity and functioning of marine ecosystems and the services they provide to society, including fisheries production, water column filtration, and nutrient cycling (Altieri & Witman, 2006; Breitburg *et al.*, 2009; Conley *et al.*, 2009; Levin *et al.*, 2009; Diaz & Rosenberg, 2011). The exponential increase in the number, size, and severity of dead zones is linked to higher rates of nutrient inputs, making the dead zone epidemic one of the strongest arguments for controlling eutrophication (Diaz & Rosenberg, 2008; Gooday *et al.*, 2009; Rabalais *et al.*, 2010). The demise of many grazer populations is exacerbating the effect of nutrient loading by reducing

their consumption of phytoplankton at the same time that nutrients are stimulating primary productivity (Jackson *et al.*, 2001; Lotze *et al.*, 2006).

The link between eutrophication and severity of hypoxia is modulated by factors including runoff, water column stratification, primary productivity, microbial activity, and organismal respiration. Based on the wide variety of ways in which climate change can influence these factors through temperature, ocean acidification (OA), sea-level rise, precipitation, winds, storm frequency, and other variables (Fig. 1), we suggest that climate change is likely contributing to the observed increase in dead zones. Many of the early studies on links between climate, eutrophication, and/or dead zones focused primarily on the potential for shifts in precipitation to affect freshwater discharge and associated nutrient dynamics. These studies highlight the important link between runoff and eutrophication, with important implications for hypoxia, but this is only one of many potential climate-related impacts on nutrients and/or dead zone formation (Howarth *et al.*, 2000; Struyf *et al.*, 2004; Justic *et al.*, 2005). Evidence is accumulating from some ecosystems that the effects of climate are sufficiently strong enough to further increase the severity of dead zones, even if rates of

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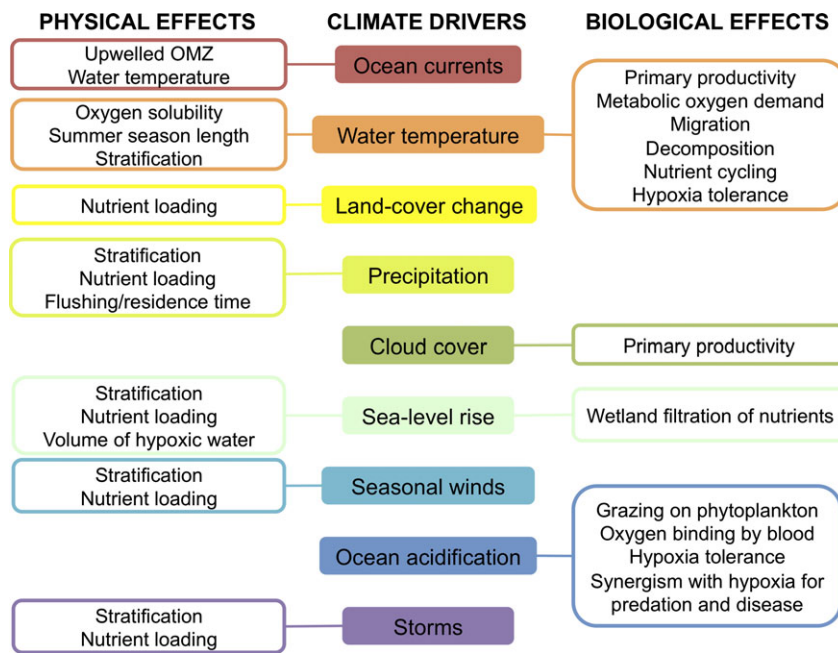
Fig. 1 A diagram that identifies the climate drivers and associated physical and biological effects that in turn mediate the severity of hypoxia. The aspects of climate change with the potential to affect dead zones extend well beyond temperature and precipitation, which are two of the most commonly identified factors. Climate change affects both the establishment and severity of hypoxia, as well as organismal responses to low oxygen, in numerous ways, and has likely contributed to the observed spread of dead zones in recent decades. Future research is needed to better understand how multiple factors, and multiple effects of a given factor, interact to drive dead zone dynamics. OMZ, oxygen minimum zone.

eutrophication are kept in check or reduced (Meier *et al.*, 2011a; Villate *et al.*, 2013; Carstensen *et al.*, 2014).

Despite growing recognition that climate, and temperature in particular, has the potential to mediate the severity of hypoxia (Conley *et al.*, 2007; Justic *et al.*, 2007; Rabalais *et al.*, 2009, 2010; Najjar *et al.*, 2010; Diaz & Rosenberg, 2011; Meier *et al.*, 2011a; Vaquer-Sunyer & Duarte, 2011), studies have often focused on a subset of drivers, such as hydrography, nutrient dynamics, or metabolic effects, and, missing the interactions and synergies between these coupled processes, have likely underestimated the magnitude of climate effects on hypoxia (Carstensen *et al.*, 2014). By reviewing the literature across a variety of perspectives and disciplines including oceanography, ecosystem and community ecology, and physiology, we examine the wide variety of climate variables that impact dead zones, highlight the multiple ways in which these variables can directly and/or indirectly affect oxygen dynamics, and consider how they modulate both the availability of oxygen and the biological responses to hypoxia. We suggest that this broad perspective is challenging in its complexity but needs to be adopted to understand the dynamics of dead zones and predict their spread.

Climate change in documented dead zones

Diaz & Rosenberg (2008) assembled a database of over 400 dead zones worldwide, and established that their number is increasing exponentially over time. To characterize the severity of climate change that these ecosystems are likely to experience over the coming century, we explored the future annual temperature anomalies predicted to occur for each of these systems. We found that the majority of documented dead zones are in regions predicted to experience over 2 °C warming (94% of sites, median = +2.3 °C) by the end of this century (Fig. 2), suggesting a broad relevance and urgency for understanding climate change to better predict and manage coastal dead zones.

Temperature effects on physical drivers of hypoxia

Temperature is perhaps the climate-related factor that most broadly affects dead zones through a variety of physical and biological mechanisms (Fig. 3). The importance of temperature in driving patterns of hypoxia is apparent in the onset of hypoxia with the warming of the summer season in most locations where dead zones are periodic or episodic (Diaz & Rosenberg, 2008). Even in models that consider how temperature
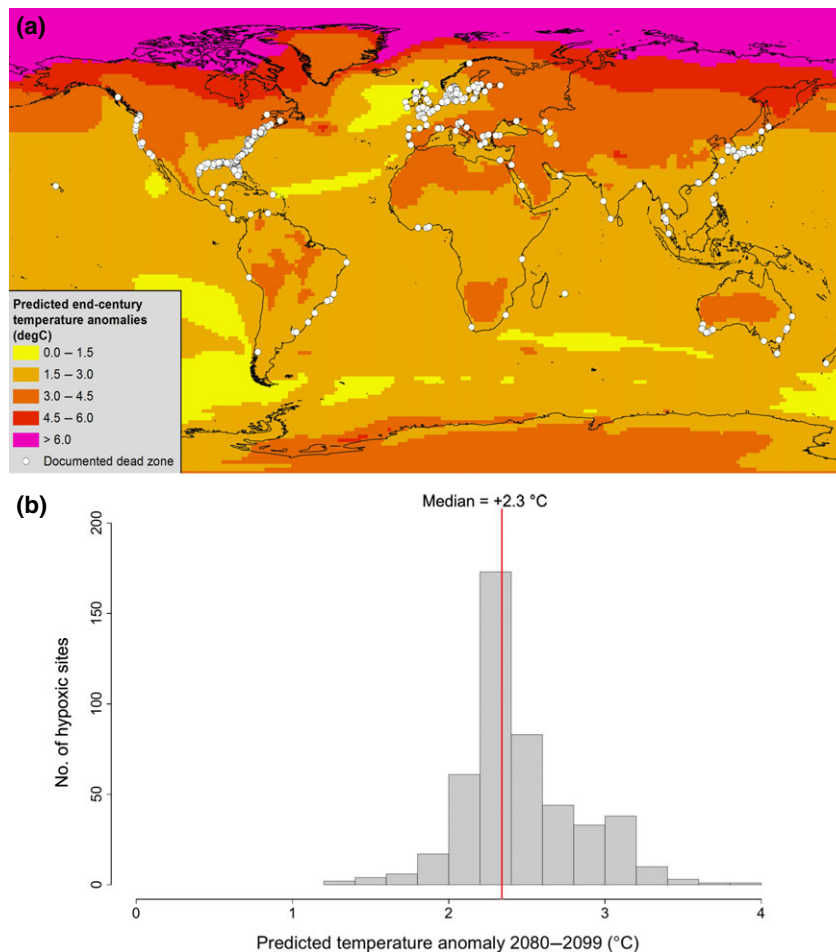
Fig. 2 (a) Map of known dead zones in relation to predicted changes in annual air temperature based on the intermediate A1B Scenario predicted to end-century (2080–2099) (Diaz & Rosenberg, 2008; NCAR GIS, 2012). (b) Histogram showing the distribution of predicted change in air temperature for known dead zones. In GIS (ArcMap 10.1; ESRI, Redlands, CA, USA), we investigated the distribution of annual air temperature anomalies predicted for the late century (2080–2099 relative to 1980–1999) under the A1B emissions scenario, a middle-of-the-road scenario in terms of fossil fuel use (IPCC *et al.*, 2007). Model results were obtained from the National Center for Atmospheric Research (NCAR GIS, 2012). Air temperature anomalies were used to approximate surface sea temperature anomalies; they are closely correlated at seasonal, annual, and longer time-scales (Cayan, 1980).

could enhance hypoxia through some pathways and reduce it through others, the net effect is that warming is predicted to expand dead zones (Conley *et al.*, 2007; Meier *et al.*, 2011a).

Lower solubility of oxygen in warmer water

Simply due to the principles of water chemistry that dictate gas solubility decreases with temperature, warming will cause a reduction in the oxygen available to aquatic organisms (Weiss, 1970). This basic relationship between oxygen solubility and water temperature is nonlinear, with greater sensitivity at lower temperatures (Fig. 4). As a consequence, the effect of warming temperatures on solubility will be especially pronounced in high latitude, temperate and arctic estuaries

where water temperatures are initially lower and predicted rates of warming are higher. Within a given estuary, the direct effects of atmospheric warming on oxygen solubility will be greater in surface waters; however, oxygen replenishment to deeper waters will also be reduced via the transport of warmer, less oxygen-rich surface waters (Meier *et al.*, 2011b).

Water column stratification

Warmer air temperatures associated with climate change will enhance stratification by heating surface waters, which in turn will promote hypoxia by preventing oxygenated surface waters from mixing to the bottom where hypoxia typically establishes (Cloern, 2001). The link between warming air temperatures
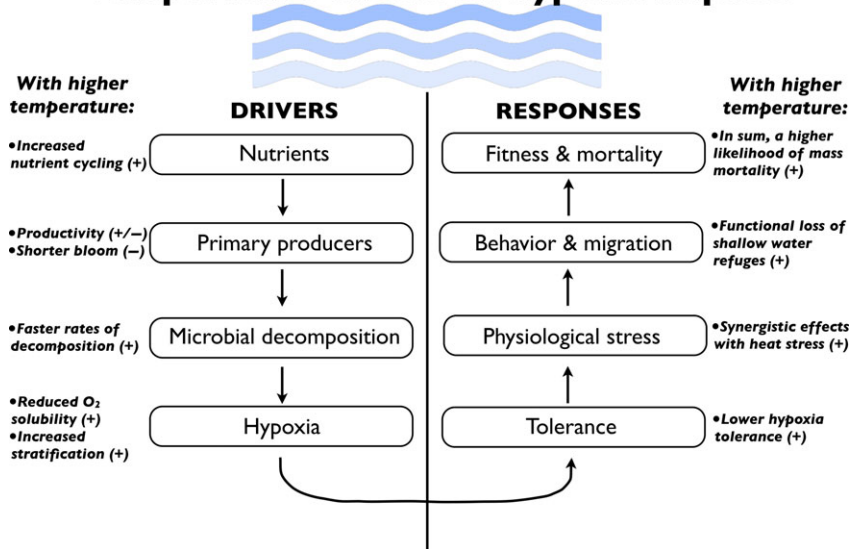
Temperature effects on hypoxia impacts

Fig. 3 A conceptual model that illustrates the numerous ways that warming temperatures will exacerbate coastal dead zones and biological responses to hypoxia. Given the linkages between the factors affected by temperature, perspectives that consider only a subset of temperature effects have likely underestimated the impact of climate change on the spread of dead zones. Symbols indicate whether each mechanism is predicted to increase (+) or decrease (−) the severity of hypoxia or biological response to hypoxia.
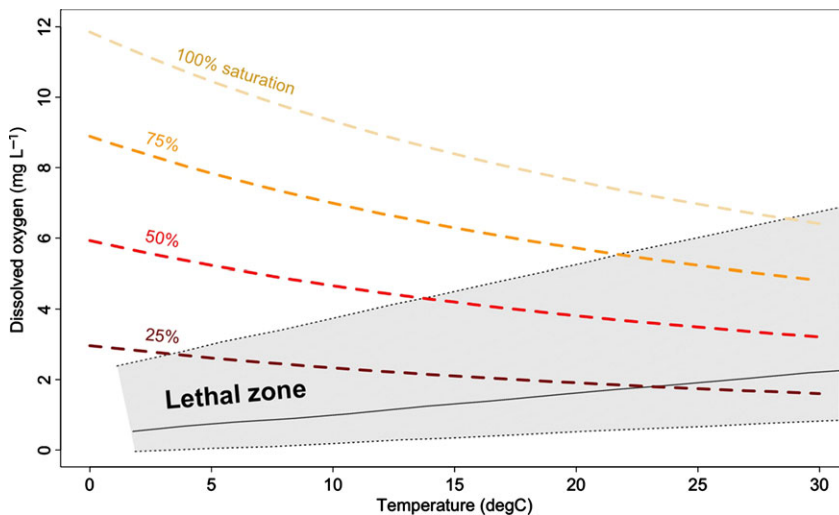

Fig. 4 The relationship between dissolved oxygen saturation and lethal dissolved oxygen dose as a function of temperature. Dissolved oxygen saturation-temperature isoclines at a salinity of 30 ppt (USGS, 2011) are mapped onto the median lethal dissolved oxygen concentration for a wide variety of marine organisms (dataset from Vaquer-Sunyer & Duarte, 2011). The black line shows the 50% quartile for all organisms and the shaded region captures 90% of all observations.

and dead zones mediated by stratification contributes to the consistent onset of seasonal summer hypoxia in long-term records from systems including the Baltic Sea and Chesapeake Bay (Conley *et al.*, 2007; Murphy *et al.*, 2011). In some systems such as the North Sea, climate-driven changes in stratification are predicted to be the dominant driver of increased prevalence of hypoxia (Meire *et al.*, 2013). The effects of climate

warming on stratification will be particularly important when warm air heats waters trapped near the surface due to a pre-existing halocline, reinforcing prior stratification through positive feedbacks. Climate warming effects on stratification will interact with changes in precipitation-related salinity, which also affect seawater density and stratification (discussed below).
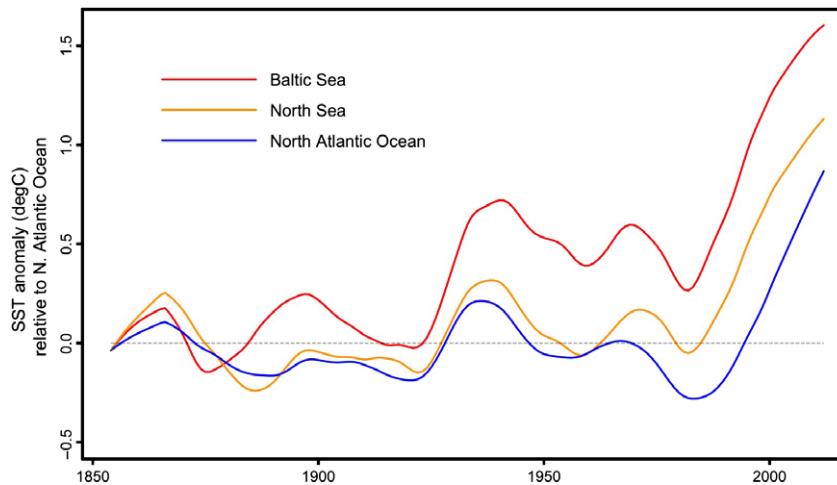
Fig. 5 Historical records of sea surface temperature (SST) change in a hypoxic sea (Baltic Sea, 56°N, 18°E) and coastal shelf area (North Sea, 56°N, 4°E), relative to the average temperature anomaly from the 1854–2012 data period of the open ocean just beyond the shelf (North Atlantic, 62°N, 2°E). SSTs in the Baltic and North Seas in the last decade are the highest in the history of their long instrument records, and warming at a faster rate than the open ocean. Moreover, summer SSTs are increasing at a rate three times that predicted for air by global climate models (Mackenzie & Schiedek, 2007). Bold lines are smoothing curves with a span of 20 years. Data are from NOAA Extended Reconstructed Sea Surface Temperatures (ERSST 3b, http://nomads.ncdc.noaa.gov/las/getUI.do).

Sensitivity of estuaries to climate warming

Because estuaries and coastal seas are often shallow and have limited exchange with the open ocean, their water temperatures are closely linked to air temperature and therefore have the potential to be more responsive to climate warming than the open ocean. This is apparent in spatial comparisons between estuaries and adjacent ocean waters such as Rio de La Plata Estuary in Argentina, where summer surface water temperatures are 4 °C warmer than the nearby ocean (Simionato *et al.*, 2010). The accelerated warming of coastal seas and estuaries is apparent in temporal trends (Fig. 5). For example, the Baltic Sea has been warming at an average rate of 0.03 °C per year since 1985, with a much more extreme rate of summer warming (0.09 °C per year), or 6–13 times the recent increase in global air temperature (Mackenzie & Schiedek, 2007; IPCC, 2013). Similarly, the Chesapeake Bay has been warming by approximately 0.03 °C per year since the 1960s (Najjar *et al.*, 2010). Increased temperatures of coastal waters expected with atmospheric climate warming will be associated with a host of temperature-dependent effects on hypoxia.

Temperature effects on biological drivers of hypoxia

Increased metabolism

Aerobic metabolic demand for oxygen is fundamentally tied to temperature, and climate warming of coastal waters of bays and estuaries will accelerate the development of hypoxia and may cause acute ecological consequences in two ways.

First, metabolic oxygen demand of organisms such as crabs, fish, and bivalves increases with temperature because of Q10 effects on basal metabolic rates and respiration. Metabolic rates increase exponentially with temperature (Brown *et al.*, 2004). This leads to rapidly decreasing hypoxia tolerances as temperatures increase (Vaquer-Sunyer & Duarte, 2011), and, conversely, decreasing thermal tolerances with increasing hypoxia (Portner & Knust, 2007). Thus, the effect of increasing temperature on metabolism leads simultaneously to lower oxygen availability and higher demand, a noxious combination that could quickly cause stress and mortality and, at larger scales, drive an ecosystem to collapse (Fig. 4). Temperature-dependent increases in respiratory oxygen consumption by habitats created by foundation species such as oyster reefs and mussel beds can further deplete oxygen locally (Dame, 1996), to a threshold where their own hypoxia and/or thermal tolerance is exceeded. Even habitats created by primary producers, such as macroalgae and seagrass, that produce water column oxygen during the day become net consumers at night when they can create pockets of hypoxic water (Raffaelli *et al.*, 1998; Polte *et al.*, 2005). Since this diel-cycling is tightly coupled to water temperature (Tyler *et al.*, 2009) the associated hypoxia would be exacerbated by warmer coastal waters.

Second, temperature will affect metabolic aspects of microbial processes such as decomposition, oxy-

gen consumption, and nutrient cycling that contribute to dead zone formation. For example, a recent modeling study of the Baltic Sea mouth found that temperature-dependent increases in benthic respiration and decreases in oxygen solubility could explain a large proportion of interannual oxygen dynamics (Bendtsen & Hansen, 2013). Heterotrophic microbes are more sensitive to temperature than primary producers (Lopez-Urrutia *et al.*, 2006). However, temperature effects on microbial nutrient transformations could enhance primary productivity by eliminating nutrient limitations on primary producers. The net effect of temperature on microbial nutrient release will depend on what substrates are available for mineralization and microbial transformations, as well as the relative temperature sensitivity of related processes such as nitrification and denitrification (Matsui *et al.*, 2013).

Effects of temperature on primary productivity

Phytoplankton, the primary carbon source to microbes that deplete oxygen in many hypoxic estuaries, are thought to be only mildly sensitive to temperature because blooms are often coupled to light availability and nutrient limitation (Sommer & Lengfellner, 2008). However, a warming climate and associated secondary changes in weather patterns affect both the timing and rates of primary productivity (Winder & Sommer, 2012). For example, warmer years have been associated with earlier phytoplankton blooms in the Baltic Sea (Alheit *et al.*, 2005) and Western Scheldt estuary (Kromkamp & Van Engeland, 2010). Overall phytoplankton biomass can be suppressed in warmer years as observed in Narragansett Bay (Oviatt, 2004), however, long-term warming causes shifts in phytoplankton species composition (Winder & Sommer, 2012), suggesting that high-temperature suppression of some species may be compensated for by an increase in other opportunistic plankton species.

Macroalgal blooms are also important drivers of localized hypoxic conditions that can be detrimental to benthic organisms (Raffaelli *et al.*, 1998). The initiation of macroalgal blooms is generally thought to be under similar resource control (e.g., light, temperature, nutrients) as phytoplankton blooms (Valiela *et al.*, 1997). As a consequence, they typically demonstrate seasonal onset in temperate estuaries in the spring and summer and can be expected to increase in magnitude with climate warming, particularly in eutrophic estuaries where excess nutrients can to increase rates of macroalgal productivity by orders of magnitude (Hauxwell *et al.*, 1998).

Effects of temperature on grazer control of algal blooms

Grazers are more responsive to temperature change than phytoplankton, and will likely exert stronger control on phytoplankton blooms as temperatures increase. This difference between phytoplankton and grazers is partly explained by metabolic theory and the greater sensitivity of heterotrophic metabolism than autotrophic metabolism to temperature (Lopez-Urrutia *et al.*, 2006). Experimentally simulated climate warming caused an increase in top-down control by copepods and reduced standing stocks of phytoplankton (O'Connor *et al.*, 2009; Gaedke *et al.*, 2010). Bivalve grazers also exhibit temperature-dependent grazing rates (Kittner & Riisgård, 2005; Gedan *et al.*, 2014), particularly in experimental eutrophication treatments (O'Connor *et al.*, 2009), and are likely to contribute to the shift in warming, eutrophic systems towards heterotrophy. Indeed, temperature-driven shifts in the timing of spring blooms are attributable to earlier disintegration of bloom conditions due to heavy grazing rather than phenological shifts in phytoplankton productivity patterns (Gaedke *et al.*, 2010; Winder & Sommer, 2012). These effects may be counteracted when warmer water also favors higher trophic levels such as jellyfish, which have the potential to indirectly enhance phytoplankton by consuming zooplankton grazerss as observed in the North Atlantic (Gibbons & Richardson, 2009).

Grazers on macroalgae can also respond positively to temperature increases as demonstrated by seasonal cycles of top-down control. However, their consumption rates can be outpaced by primary productivity rates, particularly in highly eutrophic estuaries, suggesting that herbivory can be insufficient to control macroalgal blooms, as observed in the northeastern US (Hauxwell *et al.*, 1998). One reason that grazers may be unable to keep pace with macroalgal growth is that they are stressed, die, and or flee the hypoxic conditions within the macroalgal canopy (Norkko & Bonsdorff, 1996; Norkko *et al.*, 2000). This would result in a positive feedback loop of increasing algal growth, decreasing oxygen levels, and decreasing herbivory rates once a threshold is crossed in eutrophic and warm estuaries.

These examples reveal how the ability of food web dynamics to mediate the relationship between eutrophication and hypoxia is temperature dependent. However, the exact outcome of temperature change on consumer–producer dynamics will depend on (i) the rate and timing of change in temperature and associated climate variables such as cloudiness and precipitation, which will independently affect primary productivity, (ii) the identity and turnover of species or guilds of producers and consumers in a given system,

and (iii) the potential for trophic cascades as higher trophic levels respond to temperature change. Reduced phytoplankton subsidies to the benthos, due to increased grazing or suppression of productivity, is the sole pathway by which warming temperatures will not exacerbate hypoxia and may compensate in part for some of the negative effects (Fig. 3).

Temperature related expansion of dead zones

In addition to exacerbating the severity of hypoxic conditions and ecological responses within existing dead zones, as discussed above, climate warming can lead to expansion of the duration and spatial extent of dead zones in several ways.

Sea-level rise

Rising sea levels associated with increasing annual average temperatures (due to ice melt and thermal expansion of water) is increasing the volume of bays, estuaries, and continental shelf area. This increases the overall volume of shallow coastal water susceptible to hypoxia and promotes stratification of the water column that in turn sets the stage for low oxygen in bottom waters, particularly in bays with sills at their mouths (Van Der Zwaan & Jorissen, 1991; Davies & Xing, 2007). In addition, rising sea levels could overrun wetlands, leading to higher eutrophication rates due to loss of their nutrient abatement services (Kemp *et al.*, 2005).

Season stretching

Many dead zones occur seasonally when summer temperatures reach critical levels that induce the development of hypoxia. The earlier arrival of summer air temperatures is linked to stratification, earlier onset of hypoxia, and greater dead zone area, as observed in the Black Sea (Ukrainskii & Popov, 2009). Long-term climate warming can extend the period of summertime stratification (Coma *et al.*, 2009), and earlier stratification is linked to earlier hypoxia (Murphy *et al.*, 2011). For example, increased temperatures and changes in seasonality associated with climate change are predicted to extend the duration of seasonal hypoxia in the areas of the Baltic, approximately doubling the hypoxic season by the end of the century (Neumann *et al.*, 2012).

Hypoxic-thermal kill zones

Mobile organisms including fish and crabs may lose shallow water refuges that previously provided an escape from deeper hypoxic conditions (Breitburg, 1992). As shallow water temperatures increase with atmospheric warming they may become functionally hypoxic because of decreased oxygen carrying capacity of the water and increased metabolic demand of organisms. Thus, climate change could lead to constriction of habitat because of existing hypoxia in deep water and shallow waters that are newly stressful due to high temperature and thermally induced hypoxia. This combination is predicted to reduce habitat for striped bass (Coutant, 1990). In extreme situations, the temperatures of shallow water may exceed thermal tolerance of organisms, leaving them with the dilemma of choosing death by hypoxia at depth or by thermal stress in the shallows. Other species that are migratory and/or highly mobile may exploit offshore refugia from the combined stresses of temperature and hypoxia in inshore waters, but ultimately stress avoidance may limit access to spawning grounds or may lead to increased fishing mortality when harvests are concentrated along the edge of hypoxic areas (Breitburg, 2002).

Nontemperature related climate change effects on hypoxia

Thus far, we have focused our review on the multitude of ways that temperature can drive the dynamics of dead zones. However, there are other aspects of climate change, that we discuss below, that are likely to influence the dynamics of coastal hypoxia as well.

Precipitation

Precipitation is an important climate driver of nutrient dynamics and stratification in coastal waters with direct consequences for dead zones. For example, the size of hypoxic areas in Chesapeake Bay and Gulf of Mexico are directly tied to characteristics of spring runoff (Hagy *et al.*, 2004; Turner *et al.*, 2005; Murphy *et al.*, 2011). Changes in the timing, frequency, and intensity of precipitation expected with climate change (IPCC, 2013) will influence dead zones through pulsed nutrient delivery to coastal waters (Rabalais *et al.*, 2009), changes in water column stratification (Wiseman *et al.*, 1997), and flushing/residence time of bay waters (Pilson, 1985), all of which can mediate the dynamics of nutrients, hypoxic water, and phytoplankton within estuaries and coastal shelf areas at river mouths (Howarth *et al.*, 2000; Justic *et al.*, 2005). In addition to changing the timing and volumes of freshwater runoff, altered patterns of precipitation associated with climate change will affect nutrient delivery by changing soil erosion patterns

and nutrient uptake in the watershed (Rabalais *et al.*, 2009), and by controlling patterns of snowfall and snowmelt which releases nutrients accumulated through wet deposition (Williams *et al.*, 1996). While there is high certainty that many hypoxic ecosystems will undergo significant changes in precipitation, and that those changes will affect oxygen dynamics, ecosystem-specific dynamics suggest that additional case studies may be necessary to formulate general predictions (Howarth *et al.*, 2000; Justic *et al.*, 2005).

Wind, storms, and cloud cover

Atmospheric conditions other than precipitation have the potential to affect dead zones in a number of ways. Changes in the direction and strength of seasonal wind patterns can either promote or dissipate hypoxic conditions by affecting circulation patterns that determine nutrient delivery and water column stratification (Conley *et al.*, 2007; Meier *et al.*, 2011b). Climate-driven changes in storm regimes (i.e., the timing, frequency, and intensity), will also modify hypoxic conditions by affecting runoff and associated nutrient inputs, resuspension of sediments, and stratification. However, these changes are expected to primarily occur in lower latitudes where tropical storms (e.g., hurricanes, typhoons) are more common (Rabalais *et al.*, 2009).

Since phytoplankton blooms are often light limited, changes to cloud cover expected with long-term climate dynamics will affect the timing and intensity of blooms and thereby the carbon source that fuels in coastal areas (Winder & Sommer, 2012). There is high uncertainty about how winds, storms, and cloud cover will respond to climate change (Justic *et al.*, 2005; IPCC, 2013), making their influence on future dead zone dynamics an area requiring more research.

Land-cover change and nutrient transport

Climate-driven changes in land cover will have a direct effect on nutrient inputs into coastal waters which will in turn affect rates of primary productivity that fuel hypoxia. Changes in vegetation type and cover will affect nutrient cycling and retention in the soils of coastal watersheds, as well as runoff dynamics and nutrient transport through tributaries (Kucharik *et al.*, 2000). Extreme changes in land cover resulting in vegetation loss and increased rates of desertification globally will contribute to atmospheric dust loading and enhanced atmospheric nutrient delivery to marine ecosystems (Schlesinger *et al.*, 1990; Woodward *et al.*, 2005), which could augment eutrophication in some estuaries.

Climate-driven changes to oceanic current patterns

Large-scale climate dynamics influence oceanic current patterns, which in turn affect coastal dead zones in two ways. First, hypoxic waters from deep water oxygen minimum zones (OMZs) can be shoaled onto the shelf (Grantham *et al.*, 2004) and into bays (Stauffer *et al.*, 2012) creating novel hypoxic conditions in coastal areas, a phenomenon now recognized to occur in all major OMZs (Gilly *et al.*, 2013). Second, climate-related changes in oceanic current patterns can exacerbate pre-existing dead zones by introducing additional hypoxic water, as in the St. Lawrence Estuary (Gilbert *et al.*, 2005), and/or by precluding oxygen replenishment from oxygenated oceanic waters as seen in the Saanich Inlet (Matabos *et al.*, 2012). Climate-driven changes to current patterns can also introduce warmer ocean waters into coastal areas, leading to the various temperature-dependent effects on the intensity of hypoxia (Conley *et al.*, 2007).

Hypoxia and ocean acidification

Ocean acidification has surged into the spotlight as one of the aspects of global climate change of greatest concern, since CO_2 not only contributes to a warming climate but also lowers pH due to changes in seawater carbonate chemistry (Doney *et al.*, 2009). The impacts of OA are intertwined with coastal dead zones for several reasons discussed below.

The dark side of hypoxia: nighttime hypoxia accompanied by low pH

The respiration of microbes and algal blooms that generates hypoxic conditions also generates an abundance of CO_2, which lowers pH. Thus, hypoxic dead zones are also likely to be hotspots of acidification (Duarte *et al.*, 2013). While this coupling is evident across a range of temporal and spatial scales, some of the strongest evidence that major shifts in pH and dissolved oxygen are caused by a common mechanism is their correlated diurnal cycling where the two change rapidly and dramatically, as in shallow, eutrophic estuaries (Edwards *et al.*, 2004; Beck *et al.*, 2011). Coupling can also be apparent over larger temporal and spatial scales, as observed in the Bohai Sea (Zhai *et al.*, 2012) and Western Baltic Sea (Melzner *et al.*, 2013).

Synergisms between OA and hypoxia

Ocean acidification and hypoxia can interact synergistically at the physiological level to compromise survivorship rates, reproduction, feeding activity, and larval

development, in part because decreasing pH lowers the oxygen-binding affinity of blood pigments (Portner, 2010; Doney *et al.*, 2012). These organismal responses can cascade up to have community level effects, with interactions between hypoxia and acidification increasing the susceptibility of organisms to disease due to compromised immune systems (Boyd & Burnett, 1999) and to predation due to modified behavior of stressed prey (Rosa & Seibel, 2008). The synergism between OA and hypoxia can be a potent mix acting on multiple organismal functions (Gobler *et al.*, 2014), and is thought to be responsible for the failure of scallop aquaculture in the Bohai Sea (Zhai *et al.*, 2012). There are also ecosystem level consequences as bivalves have the potential to control algal blooms, but are highly susceptible to acidified ocean conditions (Kroeker *et al.*, 2010). OA that results in bivalve population crashes would further cripple the ability of local ecosystems to regulate phytoplankton conditions that generate hypoxia.

Given the potential for hypoxia and OA, along with temperature, to interact at the ecosystem and organismal level (Somero, 2012; Bijma *et al.*, 2013), they need to be considered together in the design and interpretation of experimental and modeling studies to assess and predict changes in coastal ecosystems. For example, survivorship and behavioral thresholds established from single factor OA laboratory assays are likely overly conservative for coastal, eutrophic systems given that hypoxic and acidified conditions are likely to be encountered simultaneously in the field.

Directions for future work

While there is considerable evidence that climate change, and warming in particular, will have profound effects on the dynamics of dead zones, there are questions that demand immediate attention to better predict the future of dead zones.

At the ecosystem level, there are potential feedbacks between dead zones and climate change. What is the relative importance of the phytoplankton blooms that drive dead zone formation to act as carbon sinks? How does the recent discovery that dead zones are nitrous oxide producers (Naqvi *et al.*, 2010) feed into our understanding of climate regulation and the interaction between climate impacts and dead zones?

At the community level, how is temperature affecting the macrofauna that regulate microbial activity associated with the generation of hypoxia? Worms, amphipods, bivalves, crustaceans, and other organisms irrigate and turnover coastal sediments, altering conditions for microbes and the availability of resources

(Lohrer *et al.*, 2004; Laverock *et al.*, 2011). The shells and deposits of bivalves also support microbes with significant effects on nitrogen cycling and therefore primary production (Newell *et al.*, 2002; Welsh & Castadelli, 2004). The effects of temperature on the activity of these macrofauna therefore have important direct and indirect consequences on oxygen fluxes and nutrient levels that trigger algal bloom and dead zone conditions.

At the population and species levels, can species persist by shifting their ranges to evade ecosystems where the synergistic effects of climate change and hypoxia exceed tolerance thresholds? The multiple factors that determine ecosystem dynamics and organismal responses, combined with the geographic mosaic of ecosystem change expected in coastal habitats, suggests that predictions are not straightforward and will require detailed study from a number of perspectives (Harley *et al.*, 2006). For example, hypoxia and climate change together could lead to the demise of foundation species which in turn would produce negative effects on dependent inhabitants (Altieri & Van De Koppel, 2013). These indirect effects of climate change and dead zones would not be predicted based on physiological tolerance of inhabitant species alone.

At the organismal level, how are the mechanisms and constraints of physiological adaptation to hypoxia affected by temperature and OA? Will rates and ranges of organismal responses to these multiple stressors be sufficient to keep pace with climate change? How do the multiple stressors associated with hypoxia and climate change interact additively, synergistically, and hierarchically through space and time? Answering these questions will require an understanding of metabolic pathways and the functional genomics underlying their regulation. Can we expect constraints on adaptability because some species or populations already exist near tolerance thresholds, as seen for temperature (Stillman, 2003)?

Some of the greatest uncertainty lies in the potential synergisms among climate change factors, particularly because a given factor has several effects. For example, sea level rise will affect the volume of bays and estuaries which influences the potential volume of hypoxic water, the depth of water that contributes to stratification of the water column, and the persistence of wetlands which influence the input of terrestrial inputs. All of those factors could interact with one another, and the nature of that interaction could depend on system-specific characteristics. This adds another dimension to the perspective of multiple stressor effects in marine ecosystems (Breitburg & Riedel, 2005; Crain *et al.*, 2008) – when a given stressor itself has multiple effects.

As our understanding of dead zone dynamics becomes more sophisticated and we develop a better understanding of direct and indirect effects in coupled bio-physical perspectives in coastal habitats, it is increasingly apparent that comprehensive modeling techniques will be necessary to predict the dynamics of dead zones. The need for such multi-parameter approaches is apparent when considering that while hypoxia can be expected to worsen for the most part with climate warming (e.g., decreased solubility and simultaneous increases in metabolic demand, microbial activity, and stratification), some changes may partially counteract that trend (e.g., higher rates of grazing on phytoplankton blooms). For other factors (e.g., changes in storm/wind regimes) there is a high certainty that they will have a strong impact on hypoxia, but low certainty as to the nature of those changes. Multi-parameter physical and biological monitoring will be necessary to verify models and establish rates of responses to climate change. In some cases, the most obvious indicators of interactions between climate change and hypoxia may have already passed or been masked by apparently positive indicators of ecosystem status (Altieri, 2008). This risk of a 'sliding baseline' (*sensu* Dayton *et al.*, 1998) suggests that historical ecology, paleoecology, and geological approaches will have a prominent role in understanding the trajectory of coastal dead zones and predicting their future.

Conclusions

Climate change can have a variety of direct and indirect effects on ocean ecosystems, and the exacerbation of dead zones may be one of the most severe. Temperature is an integral component of how ecosystems and organisms generate hypoxic conditions and how they respond to dead zones. There is a multitude of ways in which dead zone dynamics are sensitive to temperature, as well as other aspects of climate change related to meteorological conditions, sea-level rise, and OA. We suggest that climate change will drive expansion of dead zones, and has likely contributed to the observed spread of dead zones over recent decades. It is also possible that eutrophication thresholds that existed decades ago for the establishment of hypoxia may have been lowered as climate change has made coastal areas more susceptible to hypoxia, suggesting that reductions in nutrient loads will have to be more aggressive when a multifactor perspective is taken into consideration. We suggest that integrating across the full set of climate variables that affect dead zones is necessary to better predict the future of dead zones and to motivate action to confront climate change and its interactions with eutrophication and other anthropogenic impacts.

Authorship

AHA and KBG designed, wrote, and revised earlier drafts of the manuscript. KBG performed the GIS analysis.

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