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Unnatural hypoxic regimes

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Abstract. Coastal hypoxia is increasing worldwide in response to human-caused changes in global climate and biogeochemical cycles. In this paper, we view anthropogenic trends in coastal hypoxia through the lens of disturbance ecology and complexity theory. Complexity theory provides a framework for describing how estuaries and other coastal aquatic ecosystems respond to hypoxia by understanding feedback loops. Can it also be valuable in understanding how these ecosystems behave under shifting (i.e., unnatural) disturbance regimes? When viewed as a disturbance regime, shifts in the spatial (areal extent and fragmentation) and temporal (frequency and duration of events) characteristics of coastal hypoxia can be used to track changes into a non-stationary future. Here, we consider options for increasing the resilience of coastal aquatic ecosystems to future, unnatural hypoxic regimes. To start, we define desirable states as ecosystems with long trophic chains and slow nutrient and carbon dynamics that produce many ecosystem services. We then work backward to describe circumstances dominated by positive feedbacks that can lead ecosystems toward an undesirable state (i.e., depauperate communities and chemically reduced sediments). Processes of degradation and recovery can be understood in the context of island biogeography where species diversity in habitats fragmented by hypoxia is determined by the balance between rapid local extinction, slow recolonization from the edges of hypoxic patches, and opportunities for ecological succession during between disturbance events. We review potential future changes associated with changing global climate and highlight ways to enhance coastal resilience. In addition to efforts to slow climate change, potential interventions include reduced nutrient and carbon loadings from rivers, restoration of aquatic vegetation, and managing for key species, including those that promote sediment oxygenation, that enhance water clarity, or that promote grazing on epiphytic algae through top-down control.

Key words: acidification, positive feedbacks; aquatic vegetation, trophic cascade; climate change disturbance; hypoxia; regime shift; resilience; thresholds, tipping points.

INTRODUCTION

Disturbance, once seen exclusively as an external threat, is now viewed by ecologists as an integral and necessary part of many ecosystems, so long as the disturbance regime provides the conditions needed to perpetuate an ecosystem and its associated ecological community (Clements...
Complexity theory

The dynamics of complex systems are controlled by negative (damping) feedback loops that maintain the system within the basin of attraction to a particular state and positive (amplifying) feedback loops that push the system out of one basin and into the basin of an alternative attractor with its own negative feedbacks. Disturbance regimes mediate the relationship between exogenous environmental drivers and system dynamics. Describing shifts in disturbance regimes can help society to understand how it might prevent environmental drivers from pushing an ecosystem dominated by negative feedbacks (promoting homeostasis) into a new configuration dominated by positive feedbacks that produce large and sometimes undesirable changes in ecosystem state (Seidl et al. 2016). Sometimes, positive feedbacks manifest themselves as cascading or domino effects, and these can be identified through network analyses that reveal two-way interactions (Rocha et al. 2015).

It is easier to monitor and avoid exceeding thresholds caused by human activities (see the next section) if a consistent framework is used to characterize hypoxic regimes and feedback loops that lead to irreversible changes in ecological communities. Management interventions can be designed to strengthen negative (homeostatic) feedback loops and weaken positive feedbacks that shift the community toward simplification (shorter trophic links). Such a framework will improve prediction and monitoring while addressing future challenges to aquatic ecosystems.

Anthropogenic changes.—There is a concern that anthropogenic changes will cause environmental drivers to pass thresholds (the value of a driver, e.g., nitrogen loading or temperature, that, when exceeded, triggers large changes in the ecosystem) beyond which ecological communities cannot recover. Already, hypoxic conditions have expanded in occurrence and duration in coastal waters worldwide (Diaz and Rosenberg 2008, Breitburg et al. 2018), with evidence of greater declines in oxic conditions in coastal areas than in marine systems (Gilbert et al. 2010). The past few decades have seen a drastic increase in the number of coastal areas with episodic or seasonal hypoxia (over 245,000 km² of oceanic hypoxic zones worldwide; Howarth 2008, Conley et al. 2011, Fennel and Testa 2018). For most of these areas, hypoxia was spatially more restricted and less frequent when they were first studied (Diaz and Rosenberg 1995, 2008). Increasing warming trends, combined with upward trends in reactive nitrogen, Nr, and organic carbon loadings, lead to concern that hypoxic disturbance regimes will continue to diverge from pre-anthropogenic norms in directions that lead away from our desired future condition (Boyer et al. 2006, Justic et al. 2007, Diaz and Rosenberg 2008). Below, we briefly review the influences of climate warming, stratification, sea-level rise, acidification, and
nutrient enrichment on the projected growth of hypoxic zones in time and space.

Climate warming is projected to increase the geographic occurrence, frequency, and severity of hypoxia in coastal waters (Breitburg et al. 2018). Melzner et al. (2013) determined that 94% of existing dead zones in estuaries and coastal seas will experience warming of at least 2°C. The duration of hypoxia is expected to increase because of reduced solubility of oxygen and increased heterotrophic respiration (Schmidtko et al. 2017), leading to earlier seasonal stratification (Coma et al. 2009). Among the many consequences, loss of the nursery function that estuaries, marshes, and other coastal ecosystem provide is likely to be disrupted (Hughes et al. 2015).

Increased use of fertilizers in agriculture has increased export of nitrogen (Nr) from rivers and into coastal waters, stimulating algal blooms that decay, causing hypoxia (Howarth 2008). Rocha et al. (2015) used network analysis to show the interacting effects of multiple drivers (including climate, increased nutrients, and fishing) on coastal and marine ecosystems and showed how cascading regime shifts can reduce the ecosystem services available to society (Fig. 1).

Historical observations show a widespread negative trend in dissolved oxygen in the upper ocean driven by changes in ocean circulation, mixing, and biochemical processes (Ito et al. 2017). Hypoxic regimes are mediated by climate changes that drive multi-decadal ocean cycles, such as the Atlantic Multi-decadal Oscillation (Karnauskas et al. 2015), and coastal wind speeds (Pryor and Barthelmie 2011). In coastal estuaries, stratification and mixing processes can be as important as surface oxygen solubility, especially in deeper waters. Strong longitudinal salinity gradients drive gravitational circulation (net up-estuary flow of denser, saltier water near the bottom), leading to differences in the frequency, duration, and severity of hypoxic conditions among estuaries (Kuo and Neilson 1987).

Future climate trends, including warming waters, slowing winds, and increased freshwater inflows (especially during warm seasons), are likely to increase hypoxia (Obenour et al. 2015). High winds, however, increase mixing and could reduce the persistence of hypoxia (Zheng et al. 2016). Future predictions of the Representative Concentration Pathways (RCP 8.5) scenario suggest there will be 5–10% decreases in summer wind speed in coastal areas in the United States (Kulkarni and Huang 2014), which could lead to a decrease in mixing and thereby an increase in the duration and spatial extent of hypoxic events.

Fig. 1. Conceptual transitions from anthropogenic changes to environmental drivers, the spectral signature of a disturbance regime influenced by drivers, and the response of a coastal community leading to changes in ecosystem services. “Environmental drivers” column: global anomalies (top) from U.S. NOAA; trends in nitrate (bottom) from Stets et al. (2015). “Ecological community” and “Ecosystem services” columns: images from creative commons.
(The RCP scenario 8.5 combines assumptions about high population and modest income growth with modest rates of technological change and improvements in the intensity of energy use. These assumptions lead to high energy demand and greenhouse gas (GHG) emissions in the absence of climate change policies; Riahi et al. 2011.) Moreover, some of the largest hypoxic zones are expected to experience increased nutrient loadings. For example, the hypoxic zone in the Gulf of Mexico is fueled by nutrient loadings from the Mississippi River, and the river discharge from the Mississippi River is expected to increase by as much as 23% under a CO2-doubling scenario (Zheng et al. 2016). If this increased discharge occurs during spring and summer, depth stratification will increase in the Gulf of Mexico, decreasing the renewal of surface oxygen levels available for mixing (Tao et al. 2014). Increased freshwater inflow could also prevent the formation of dense deep water that powers the global conveyor belt oceanic currents that regulate climate at broad, global scales (Scheffer et al. 2001). Homogenization of coastal upwelling has also been predicted, and this could have significant implications for ocean fishes and fisheries (Wang et al. 2015). These results highlight the importance of understanding influences of climate on stratification and upwelling (Wang et al. 2015, Meier et al. 2017).

Sea-level rise might be expected to increase hypoxia by increasing stratification (due to salinity increase) and elevating dissolved carbon and nutrient influxes from inundated coastal wetlands. However, over time, coastal seagrass beds and mangroves can slowly migrate toward newly inundated areas with suitable salinities and depth through accretion of sediment (Kirwan et al. 2016, Sasmito et al. 2016), so long as their migration is not impeded by barriers (i.e., coastal infrastructure). Changes in the composition and distribution of mangroves (Sasmito et al. 2016) and marsh grasses and seagrasses (Adam 2002, Koch et al. 2013, Crosby et al. 2016) are expected. Finally, the lack of agreement between observations and hindcast projections by models of ocean circulation, sea-level rise, and other important processes emphasizes that much uncertainty remains (Frollicher et al. 2016).

Ocean acidification caused by CO2 uptake from the atmosphere is another concern associated with future climate change (Altieri and Gedan 2015). Simulating carbon cycle feedbacks shows an acceleration of acidification under future climate (Matear and Lenton 2018), with acidification amplified by coastal hypoxia (Melzner et al. 2013). Spatially, variation in pH reflects locally dominant biological and chemical processes. For example, river plumes tend to have higher pH due to high biological productivity (Guo et al. 2012). Coastal ecosystems with aquatic vegetation (e.g., mangroves) also elevate pH by consuming CO2. Hypoxic zones, however, create hotspots of acidification because microbes that decompose algal blooms produce CO2 and thereby lower pH (Hughes et al. 2015). The negative ecological consequences of acidification on biota are likely to further exacerbate hypoxia—a positive feedback loop.

**Desired ecosystem state and function.** Following Crepin et al. (2012), we define a desired regime as a range of conditions in which the ecosystem maintains a set of structural and functional properties and produces a consistent suite of ecosystem services. Here, we define the desired coastal ecosystem as one that supports long trophic chains and high biodiversity. In such an ecosystem, a small fraction of energy flows through a microbial shunt leading to quick recycling of nutrients involving only primary producers and bacteria. In contrast, communities exposed to persistent hypoxic conditions develop chemically reduced sediments that support small, opportunistic species tolerant of low-redox conditions, including high sulfide levels.

As a reference condition, it is tempting to define a range of desired ecosystem states and functions by describing hypoxic disturbance regimes during historical periods. In other words, during periods not influenced by the relatively recent anthropogenic effects of global warming or disruption of nitrogen cycles by creation of Nr through the Haber–Bosch process (Galloway et al. 2014). However, setting a desired baseline based on historical conditions has several problems. When historical conditions are used as a baseline, already-degraded conditions may be established as a baseline (Villnas and Norkko 2011). This can occur when changes in perspective occur over time due to scientific observation after an ecosystem has changed. As a result, expectations (e.g., for fish abundances) have lowered over time; that is, the baseline has shifted (Pauly 1995, Dayton
et al. 1998). Furthermore, anthropogenic impacts can severely compromise the ability of a system to recover and simply reproducing the signature of prior disturbances may not lead back to the original coastal ecosystem’s state.

Signatures of disturbance regimes in time and space.—Spectral signatures of disturbance regimes can be used to characterize their temporal and spatial patterns. Changes in the spectral properties can be used to track changes in disturbance regimes due to anthropogenic influences. Two temporal descriptions of seasonal hypoxia are its recurrence interval and duration (Fig. 2). In the case of oxygen stress, severity is often measured by the duration of waters with dissolved oxygen concentrations below a threshold, for

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**Fig. 2.** Example of dimensions describing proposed statistical indicators to characterize hypoxic disturbance regimes; (A) recurrence–duration curves are proposed to summarize baseline historical (solid) and future (dashed) regimes; (B) physicochemical changes as the duration of hypoxia increases; (C) changes in ecological community as the duration of hypoxia increases. Taxa vary in sensitivity to the duration of hypoxia, with low tolerance among fishes and crustaceans, higher tolerances among echinoderms and annelids, and the highest tolerances among cnidarians and mollusks (Nystrom et al. 2012, Stets et al. 2015).
example, 2 mg/L (Shields and Weidman 2008). Once this threshold is selected, duration becomes the main indicator of intensity. Similar descriptors have been suggested for other disturbance regimes, such as wildfire in terrestrial ecosystems (Malamud et al. 2005, Keitt 2008, Gooday et al. 2009) and extreme flows in rivers (Poff et al. 1997).

The spatial extent of hypoxia is a second dimension of interest. Spatial extent can be quantified by examining the spatial distribution of low-oxygen recurrence intervals, where annual recurrence is expected in the geographic epicenter of the hypoxic zone, but lower frequencies are possible farther from the center (Fig. 3).

System feedbacks and tipping points.—Complexity theory suggests that ecosystems can shift abruptly among regimes or alternative stable states (Scheffer et al. 2001). Thresholds can appear when positive feedbacks among elements of the ecosystem dominate stabilizing negative feedbacks (Shields and Weidman 2008). Previous work has described positive feedbacks associated with community responses to hypoxia, suggesting the presence of thresholds or tipping points beyond which the trajectory of ecosystems is not easily reversible (Pihl et al. 2006, Conley et al. 2009).

Ecosystem responses to oxygen stress can be described in terms of recurrence interval, duration, spatial fragmentation, and spatial extent. Unlike the other statistics, indicators of intensity are disturbance specific. In this case, dissolved oxygen is used, and ecosystem responses to different ranges of oxygen depletion have been documented (Diaz et al. 2012). Pearson and Rosenberg (1978) developed a paradigm describing biological degradation and recovery patterns for benthic communities in relation to organic enrichment and consequent changes in oxygen availability. The scientific challenge is to define thresholds beyond which recovery is impeded or prevented (Diaz and Rosenberg 2008).

In the case of hypoxia, environmental drivers may cause indicators, such as the duration of hypoxia, to pass a threshold beyond which the ecosystem falls into a new regime dominated by positive feedbacks between physicochemical processes and ecological communities (Pihl et al. 2006, Conley et al. 2009, Fig. 4). The alternative attractor or regime in this case is a depauperate benthic community lacking most taxonomic groups other than bacteria that tolerate highly-reduced and anoxic conditions. We refer to the transition to this hypoxic regime as community collapse (Fig. 4). The resulting ecosystem operates differently in that significant amounts of the system’s energy are shunted to microbial decomposition.

Fig. 3. Frequency of occurrence of midsummer hypoxia in northern Gulf of Mexico based on a 60–90 station grid. Data were available for a multi-transect cruise typically during late July in each year from 1985 to 2008. The white star indicates a continuous data collection site (Station C6). Map from Babin and Rabalais (2009). The northern Gulf of Mexico receives nutrient-laden inflows from the Mississippi river basin, which drains the agricultural Midwest, USA (Vaquer-Sunyer and Duarte 2011). Models suggest that a 59% reduction in nutrient exports is needed to achieve a target of reducing the dead zone to 5000 km² by 2035 (Scavia et al. 2017).
Physicochemical changes can alter how organic matter is processed in sediments, increasing the risk of further hypoxia (Conley et al. 2007). Recovery is inhibited by positive feedbacks by which low-oxygen conditions are caused by an excessive amount of nutrients, stimulating algal growth. The subsequent decay of algae leads to physicochemical changes to sediments, which then become less favorable as habitat to important benthic bioturbating species (Fig. 5).

This phenomenon might have profound consequences for the functioning of the benthic ecosystem. Structural equation modeling used with experimental data to describe interaction networks (Thrush et al. 2014) suggests that critical alterations in benthic ecosystem interactions occur in response to shading, which often is a consequence of increased turbidity due to sedimentation or eutrophication in coastal marine ecosystem (Thrush et al. 2012, 2014). Such changes in important environmental drivers can interrupt positive feedbacks that could lead to shifts in ecosystem functionality. For example, shading can decouple the relationship between sediment biogeochemical fluxes, productivity, and bioturbation by sediment-dwelling bivalves (Thrush et al. 2014). A similar decoupling of nutrient effects has also been reported for ecosystems gaining piscivorous predators (Donadi et al. 2017).

**Community Collapse (Regime Shift)**

**Ecological dynamics**

The time to community collapse (Fig. 2) depends on the composition of the initial community and the sensitivity of the resident species to the chain of events initiated by hypoxia. The first ecological response to decreased oxygen near the bottom is interruption of diel vertical migration by anchovy and other planktivorous fish (Ludsin et al. 2009). Next, mobile benthic species move away from the hypoxic zone (Bell and Eggleston 2005), followed by pelagic species (Rose et al. 2009, Craig 2012). This movement is followed by responses (e.g., reduced growth and increased mortality of individuals or shifts in species) by non-mobile taxa in the benthic community. The loss of top-down control by piscivorous fishes, resulting either from temporary movements to avoid hypoxic zones or from mortality, can trigger threshold-like shifts in ecosystem function (Craig 2012).

Nutrient stimulation of short-lived epiphytic filamentous algae leads to shading perennial...
species of submerged aquatic vegetation (Hughes et al. 2016), as depicted in Fig. 6. However, when piscivorous fish were abundant, they exert top-down control on grazer biomass (i.e., epiphytic algae decrease as grazer biomass increases; Baden et al. 2012, Hughes et al. 2013). In bays of the Baltic Sea, Donadi et al. (2017) noted that piscivores (perch and pike) in a four-level trophic cascade controlled mesopredators (three-spined stickleback), and increased epifaunal grazers which, in turn, benefitted aquatic vegetation. This consistent with the idea that food webs are polarized (Jager and Gardner 1988, Polis et al. 2000), creating trophic cascades. Ecosystems can shift from top-down control by predators to bottom-up (nutrient-limited) control perpetuating hypoxic conditions (Daskalov 2008, Moksnes et al. 2008). Loss of piscivorous fishes through overfishing (Baden et al. 2012) is one factor that has contributed to a worldwide decline in seagrass ecosystems (Orth et al. 2006). Seagrass ecosystems have very high biodiversity relative to surrounding coastal waters (Duffy et al. 2015) and can help to promote coastal resilience (Guan et al. 2016).

Ocean acidification has negative effects on biota ranging from copepods (Wang et al. 2018) to burrowing bivalves, coral reefs, and fishes. Studies suggest that ocean acidification will compress food webs and simplify ecological communities (Kroeker et al. 2011, Vizzini et al. 2017). Acidification may exacerbate biotic feedbacks that prevent recovery of coastal aquatic ecosystems affected by hypoxia. However, mangroves and other aquatic vegetation may be able to increase resilience by taking up CO₂ and raising pH locally (Sippo et al. 2016).

Following prolonged hypoxia over an area of several thousands of km², benthic communities in a Danish estuary transitioned from slower growing, burrowing species to fast-growing, surface-dwelling species (Conley et al. 2007). Collapse of benthic communities can occur with hypoxia after several days or week(s) due to a
combination of oxygen deprivation and release of toxic hydrogen sulfide from sediment (Vaquer-Sunyer and Duarte 2010, Villnas et al. 2012, Fig. 4). The resistance of key species and functional groups to disturbance, for example, via sulfide tolerance (Karlson et al. 2005), largely influences when the regime shift occurs (Lundquist et al. 2004).

Nitrogen dynamics

Positive feedbacks also drive nitrogen dynamics under hypoxic conditions (Fig. 5, loop). Anoxic condition halts the most important process for N-removal in coastal waters, coupled nitrification–denitrification (Jäntti et al. 2011). Following short seasonal anoxic events, coupled nitrification–denitrification can be restored to baseline levels after reoxygenation (Hietanen and Lukkari 2007, Fig. 7, thin lines). However, prolonged events create a positive feedback whereby sediment demand for oxygen increases and nutrients are remobilized into the water column from the sediment (Hietanen and Lukkari 2007). After an extended period of anoxia, denitrifiers may be lost from the microbial community causing denitrification to remain low even after oxygen returns to the system (Karlson et al. 2005, Fig. 7, thick lines). Remineralization of benthic algae has a positive feedback on the system as it further increases the amount of available nitrogen and stimulates additional algal production and subsequent decay (Karlson et al. 2005, Conley et al. 2007).

Loss of macrobenthic species following hypoxia has been shown to reduce benthic bioturbation potential (Villnäs 2013), which reduces the oxic–anoxic interface in the sediment where coupled nitrification–denitrification processes take place (Kristensen 2000). Indeed, Douglas et al. (2017) found that decreased diversity and abundance of important nutrient-processing benthic species reduced denitrification following nutrient stress. Microcosm experiments suggest that acidification could prevent bioturbation from promoting oxidation of ammonia (Laverock et al. 2013). We note that duration of seasonal hypoxia is likely to be affected by seasonal patterns in temperature due to climate warming.
Anticipating regime shifts under unnatural hypoxic regimes

Anthropogenic impacts can severely compromise the ability of a system to recover and simply reproducing the signature of prior disturbances may not lead to the desired basin of attraction. As Conley et al. (2009) submit, a return to “Neverland” is not possible after a system progresses beyond thresholds of various hypoxia measures. For example, none of the coastal aquatic ecosystems examined by Conley et al. (2009) returned to their reference chlorophyll-a levels even after nutrient reduction and decades of time for recovery. Beyond a threshold of frequency, duration, or spatial scale in hypoxic events, altered community structure and function makes recovery difficult. In terms of complexity theory, the ecosystem has moved into a new basin of attraction.

With the expected expansion of hypoxia under non-stationary global climate drivers and nutrient loadings, how will we know when a transition to an undesirable state (i.e., tipping point) is on the horizon? Developing leading indicators of such ecological regime shifts has been an active area of theoretical research (Scheffer et al. 2012). However, the empirical testing of these indicators to see how well they predict regime shifts has lagged theoretical modeling efforts (Groffman et al. 2006).

One leading indicator identified using theoretical models is critical slowing down, signaled by increased autocorrelation in ecosystem state (reduced resilience defined as the ability of an ecosystem to withstand or recover quickly from a disturbance) as the system approaches the basin of a new attractor (Dakos et al. 2008, Biggs et al. 2009). Yet, regime shifts can be slow (Karssenberg et al. 2017). Slow shifts occur when the positive feedbacks involve pools that have slow dynamics, producing long lags (e.g., flux of phosphorus from sediment, slow recolonization of dominant macrofaunal from distant sources; Lundquist et al. 2004, Karssenberg et al. 2017).

Estuarine and other coastal aquatic ecosystems have often responded gradually to historical declines in key species and functions that foreshadowed community collapse (Conley et al. 2007, Thrush et al. 2009).

Deviation from historical power laws describing spectral properties of ecosystems has been noted as a promising temporal indicator of an impending tipping point (Kéfi et al. 2014). Increasing spatial variability has also been suggested as one harbinger of regime shift (Lundquist et al. 2004). Following the loss of
functionally important species, an increase in spatial variance, that is, in beta diversity or heterogeneity, can foreshadow collapse into a homogeneous community dominated by opportunistic species (Lundquist et al. 2004, Thrush et al. 2009, Kéfi et al. 2014).

The best leading indicator may be a trend in the recurrence interval of hypoxia in coastal waters. Disturbance regimes with recurrence intervals of hypoxia shorter than recovery rate of the least-resilient taxa are most at risk of an extended, if not permanent, shift to a less desirable state. For example, the diversity and abundance of benthic fauna in a Norwegian study was lowest in areas that experienced more frequently recurring hypoxic events because the time for complete recovery before the next event was insufficient (van Son et al. 2014).

COMMUNITY RECOVERY

Successional recovery of the benthic community is an example of hysteresis; that is, it does not typically follow the reverse path of degradation (Rosenberg et al. 2002, Diaz and Rosenberg 2008, Steckbauer et al. 2011). Recovery can be delayed by anoxic sediment conditions, tending to the release of P and decomposition of organic carbon. This refuels primary production, which subsequently increases the oxygen demand of the sediment (Middelburg and Levin 2009). Furthermore, the first colonizers of benthic communities must tolerate the reduced sulfur compounds that have accumulated, and therefore, sulfide-oxidizing microbes may be important (Fig. 5). Diatoms are also relatively tolerant of hypoxic conditions and have been found to be pioneer species that colonize artificially defaunated benthic plots in a shallow area within a week, adding oxygen (Larson and Sundback 2008, Montserrat et al. 2008). The earliest observed animal colonists have been small, surface-deposit feeders, followed by subsurface feeders and later, large, deep-burrowing animals (Middelburg and Levin 2009).

Timing of community recovery

Across disturbance regimes, timescales of recovery processes define threshold behavior (Turner and Dale 1998). There are important differences in the dynamics of hypoxia between shallow, well-mixed estuaries and deeper, stratified coastal aquatic ecosystems. Time series have shown recovery in response to simultaneous decreases in nutrient and organic carbon loadings in shallow, but not in deep-water offshore ecosystems (Middelburg and Levin 2009). A lack of response can be due to a trophic cascade that decouples algae from nutrients through top-down control, for example.

Recovery of fauna typically takes longer than recovery of chemical sediment dynamics. Recovery in response to hypoxia caused by organic enrichment can take much longer than that caused by nutrient pollution alone because redox potentials change and undegraded organic matter accumulates in sediment (Gammal et al. 2017). Recovery of benthic fauna from hypoxia (<2 mg/L O2) can take months to years (Rosenberg et al. 2002, Van Colen et al. 2010, Steckbauer et al. 2011). In the Scheldt estuary, recovery of small, opportunistic foraminifera feeding on bacteria occurred within two weeks, followed by a bloom of microphytobenthos and recovery of nematodes by eight weeks (Brouwer et al. 2015). Larger macrofauna (>5 mm) were slow to recover after complete extirpation (Brouwer et al. 2015). The recovery of benthic macrofauna (e.g., bivalves, polychaetes) is important because these organisms are known to facilitate recovery of meiofauna through sediment bioturbation and reoxygenation (Van Colen et al. 2012, Brouwer et al. 2015). Divergence in community assembly following disturbance creates patchiness whereby some patches are reached first by bioturbators and other patches are settled by deposit feeders that are negatively affected by bioturbation (Van Colen et al. 2012).

Spatial and temporal influences on recovery

Temporal recovery in shallow disturbance-driven ecosystems has been described by the windows of opportunity (WoO) theory. Originally developed to understand vegetation recovery in disturbance-driven floodplains, WoO can help to interpret how the spectral signature (e.g., frequency) of disturbance will influence recovery. After a disturbance leaves bare sediment, the WoO theory predicts that recolonization will occur when the duration of time (i.e., the window) with no physical disturbance is long enough to permit seedling establishment (Balke
et al. 2014). The WoO theory correctly predicted a sudden vegetation recovery event in a salt-marsh (Balke et al. 2014). We suggest here that this idea may also apply to non-physical disturbances that remove vegetation, such as hypoxia or changes in salinity (e.g., sea-level rise; Fig. 6).

Spatially, we expect communities to recover more slowly at the center of larger hypoxic zones than at its edges or at the centers of smaller zones. Theory predicts that the duration of successional recovery of benthic communities should increase as the spatial scale of disturbance increases (Balke et al. 2014), and field studies that simulated disturbance by smothering sediment support this prediction. At a finer scale, intertidal patches with low diversity dominated by opportunistic species tended to recover more quickly than those without opportunistic species in Mahurangi Harbor, New Zealand. However, recovery of biomass was slow (<80% of biomass after 394 d), and resilience was enhanced by maintaining ecological connectivity to a broad, regional pool of species (Thrash et al. 2008). Recolonization depends on life-history traits, such as mobility, timing of reproduction, mode of development, and dispersal strategies (Valanko et al. 2010, Heino et al. 2015). Depending on the assemblage, post-disturbance recolonization of benthic communities in coastal systems can be accomplished through larval drift and post-settlement dispersal as well as by adult movement (Norkko et al. 2010, Pratt et al. 2015). Whitlatch et al. (1998) found that immigration of juveniles had a much more dramatic effect on patch recovery time and population dynamics than did immigration by adults.

The spatial extent of bottom-water hypoxia is a frequently reported measure (Buzzelli et al. 2002). Several studies have addressed how the spatial extent of hypoxic areas influences the ability of benthic communities to recover (Thrash et al. 1996, Norkko et al. 2006, 2010). Norkko et al. (2006) defaunated patches of different sizes to study macrofauna recovery in the intertidal zone. Most taxa showed the expected pattern, with recolonization proceeding from the edges leading to faster colonization of smaller defaunated patches. However, the amphipod, Corophium volutator, which showed the opposite pattern, recolonized areas not yet reached by the bioturbating lugworm, Arenicola, that exposes the amphipod to predators. This negative species interaction is typical between opportunistic species that colonize early and bioturbating species that appear later in succession.

Such studies are needed to establish spatial thresholds in patch-size statistics (Kéfi et al. 2014). Many natural hazards have fractal or scale-independent spatial distributions (Norkko et al. 2006). As one example, a frequency–area distribution is considered to follow a power law if the frequency of disturbed area $A$ is $f(A) \sim A^{-\beta}$ (Kéfi et al. 2014). More research is needed to establish scaling relationships and characteristic recolonization times following hypoxic events for different sized hypoxic zones in coastal waters.

**Comparison of Hypoxia with Wildfire Disturbance Regimes**

It is interesting to consider similarities and differences between hypoxic regimes and other disturbances. The spectral signature of disturbances is a canonical framework for comparing disturbances and transferring knowledge gained by studying one type of disturbance regime to another.

In the case of wildfire, high-intensity wildfires have increased in frequency and size (Smith et al. 2009, Barbero et al. 2015). Wildfire regimes can be described by frequency–area distributions for burns of different sizes, and the consensus is that these distributions are heavy tailed (i.e., there are more large burns than under an exponential distribution; Millington et al. 2006). A critical transition threshold in wildfire spread corresponds to the amount of fuel expected to grow between sparks (i.e., a measure of recovery rate), a threshold that many forests in Canada are now approaching (Millington et al. 2006). Spatially, this tipping point is related to the percolation threshold; that is, the probability of finding a cluster of fire-susceptible cells spanning a large area increases dramatically, along with the average area burned (Malamud et al. 2005).

The spatial dynamics of feedbacks characteristic of hypoxia may be fundamentally different from those of terrestrial ecosystems affected by wildfire. Whereas burning of a patch in one year lowers the risk of a wildfire in the next years (negative feedback during recovery; Sturdivant et al. 2013), hypoxic events elevate future risk (positive feedback during recovery). Thus,
hypoxia does not share the spatially self-limiting qualities of wildfire. Nevertheless, spatial strategies can be devised to avoid “cascades of failure” for networks of hypoxic patches. It may also be possible to develop recovery-time relationships as functions of hypoxic patch size and to discover size thresholds that permit recolonization within the interval between seasonal events.

RESILIENCE IN THE FACE OF ANTHROPOGENIC CHANGE

Under global climate change, the severity, duration, frequency, and spatial extent of disturbances, including hypoxia, are expected to increase (Dale et al. 2001, Intergovernmental Panel on Climate Change 2007, Zinck et al. 2011). For example, simulations of a doubled-\text{CO}_2 climate predicted a 30–60\% decrease in average summer deep-water oxygen content from a 1985–1992 baseline (Breitburg et al. 2018). Warm water has lower oxygen solubility than cold water and leads to higher oxygen (respiration) requirements of aquatic organisms (Carpenter 1966, Buzzelli et al. 2002, Conley et al. 2007, 2009, Middelburg and Levin 2009); these combined effects intensify the influence of hypoxia on aquatic communities (Steckbauer et al. 2011).

In some cases, global increases in hypoxia in coastal waters may have followed, rather than preceded, declines in species diversity due to losses of aquatic vegetation (e.g., wetlands, seagrasses; Lotze et al. 2006). Algal over-growth, stimulated by excess nutrients, can lead to shading and loss of vegetation (Burkholder et al. 2007). Efforts to restore coastal habitats can lead to more resilient ecosystems that will be able to absorb future more frequent or more intense disturbances (Lotze et al. 2006). This response is possible because coastal vegetation (e.g., saltmarshes, seagrasses, and mangroves) provides critical nursery habitat (Fig. 6) and serves as a sink for nutrients and sediment. More generally, positive feedbacks initiated by hypoxia can be interrupted by ensuring that critical taxa (e.g., piscivorous fishes, benthic bioturbating species, water-filtering species) occur at abundances needed to foster ecosystem resilience (Thrush et al. 2008). For example, recruitment of suspension-feeding mussels or oyster reefs can push the system from a turbid to a top-down controlled state (Nystrom et al. 2012). Trophic controls, such as protecting piscivorous fishes, may also be effective. Another path to promoting resilience is to promote functional diversity of nutrient-processing species and benthic macrofauna that perform bioturbation (Douglas et al. 2017).

Ecosystem resilience is challenged by ongoing anthropogenic pressures that are inducing changes in natural disturbance regimes such as hypoxia in coastal waters. Enhancing the ability of an ecosystem to withstand or recover quickly from a disturbance will be critical as disturbance regimes change. Complexity theory offers one tool to understand and evaluate system feedbacks and to define thresholds in the face of these changes. Building that understanding requires defining desired future conditions and quantifying system feedbacks and responses to exogenous drivers.

CONCLUSIONS

In this synthesis, we considered options for increasing the resilience of coastal aquatic ecosystems to future, unnatural hypoxic regimes. By interrupting positive feedback cycles (Nystrom et al. 2012), as shown in Fig. 5, we can restore more natural hypoxic disturbance regimes and foster resilient coastal aquatic ecosystems.

Table 1. Potential interventions suggested by feedback loops that prolong hypoxia.

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<th>Intervention Description</th>
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<tr>
<td>1. Change abiotic drivers</td>
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<td>• Reduce nutrient and carbon runoff from rivers</td>
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<td>• Slow warming through reduced carbon emissions</td>
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<td>• Decrease freshwater flow from rivers</td>
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<td>2. Restore aquatic vegetation</td>
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<tr>
<td>• Restore seagrass beds, saltmarsh, and mangroves</td>
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<td>• Remove barriers to expansion of vegetation</td>
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<tr>
<td>• Manage for bioturbating macrofauna that promote aeration of sediment</td>
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<tr>
<td>• Protect oyster and mussel beds</td>
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<tr>
<td>• Create coastal protected areas for piscivorous fishes that control grazers</td>
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<tr>
<td>3. Increase oxygen exchange in sediment</td>
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<td>4. Increase water clarity</td>
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dominated by long trophic chains and a strong portfolio of ecosystem services. We conclude by offering suggesting paths to promote resilience that were identified from this analysis and review (Table 1). These include changing the abiotic drivers (i.e., warming and nutrient inputs) that control salinity gradients and mixing, restoring aquatic vegetation, removing barriers that permit seagrasses, saltmarsh vegetation, and mangroves to track suitable habitat conditions, managing for benthic species whose presence supports oxygen exchange in sediments, increased water clarity (e.g., mussels, oysters), or control of other ecosystem processes (e.g., protected areas to support piscivorous fishes that exert top-down control). Understanding feedbacks is the key to building resilience into coastal ecosystems facing unnatural disturbance regimes.

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LITERATURE CITED


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