Massive oyster kill in Galveston Bay caused by prolonged low-salinity exposure after Hurricane Harvey

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Abstract

Extreme precipitation events are projected to occur more frequently under a warming climate, posing increasing threats to coastal ecosystems. Hurricane Harvey (2017), the wettest tropical cyclone in the U.S. history that caused a 1000-year flood in the Houston metropolitan area, provides an opportunity to study the response of coastal ecosystems to extreme events. As sessile, epibenthic filter-feeding organisms, oysters are inherently sensitive to changes in environmental and water quality conditions, making them a good indicator for ecosystem health. Oyster measurements at 130 sites in Galveston Bay show that the mean oyster mortality drastically increased from 11% before Harvey to 48% after Harvey. Post-Harvey oyster mortality exhibited large spatial variability and was up to 100% at some major reef complexes. For all the oyster sampling sites, brown shells were dominant, while black shells indicating mud burial were rare. Considering the little impact from sediment deposit, we hypothesized the low-salinity exposure as the main cause for the massive oyster kill. We conducted a multidisciplinary (biological-geological-physical) investigation combining the oyster data with bay-wide sediment core data and results of a previously-validated high-resolution numerical model. Oyster mortality was found to be significantly and positively correlated with the bottom low-salinity exposure time (duration of bottom salinity continuously less than 5 PSU), while there was no significant relationship with the thickness of storm-induced sediment deposit. The physiological aspects for the impact of low-salinity exposure, the underlying physical mechanisms for the prolonged salinity recovery, and wider implications of oyster kill in Galveston Bay in the context of global oyster reef conditions were discussed. The worldwide reported oyster kill events due to extreme weather events suggest additional pressure posed by future climate on the native coastal oyster

reefs that are already at the brink of functional extinction worldwide due to centuries of resource extraction and coastal habitat degradation.

Keywords: oyster mortality; low-salinity exposure; extreme precipitation; Galveston Bay; Hurricane Harvey

1. Introduction

Extreme precipitation and subsequent flooding resulting from intense tropical cyclones have become more frequent over the past few decades (Knight and Davis, 2009; Donat et al., 2016; Pfahl et al., 2017). Historic amounts of rainfall have been reported more often recently. For example, Hurricane Floyd (1999) brought up to 61 cm of precipitation in North Carolina (Atallah and Bosart, 2003), Hurricane Harvey (2017) 130 cm in Texas (Du et al., 2019a) and Hurricane Florence (2018) 91 cm in North Carolina (Feaster et al., 2018). The likelihood of extreme precipitation events is projected to increase under a warming climate due to increased upper ocean heat content and atmospheric humidity (Knight and Davis, 2009; Donat et al., 2016; Pfahl et al., 2017). In the future, the climate is likely going to be characterized by more extreme intra-annual precipitation regimes (Knight and Davis, 2009; Risser and Wehner, 2017; Trenberth et al., 2018).

Extreme precipitation events and the resulting flooding in coastal areas are posing increasing threats to human society and have acute impacts or long-lasting influences on coastal ecosystems (Paerl et al., 2001; Holmgren et al., 2007; Wetz and Yoskowitz, 2013; Biggs et al., 2018). In addition to the dramatic responses in hydrodynamic processes, significant shifts in phytoplankton and fish communities have been widely observed after heavy floods (Hughes, 2000; Weyhenmeyer et al., 2004; Cardoso et al., 2008; Steichen et al., 2020). The timescales of their influence on coastal ecosystems range from days to years and vary from one system to another, depending on the event's intensity and the resiliency of the system in both hydrodynamic and biological processes. Advancing our understanding of the ecosystem's response and resiliency to extreme perturbation is of urgent importance in guiding living resource management and can be facilitated by establishing and assessing appropriate indicators for ecosystem function and health.

As sessile, epibenthic, filter-feeding organisms, oysters are inherently sensitive to changes in environmental and water quality conditions (Lowe et al., 2017), making them an excellent sentinel organism to examine how extreme weather events may impact the ecosystem health (Volety et al., 2003). Oysters play an important role in the ecosystem by filtering phytoplankton, removing particles in the water column, providing food, shelter, and habitat for fish and invertebrates (Newell and Jordan, 1983; Lenihan et al., 2001), and protecting the shoreline from erosion (Piazza et al., 2005). Along the northern coast of Gulf of Mexico and the Atlantic coast of the United States, the eastern oyster (*Crassostrea virginica*) is the primary commercially valuable species of oyster (MacKenzie et al., 1997; zu Ermgassen et al., 2013).

Hurricane Harvey (hereinafter referred to as Harvey) provides an ideal opportunity to investigate how eastern oysters in natural waters respond to acute external perturbations. The oyster industry in Galveston Bay made up as much as 22% of the total U.S. harvest and brought in $14.7 million ex-vessel value in 2004 (NOAA Fisheries landings data: https://foss.nmfs.noaa.gov/apexfoss/f?p=215:200:641675228657, accessed on November 17, 2020), but oyster landings have significantly decreased since that time. An average annual ex-vessel value was just $7.7 million for 2007-2016 with the landings accounting for only 8.7% of the national oyster harvest (Texas Parks & Wildlife Department, unpublished data). In 2017, Harvey (Fig. 1a) brought record-breaking precipitation (maximum 130 cm over a 5-d period) and, together with wind-induced storm surge, it caused unprecedented compound flooding in the Houston-Galveston area (Valle-Levinson et al., 2020; Huang et al., 2020). It delivered a huge volume of freshwater (14×10^9 m^3) and sediment (9.86×10^7 metric tons) into Galveston Bay (Du et al., 2019a, 2019b). The enormous volume of freshwater input, about 3.7 times the bay volume, made the entire bay virtually fresh for days (Fig. 1), exerting potentially high pressure on the wild eastern oysters in the bay. Eastern oyster populations thrive at intermediate salinities (10-20 PSU) in most estuaries (Cake, 1983), even though adults can survive under a wider salinity range (0-42.5 PSU) (Menzel et al., 1966). Prolonged exposure to low-salinity water has been observed to cause substantial oyster mortality, and oysters are more vulnerable to low-salinity exposure in warmer water (Levinton et al., 2011; Pollack et al., 2011; Munroe et al., 2013).

We conducted a multidisciplinary (biological-geological-physical) investigation to identify the underlying mechanism(s) for the massive oyster kill after Harvey. The observed post-Harvey mortality rate of eastern oyster at 130 sampling sites is high with large spatial variability. Previous studies have shown that low-salinity exposure and/or sediment deposit (smothering) can increase oyster mortality (Volety et al., 2003; Munroe et al., 2013; Colden and Lipcius, 2015). We applied a validated hydrodynamic model to calculate the "low-salinity exposure time," the duration when bottom salinity was continuously below a given threshold, and examined the relationship between the oyster mortality and the low-salinity exposure time. We found a significant relationship between the oyster mortality and the low-salinity exposure time but not with the storm sediment deposit estimated from 56 push cores collected throughout the entire bay. The physiological mechanisms for the impact of low-salinity exposure and how the Harvey case implicates coastal ecosystems' response to extreme weather events were discussed. Our findings explain how hydrodynamic processes affect oyster survival under natural setting during an extreme precipitation event.

2. Material and Methods

2.1. Measurement of eastern oyster mortality

Texas Parks & Wildlife Department measured oyster mortality at 130 sampling sites, covering most of the harvestable public oyster reefs in Galveston Bay on October 2 and 11, 2017, about one month after Harvey made landfall along the mid-Texas coast. Ten samples were collected at each of the 12 major reef complexes (Fig. 2a) using a 0.5 m-wide “Biloxi style” oyster dredge, with each dredge pulled at 4.8 km h^{-1} for 30 sec. All oysters greater than 25 mm were categorized as live or “boxes”. Boxes here mean recently dead oysters with shells still attached at the hinge (articulated) and thus were presumably alive before Harvey. Mortality was determined for each sample based on the number of boxes relative to the total number of live oysters before Harvey (i.e., live + boxes).

For comparison, the oyster mortality rate was also determined for pre-Harvey normal conditions using another 130 samples collected in the fall of 2016. Of them, 100 sites were sampled in September 2016, but the other 30 sites in the middle of the bay were sampled in November 2016. Nonetheless, the results are typical of what we usually observed in those areas prior to Harvey.

2.2. Storm sediment deposit thickness

From October 2017 to May 2018, 56 push cores were collected using 7.62-cm diameter, 0.6-cm long polycarbonate core barrels. Upon returning to the lab, the polycarbonate push cores were x-rayed using a large animal veterinarian x-ray machine with a digital panel. The thickness of the Harvey flood layer was visually determined from the x-radiographs based on textural variations in the strata (see Fig. 5 in Dellapenna et al., 2020). For most cores, the base of the Hurricane Harvey deposit was easily identified from the x-radiographs as an anomalous erosional surface with a shell and sand layer (representing the bedload deposit) sitting atop of it and above this a high-water content mud deposit (representing the suspended load deposit). The sand layer was clearly evident as a lighter tone in the x-rays and is an anomalous feature within these cores as they were all collected in areas where the remainder of the cores were mud dominated. We examined the relationship between the oyster mortality rate and the storm deposit thickness.

2.3. Numerical model and simulations

We employed a pre-calibrated 3D hydrodynamic model (Du et al., 2019c), with the model domain covering the northwestern Gulf of Mexico (Fig. 1a). The purpose of using the hydrodynamic model is to overcome the limitation of salinity observations as only a handful of water quality monitoring stations are maintained for the entire Galveston Bay and data from these monitoring stations are insufficient to cover the widely-spreading oyster reef areas. The model is based on the Semi-implicit Cross-scale Hydroscience Integrated System Model (SCHISM: Zhang et al., 2015, 2016). The model grid contains 142,972 horizontal elements, with the horizontal resolution ranging from 40 m in the narrow ship channel (surface width of 150 m) of Galveston Bay (Fig. 1b) to 2.5 km on the shelf and 10 km in the open ocean. The fine grid for the ship channel is carefully aligned with the channel orientation to faithfully capture the sharply-changing bathymetry near the channel edge, which is important to accurately simulate the salt intrusion process (Ye et al., 2018). Vertically, a hybrid *s*-*z* grid is used, with 10 sigma layers for depths less than 20 m and another 30 *z* layers for depths from 20 to 4000 m. When forced by realistic boundary conditions, including the open boundary conditions from FES2014 global tide (Carrere et al., 2015) and global HYCOM model output (https://www.hycom.org/data/glbu0pt08), atmospheric forcing from the European Centre for Medium-Range Weather Forecasts (ECMWF: https://www.ecmwf.int), and river discharges from 15 USGS gaging stations, the model gives a satisfactory reproduction of the observed hydrodynamic conditions in 2007-2008 inside the Galveston Bay and over the Texas-Louisiana shelf in terms of water level, salinity, temperature, vertical stratification, and shelf currents. A more detailed description of the model configuration, including the grid system, bathymetry, and forcing boundary conditions, and the 2007-2008 model validation results can be found in Du et al. (2019c).

This model was applied to simulate the hydrodynamic response of Galveston Bay to Harvey (Du and Park, 2019). For the Harvey simulation, not only the surface runoff but also the groundwater discharged were carefully incorporated in the model. Based on a freshwater-fraction method using measured salinity and velocity at the bay entrance, Du et al. (2019a, 2019b) estimated that 47% (6.63×10^9 m^3) was through diffusive surface runoff and groundwater discharge along the bay's coastline. By adding point sources of freshwater along the bay's coastline line to account for this part of freshwater load, the model reproduced well the notable estuarine responses to Harvey, including long-lasting elevated water level, extraordinarily strong along-channel velocity with the seaward speed exceeding 3 m s^{-1}, sharp decreases and long recovery of salinity, and huge river plumes on the shelf. Particularly, this model application reproduces the temporal and spatial variation of salinity during Harvey very well, with the mean absolute error of 1.4 PSU at MIDG at the middle of the bay and TRIN inside Trinity Bay (see Fig. 1b for their locations) (Du and Park, 2019). The hydrodynamic simulation for Harvey has been used to examine the dispersion of leaked pollutants in Galveston Bay (Du et al., 2020). The output of the validated hydrodynamics, specifically the bottom salinity, was used in this study to quantify the spatially-varying low-salinity exposure.

A salinity of 5 PSU has been suggested as a critical threshold value for oyster recruitment, survival, and growth, although the threshold value varies with water temperature. Soaking in water with salinity at 5 PSU and temperature of 23-25°C can lead to very high mortality of juvenile oysters, 75% and 96% after 2 and 9 weeks, respectively (Volety et al., 2003). Even for adult oysters, prolonged exposure to low-salinity (<5 PSU) water can lead to high moralities (Chanley, 1957; Powell et al., 1994).

We used the validated hydrodynamic model to estimate the low-salinity exposure time (T_{E5}), defined as the duration for bottom salinity to be continuously lower than 5 PSU, during Harvey and examined the relationship between the oyster mortality rate and T_{E5}. We then conducted seven numerical experiments with 0%, 10%, 20%, 30%, 40%, 50%, and 200% of Harvey's stormwater ΔQ (the freshwater load due to Harvey, defined as the difference between the discharge during Harvey and the pre-storm condition: see Fig. 4 in Du and Park, 2019) and calculated the corresponding T_{E5} to further investigate the system's response to different amounts of stormwater input. The extraordinary amount of Harvey's stormwater (ΔQ) is rare, with the return period exceeding 1,000 years (van Oldenborgh et al., 2018), but precipitation events with smaller intensities (e.g., 10%-50% of ΔQ) are likely to occur more frequently. The results from model scenario runs were used to examine the relationship between T_{E5} and stormwater input.

3. Results

3.1. High oyster mortality after Harvey

Relative to the pre-Harvey surveys, oyster mortality rate increased dramatically after Harvey (Fig. 2). Of the 130 sampling sites at 12 major reef complexes, oysters (boxes or live) were found at 117 sites, while old dead shells (disarticulated shell halves) and some buried shells were found at the remaining 13 sites. The mean mortality rate for all sites increased from 11% in the pre-Harvey surveys to 48% in the post-Harvey surveys. The mortality rates after Harvey exhibit a very large spatial variability, ranging from 10% to 100% (Fig. 2b). Mortality rates higher than 75% were found at several reef complexes in East Bay (reefs #10 and #11) and west of the Houston Ship Channel (reefs #1 and #3). In particular, no live oyster was found at reef #11 in the inner part of East Bay. Oyster reefs in Galveston Bay have been recovering since Harvey, which also varies spatially, with a rapid recovery along the ship channel and a slow recovery in East Bay, such as reefs #9, #10, and #11 (Texas Parks & Wildlife Department, unpublished data).

The disarticulation rates of boxes, which depend on salinity and temperature, have been found to take less than a year (Ford et al., 2006). However, for the overwhelming majority of the boxes in the post-Harvey samples, their insides were relatively clean with no fouling organisms or oyster spat observed, indicating that the oysters had been dead for only a short period of time prior to sampling. Additionally, there was a dramatic increase in the number of these clean, empty boxes observed in the post-Harvey samples, indicating a massive mortality event after Harvey.

3.2. Oyster mortality vs. low-salinity exposure time and storm sediment deposit

It has been shown that low-salinity exposure and/or sediment deposit (smothering) can increase the oyster mortality (Volety et al., 2003; Munroe et al., 2013; Colden and Lipcius, 2015). The observed Harvey flood deposit sediment thickness exhibit large spatial variability (Fig. 3b). For all oyster sampling sites, brown shells were dominant, while black shells that have been buried by mud were rare, indicating little impact from sediment smothering despite the large input of sediment during Harvey. This is confirmed by regression analysis between oyster mortality rate and the storm sediment deposit thickness, which shows no significant relationship between them (Fig. 3d). This is likely because oyster reefs are bathymetrically high features, i.e., they have positive bathymetric relief. The storm flood deposits were mud dominated and settled out from the suspended load of the flood waters on the seabed, primarily within bathymetrically low areas. Therefore, there was not much deposition on top of the oyster reefs, with the noted exception of the area just upstream of the Texas City Dike, where flood deposit was thickest (Fig. 3b) (Du et al., 2019a; Dellapenna et al., 2020).

We hypothesized the controlling factor for the spatially varying oyster mortality is the low-salinity exposure. To quantify the impact of low-salinity exposure, we calculated the low-salinity exposure time based on bottom salinity outputs of the validated numerical model (Du and Park, 2019). The calculated low-salinity exposure time with a critical threshold of 5 PSU (T_{E5}) exhibits a very large spatial variability, ranging from a few days to >30 d, with the longest T_{E5} in East Bay, Trinity Bay and the upper Galveston Bay (Fig. 3a). Regression analysis revealed a significant positive linear relationship (r^2 = 0.51; p-value = 0.02), indicating a strong spatial coherence between oyster mortality and T_{E5} (Fig. 3c). Note that reefs #1 and #12 were regarded as outliers (see below) and excluded from the regression analysis. We also conducted a regression analysis between the mortality and low-salinity exposure time using a critical salinity ranging from 1 to 10 PSU. A critical salinity of 5-10 PSU gave similar significance of positive relationship, but no significant relationship was found for a critical salinity of 1-4 PSU with all p-values > 0.17.

Of the 12 reef complexes, reefs #1 and #12 were identified as outliers for the linear regression between oyster mortality and T_{E5}. Reef #1 is located close to the Texas City Dike, a levee extending 8 km southeast into the mouth of Galveston Bay. It was constructed in 1930s to protect the Texas City Channel from siltation by sediments transported downstream in the bay. The sediment core data show that more than 35 cm of Harvey sediment deposited just upstream of the dike in the area around reef #1 (Fig. 3b). It is at least in part due to the presence of the Texas City Dike, which hinders the transport of sediments from the main bay to West Bay and thus facilitates the accumulation of sediments on the upstream side of the dike. The main reason for the oyster kill at reef #1 is therefore likely sediment smothering rather than freshwater soaking. As for reef #12 in Trinity Bay, poor conditions have been observed for many years prior to Harvey with low abundance of live oysters and large amounts of black, buried shells (Texas Parks & Wildlife Department, unpublished data). Our post-Harvey survey data also show that most shells were empty and old at reef #12, for which a recent event like Harvey was not likely to be responsible.

4. Discussion

4.1. Cause(s) for the massive oyster kill

Oyster kill in the coastal sea can be caused by a variety of processes, including viral infection, sediment smothering (or siltation), reduction of river flow (leading to high salinity), flooding (leading to low salinity), extreme weather, habitat destruction, and hypoxia (Mackenzie, 2007; La Peyre et al., 2013). During a storm event, the storm-induced sediment deposition and flooding are presumably regarded as the two prominent causes for the subsequent oyster kill in Galveston Bay. Field surveys suggest little evidence of sediment smothering, since black shells (indicting mud deposition) were rare. The most probable reason accounting for the massive oyster kill is the flooding-induced low-salinity exposure. This hypothesis is confirmed by the significant positive relationship and spatial coherence between oyster mortality and low-salinity exposure time (Fig. 3c). While it is always risky to use correlation analysis to indicate the causality, the major conclusion regarding the cause of oyster kill during the storm events is still valid as other prominent causes (e.g., hypoxia, viral infection) can be excluded. Hypoxia is rarely observed in Galveston Bay, mostly because of the bay's shallow bathymetry (mean depth of about 2.5m, see the bay's bathymetry in Fig. 1b). Viral infections are more frequently seen after severe droughts and high salinity conditions, ant thus unlikely to happen following the extraordinary freshwater load during Harvey.

The influence of exposure to low-salinity water has been examined in previous studies with laboratory experiments that usually examined the response to constant salinities (Loosanoff 1953; Volety et al., 2003). The laboratory setting is unnatural as salinity in natural coastal water fluctuates at tidal and subtidal time scales. The T_{E5}-mortality curve in Fig. 3c, therefore, would be closer to the response in natural systems. Despite uncertainties associated with spatially varying storm deposits, this curve can serve as an efficient guideline for a quick assessment of the stress imposed on oysters by flooding events during the warm summer months. For example, a 14-d exposure of low-salinity (5 PSU) may lead to 50% mortality under the water temperature of 28±2.6°C (measured at the bay entrance in September 2017). For flooding events during the cooler winter months or in cooler environments, the mortality under the same duration of low-salinity exposure is expected to be lower.

The impact of low-salinity exposure is also manifested in the typical spatial distribution of oysters along the salinity gradient in estuaries. Reefs located near the head of an estuary where salinity is low are sparsely populated due to frequent flooding and high mortality rates; the population is dense in the middle of estuaries with intermediate salinity; and the population becomes sparse toward the higher salinity waters near the mouth of the estuary where parasitic infection and predation pressure are high (Bergquist et al., 2006; Volety et al., 2009).

The effect of low-salinity exposure on oyster mortality depends highly on seawater temperature. In explaining the summer mortality event of the Pacific oyster in France, Samain and McCombie (2008) showed that mortalities occurred only when seawater temperature exceeded a threshold of 19-20°C. Once temperatures exceed this threshold, oysters usually reach the pre-spawning stage characterized by a negative energy budget: energetic resources attain their lowest level whereas energy demand and reproductive effort are at their highest. In addition, the haemocytes, the invertebrate blood cells involved in defense mechanisms, also show their lowest performance when the temperature is high (Gagnaire et al., 2006). As a result, the flooding event during the summertime, such as the case of Harvey, will have a more negative impact on oyster survival compared to those during cooler seasons. A comparison study (La Peyre et al., 2013) also showed dramatically different impacts on oysters at Breton Sound (near Mississippi River outflow) of two flooding events, one during the hot summer month of 2010 (temperature > 25°C, high mortality) and the other during the spring of 2011 (temperature < 25°C, low mortality). It is worth noting that the influence of temperature during Harvey is unlikely contribute to the spatial heterogeneity of oyster mortality, since the air and water temperature are usually identical among different regions due to the limited length (~40 km) and width (~40 km) of the bay.

Bivalves including oysters can cope with low salinity for a short period by releasing a suite of stress response genes, closing their valves, and shifting to anaerobic metabolism to isolate their internal tissues in order to maximize their survival under extreme conditions (Michaelidis et al., 2005; Zhang and Zhang, 2012). Short-term exposure to low salinity sometimes may even enhance the population by reducing predators (e.g., oyster drill, whelk) and parasites (e.g., *Perkinsus marinus*) (La Peyre et al., 2003; Levinton et al., 2011; Pollack et al., 2011). However, if they need to close their valves for too long, the accumulation of toxic compounds and the unfavorable energetic balance inside the shell will eventually lead to their mortality.

4.2. Mechanisms for spatially-varying low-salinity exposure time

This study shows the important physical control (low-salinity exposure) on the oyster reef ecosystem (oyster mortality). Then, what are the mechanisms for the low-salinity exposure to vary spatially over a wide range from a few days to >30 d? Based on the decomposition of salt flux at the bay entrance, Du and Park (2019) showed that it was the tidal pumping that was most important for the salinity recovery in the bay after Harvey. The salt flux induced by two-layer exchange flow was at least one order of magnitude smaller, with the exception immediately after the input of extraordinarily large freshwater when a large horizontal salinity gradient existed between the fresh bay and the salty coastal water (Fig. 9 in Du and Park, 2019). Because of a small tidal range and the resultant weak tidal pumping, the overall salinity recovery was slow in

Trinity Bay and East Bay (recovery time > 3 months), while the salinity in the lower bay and near the ship channel recovered much more quickly.

Besides the weak tidal exchange, the highly confined geometry of the coastal bay system also hinders the estuary-shelf exchange. Galveston Bay is connected to the shelf seas with three narrow outlets. Even the main entrance that accounts for 80% of the water exchange is just 2.5 km wide. The narrow outlets and confined geometry amplify the impact of flooding events. The prolonged salinity recovery after major precipitations events is likely to occur for estuaries with similar geometry in the northern Gulf of Mexico, e.g., Apalachicola Bay, Mobile Bay, Matagorda Bay, Aransas Bay, and Corpus Christi Bay.

4.3. Impact of stormwater input: Lessons learned from Harvey

Interesting and important questions for resource assessment and management are: (1) how the bay will respond to different amounts of stormwater input; and (2) how much stormwater the bay can receive without significantly increasing oyster mortality. The results for T_{E5} from a series of scenario runs with different amount of freshwater input (Fig. 4) provide valuable information for these questions. As stormwater enters from the main rivers, T_{E5} starts to increase first in the San Jacinto Estuary in the upper bay and at the mouth of Trinity River where its discharge enters Trinity Bay, and high T_{E5} expands quickly in Trinity Bay with increasing stormwater. With 50% of Harvey's stormwater (i.e., $0.5\times\Delta Q$), the entire Trinity Bay has T_{E5} larger than two weeks. The results of numerical experiments also suggest that most of the oyster reefs in the bay may be able to sustain 20-30% of ΔQ (i.e., 2.8-4.2$\times10^9$ m^3 discharge over a similar duration as with Harvey). With 20%-30% of ΔQ, T_{E5} are larger than 7 d only in the regions where there are no reefs with live oysters (Fig. 4c,d).

The relationship between the bay bottom area with $T_{E5} > 7$ or 14 d and the amount of stormwater input (Fig. 4i) provides another valuable information for the two important questions. The bay bottom area with $T_{E5} > 7$ or 14 d increases as stormwater input increases but in a nonlinear way. ΔQ is about 3.7 times of bay's volume, meaning that 1/3.7 (27%) of ΔQ would be large enough to flush the entire bay. As a result, the area with $T_{E5} > 7$ or 14 d increases rapidly and almost linearly when stormwater increases from 10% to 40% of ΔQ, beyond which the rate of increase reduces. When exceeding 27% of ΔQ, more freshwater coming in will not make the bay fresher, but it can result in fresher shelf water (Du and Park, 2019) and hence will increase T_{E5} but with a slower rate.

It is worthy noting that about half of the freshwater load into Galveston Bay during Harvey was through surface runoff along the coastline and groundwater (Du et al., 2019a). Groundwater is increasingly recognized as an important freshwater and nutrient source to coastal waters (Moore et al., 2010; Marazuela et al., 2018; Luijendijk et al., 2020). While it is hard to isolate the groundwater's contribution, the influence of groundwater input is presumably more long-lasting than the surface runoff. However, considering the intensive urbanization around Galveston Bay, the impact of groundwater is likely less than what one would expect in a rural coastal area.

4.4. Flooding induced oyster kill: a worldwide problem

Massive oyster kill caused by prolonged exposure to low-salinity water is not unique to Galveston Bay. It has been reported worldwide (Fig. 5). For example, Hurricane Irene and Tropical Storm Lee (2011) generated extreme flooding in the Delaware River and led to high oyster mortality (10-50%) in the upper Delaware Bay (Munroe et al., 2013). Most of the documented oyster kills were caused by prolonged low-salinity exposure after flooding (Table

1). Besides hurricanes, other processes could also cause flooding in coastal waters. Oyster mortality due to opening of flood-control spillways has been reported in multiple coastal waters (e.g., La Peyre et al., 2013; Gledhill et al., 2020). For instance, after the Deep Horizon drilling platform explosion in April 2010, a large volume of Mississippi River freshwater was released from diversion structures to keep oil from reaching sensitive coastal wetlands. As a consequence, oyster densities in coastal waters near the Mississippi Delta reached an extreme low in 2010, with little recovery in 2011 and 2012 (Grabowski et al., 2017; Powers et al., 2017). Note that the documented oyster kill events in Table 1 likely represent a small portion of the impact of floods on oyster reefs around the world, since oyster mortality in many coastal systems is not as systematically monitored as is done for Galveston Bay by Texas Parks & Wildlife Department.

The future climate, characterized with more frequency of extreme weather events (e.g., marine heat wave, severe drought, intense storms), is expected to pose additional pressure to the native coastal oyster reefs that are already at the brink of functional extinction worldwide due to centuries of resource extraction and coastal habitat degradation (Beck et al., 2011). More restoration and management efforts are needed to reverse the loss of oyster reefs and restore the vital ecosystem services provided by oyster reefs.

Concluding Remarks

The massive oyster kill in Galveston Bay after Harvey sheds light on how an extreme weather event could impact coastal ecosystems and resources. Changes in physical conditions, particularly the salinity, after either natural or human-controlled flooding events, could greatly affect the survival of benthic organisms, such as oysters. The impact of flooding events is particularly drastic for coastal systems with low flushing capacity (e.g., a lagoon-type estuary).

Such coastal systems are widely distributed around the world. With the increasing frequency of extreme weather events as projected by climate models, ecosystems in this type of coastal environment will likely face more challenges in the future.

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Fig. 1: Salinity variation during Hurricane Harvey. (**a**) Track of Hurricane Harvey with the model domain (red dashed rectangle), (**b**) the zoom-in of Galveston Bay showing the nodes of the unstructured model grid (colored dots showing depths), names of sub-bays, and locations of four salinity monitoring stations (solid green squares), and (**c-f**) time series of salinity at the four stations. Salinity data in (**c-f**) clearly show the entire bay had been virtually fresh over several days, with the blue shades denoting the period when salinity was continuously lower than a critical threshold value of 5 PSU.

Fig. 2: Observed oyster mortality rate. (**a**) The oyster mortality rate at 130 sampling sites in October 2017, a month after the extreme precipitation by Hurricane Harvey, and (**b**) changes in oyster mortality rate before and after Hurricane Harvey at 12 major reefs. In (**a**), the numbers indicate the 12 major oyster reef complexes with different symbols indicating different reef complexes. In (**b**), the post-Harvey mortality rates were measured in October 2017, a month after Hurricane Harvey, while the pre-Harvey values were based on measurements in the fall of 2016.

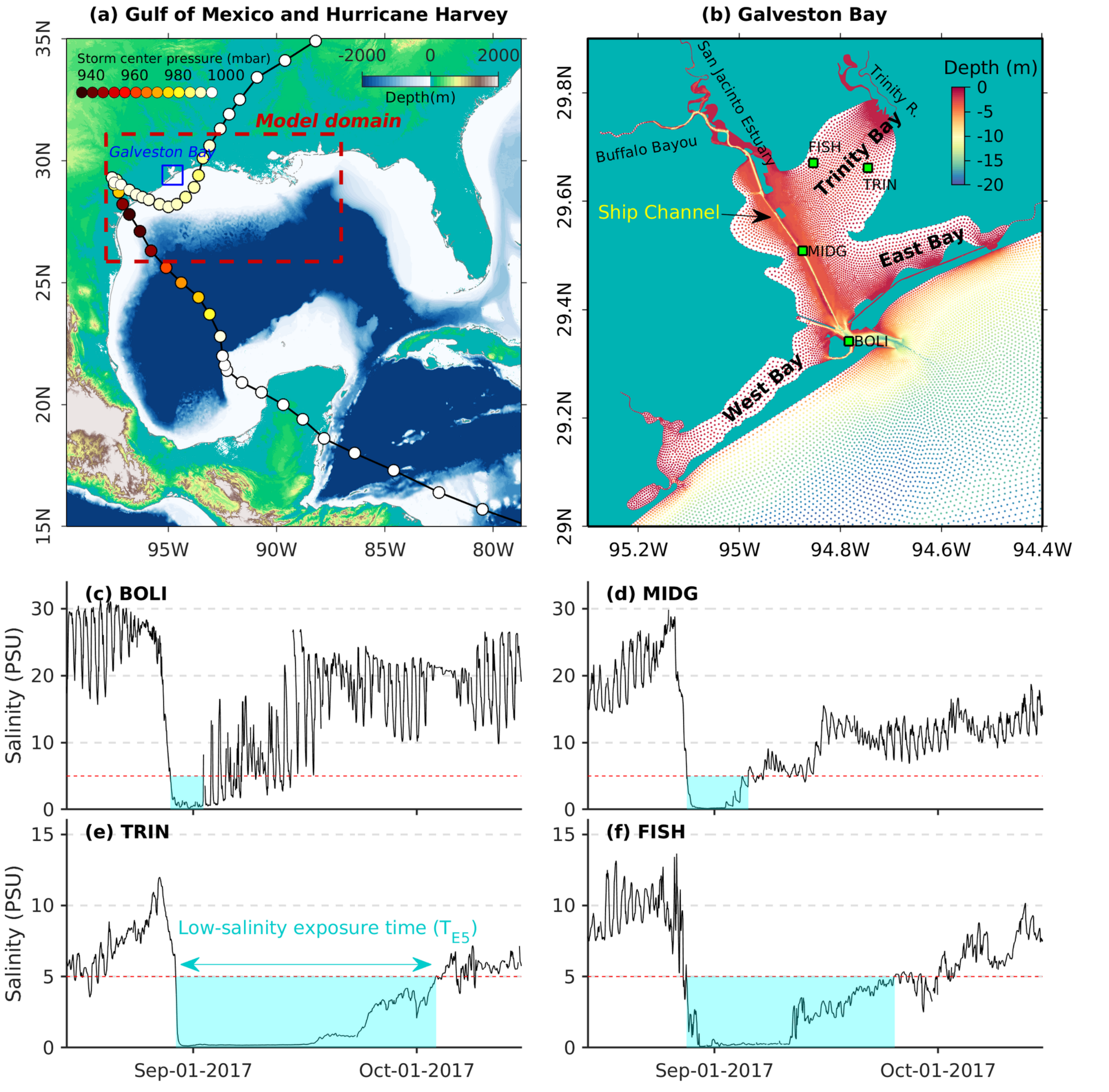
Fig. 3: Relationship between oyster mortality vs. low-salinity exposure time and storm sediment deposit. (**a**) Low-salinity exposure time for bottom water with a threshold of 5 PSU (T_{E5}) based on simulations from a previously calibrated 3D hydrodynamic model and (**b**) sediment deposit thickness based on the x-ray analysis of sediment cores collected from 56 locations (●), and (**c-d**) their relationships with the oyster mortality rate with the linear regression (solid line) and 95% confidence interval (dashed lines). Note that the regression analysis in (**c**) does not include the two outliers, reefs #1 and #12. At reef #1. sediment deposit is thicker than 35 cm, and the high mortality was likely to be caused mostly by sediment smothering (see the text). At reef #12, most of the oysters collected were old shells.

Fig. 4: Results of model scenario runs with different stormwater input. (**a-h**) Distribution of the low-salinity exposure time with a threshold salinity of 5 PSU (T_{E5}) for different amounts of stormwater, i.e., 0%, 10%, 20%, 30%, 40%, 50%, 100% and 200% of the Harvey's stormwater ΔQ and (**i**) the bay bottom area with T_{E5} > 7 d (solid line) and 14 d (dashed line) as a function of stormwater input.

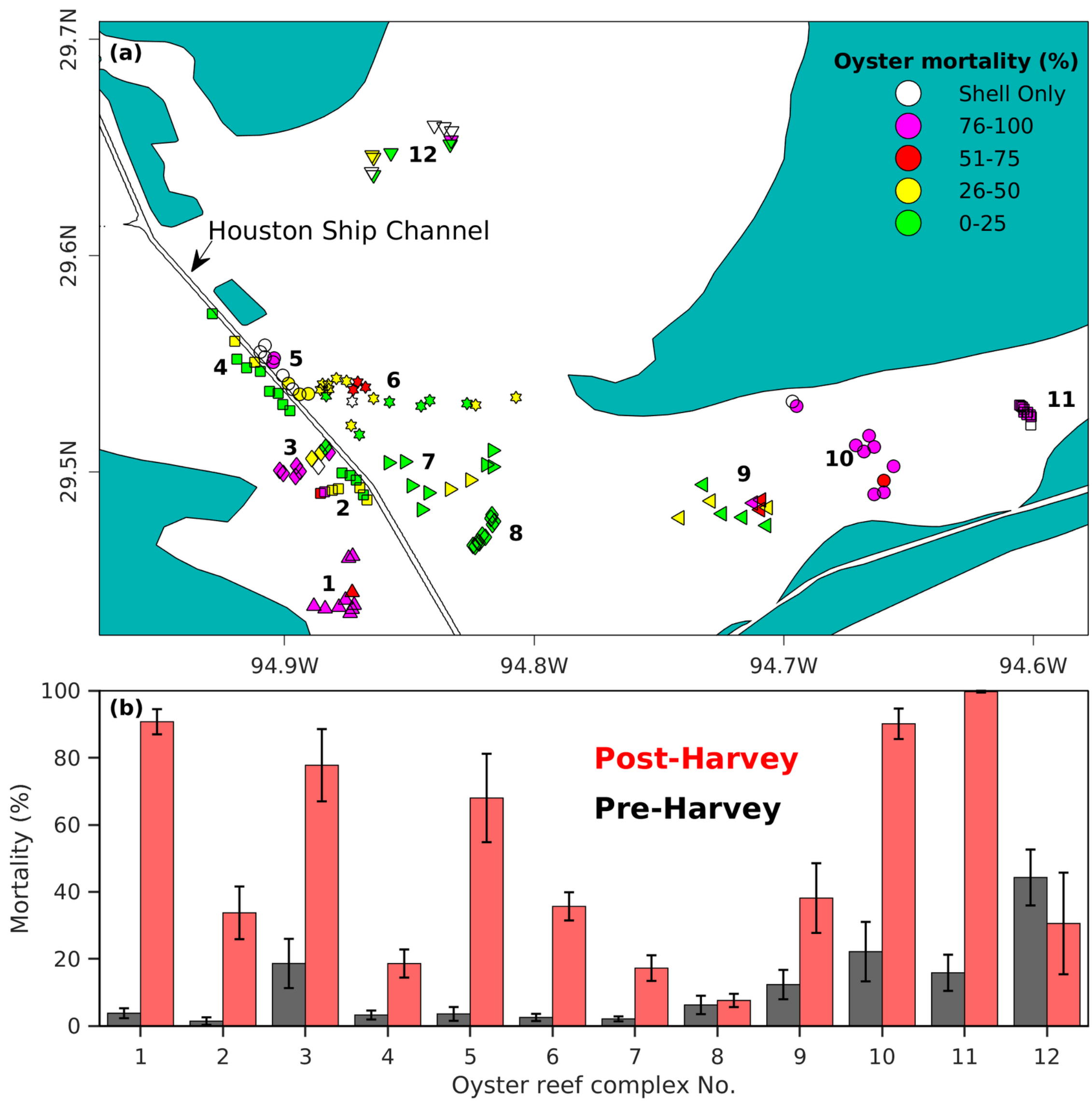
Fig. 5: Documented oyster kill (red text) and the health condition of worldwide oyster reefs (filled circles) from Beck et al. (2011).

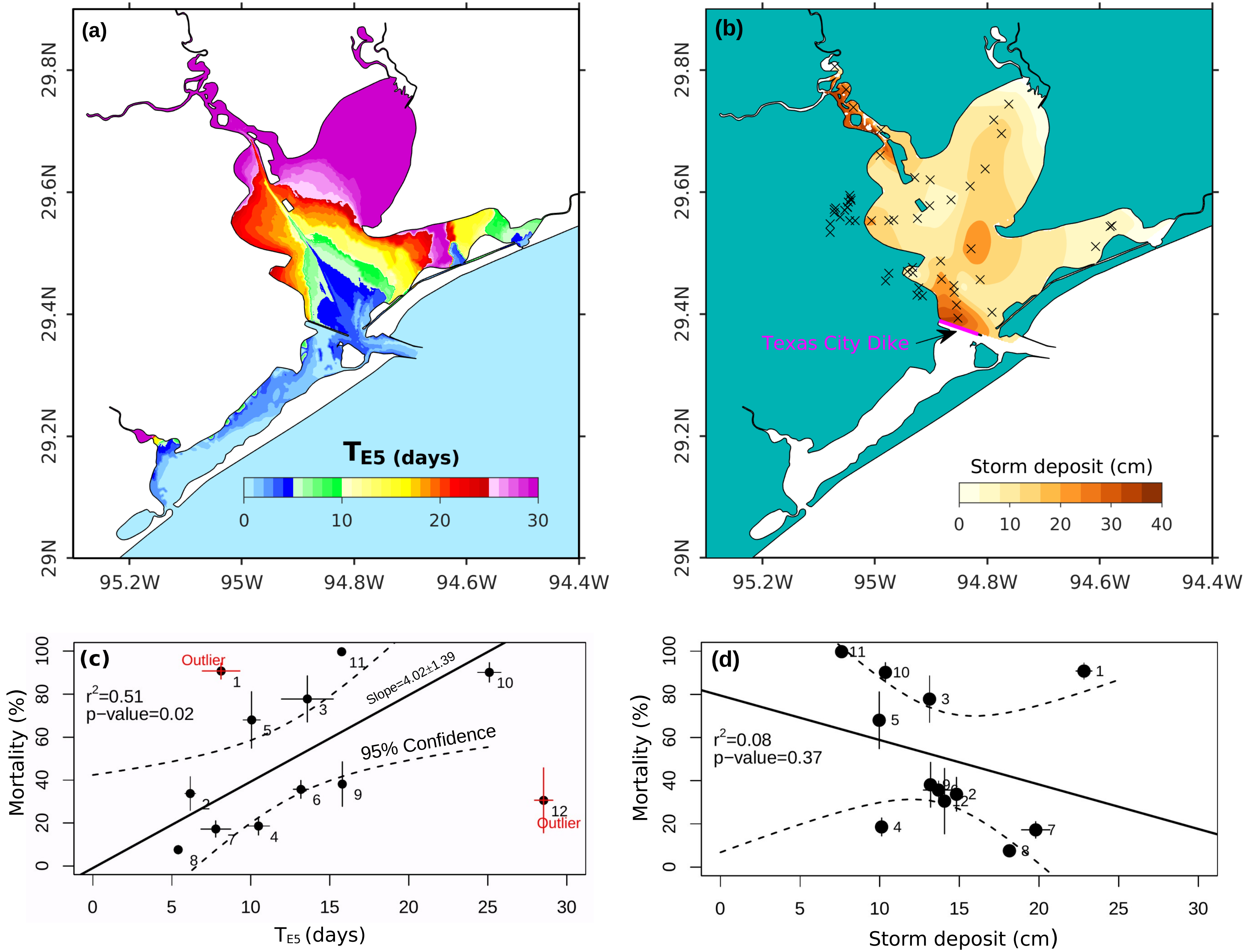
Table 1: A list of reported major oyster kill events.

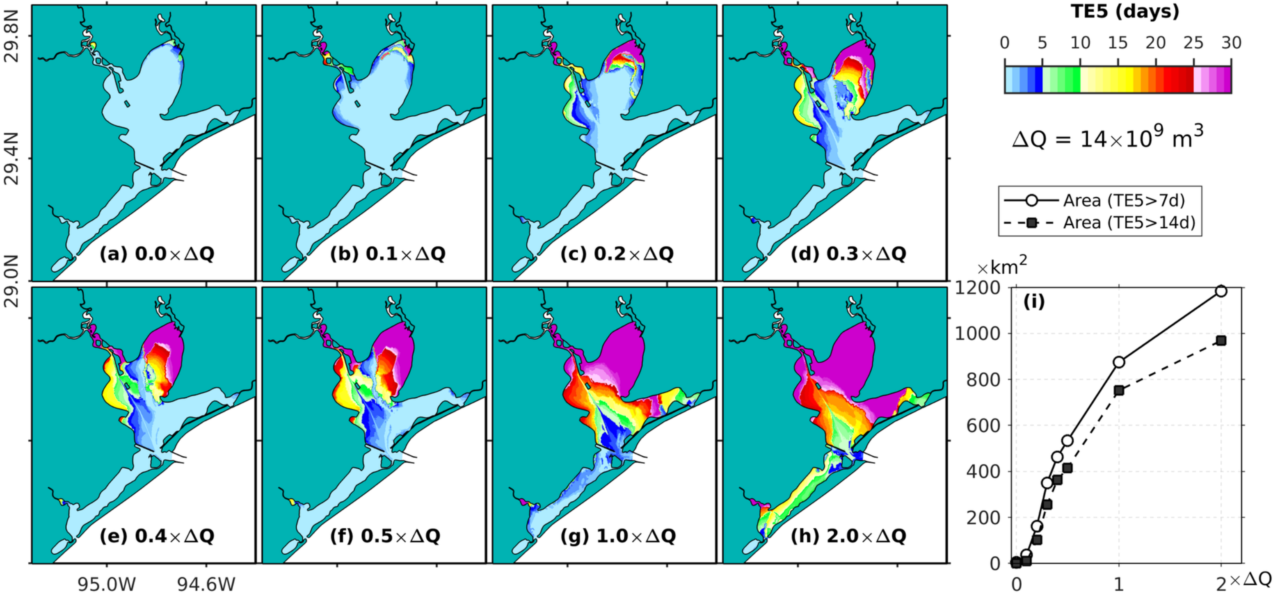
Location	**Time**	**Description**	**References**
Moreton Bay, Australia	Late 19^{th} century	Declined oyster reefs after major flood events in the late 19^{th} century.	Diggles (2013)
Matsushima Bay, Japan	1958	Severe moralities were reported following the 1958 El Nino.	Imai et al. (1965)
Apalachiocola Bay, US	1960 -1984	Oyster landing was low in years when flows exceeded 30,000 cfs for 100 days or more.	Wilber (1992)
Northern Gulf of Mexico, US	1950 -2003	Oyster harvests in five major estuaries were inversely related to freshwater inflow. Most of the lows in landing (17 of 19) coincided with peaks in discharge of major rivers feeding their estuaries. Opening of Bonnet Carré spillway lowered oyster landing in Mississippi.	Turner (2006)
Puget Sound, US	1998	Oyster mortality was high in the late summer when dissolved oxygen was low.	Cheney et al. (2000)
Morlaix Bay, France	1999	The mortality was associated with *Vibrio* strain, whose effect was more serious under higher temperature.	Lacoste et al. (2001)
Wonboyn Lake, Australia	2002	An unprecedented mortality (15-100%) of Sydney rock oyster in aquaculture zones was associated with severe inflammation, which was possibly caused by bloom of dinoflagellate.	Ogburn et al. (2007)
Tomales Bay, US	2003	High levels of mortality were observed and related to the presence of *Ostreid herpesirus*, whose impact appeared to be stronger when temperature was higher.	Burge et al. (2006)
Bannow Bay and Dungarvan Harbour, Ireland	2003	Mass mortality event (>20%) of oyster occurred and was associated with high temperature and high nutrient.	Malham et al. (2009)
Mission–Aransas Estuary, US	2007	Flood event caused reduction of oyster abundance. Oyster population recovered within 1 year.	Pollack et al. (2011)
Thau lagoon, France	2008	A major oyster mortality event coincided with a nationwide increase of ~1.5°C in winter seawater temperature.	Pernet et al. (2010)
Breton Sound, Louisiana, US	2010	Management responses to Deepwater Horizon oil spill caused an extended low-salinity (<5 PSU) in hot summer months, which led to a high mortality and low recruitment of oyster.	La Peyre et al. (2013)
Delaware Bay, US	2011	Two storm events (Hurricane Irene and Tropical Storm Lee) generated extreme flooding in Delaware River and caused prolonged baywide low salinity. Monthly mortality was up to 55%.	Munroe et al. (2013)
Sanfrancisco Bay, US	2011	A series of atmospheric river made landfall within California, driving an extreme freshwater discharge and leading to nearly 100% of oyster mortality at the northern bay.	Cheng et al. (2016)
Port Stephens, Australia	2013 -2014	Spatial variations in oyster microbiome were characterized by the relative abundance of pathogenic bacteria.	King et al. (2019)
Tasmania, Australia	2016	*Ostreid herpesvirus*-derived mortality linked with the long and intense marine heat wave.	de Kantzow et al. (2017)
Mississippi Sound, US	2019	The mortality event was caused by opening of Bonnet Carré Spillway to release pressure from high discharge of Mississippi River on New Orleans.	Gledhill et al. (2020)

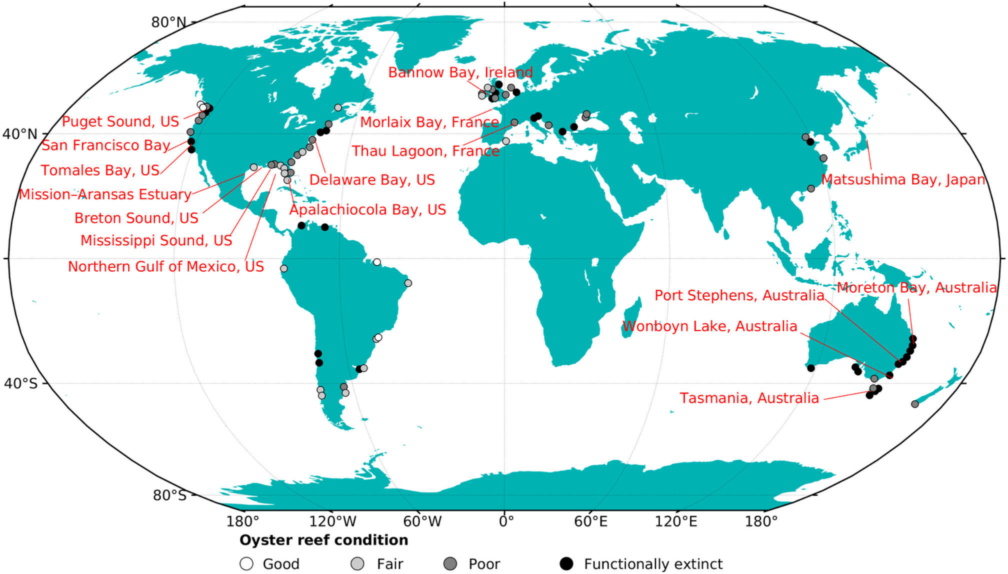


(a) Gulf of Mexico and Hurricane Harvey
Storm center pressure (mbar)
940 960 980 1000
-2000 0 2000
Depth(m)
Model domain
Galveston Bay
35N
30N
25N
20N
15N
95W 90W 85W 80W
(b) Galveston Bay
San Jacinto Estuary
Trinity R.
Depth (m)
0 -5 -10 -15 -20
Buffalo Bayou
FISH
Trinity Bay
TRIN
Ship Channel
MIDG
East Bay
BOLI
West Bay
29.8N 29.6N 29.4N 29.2N 29N
95.2W 95W 94.8W 94.6W 94.4W
(c) BOLI
(d) MIDG
Salinity (PSU)
(e) TRIN
(f) FISH
Low-salinity exposure time (T_{E5})
Sep-01-2017 Oct-01-2017

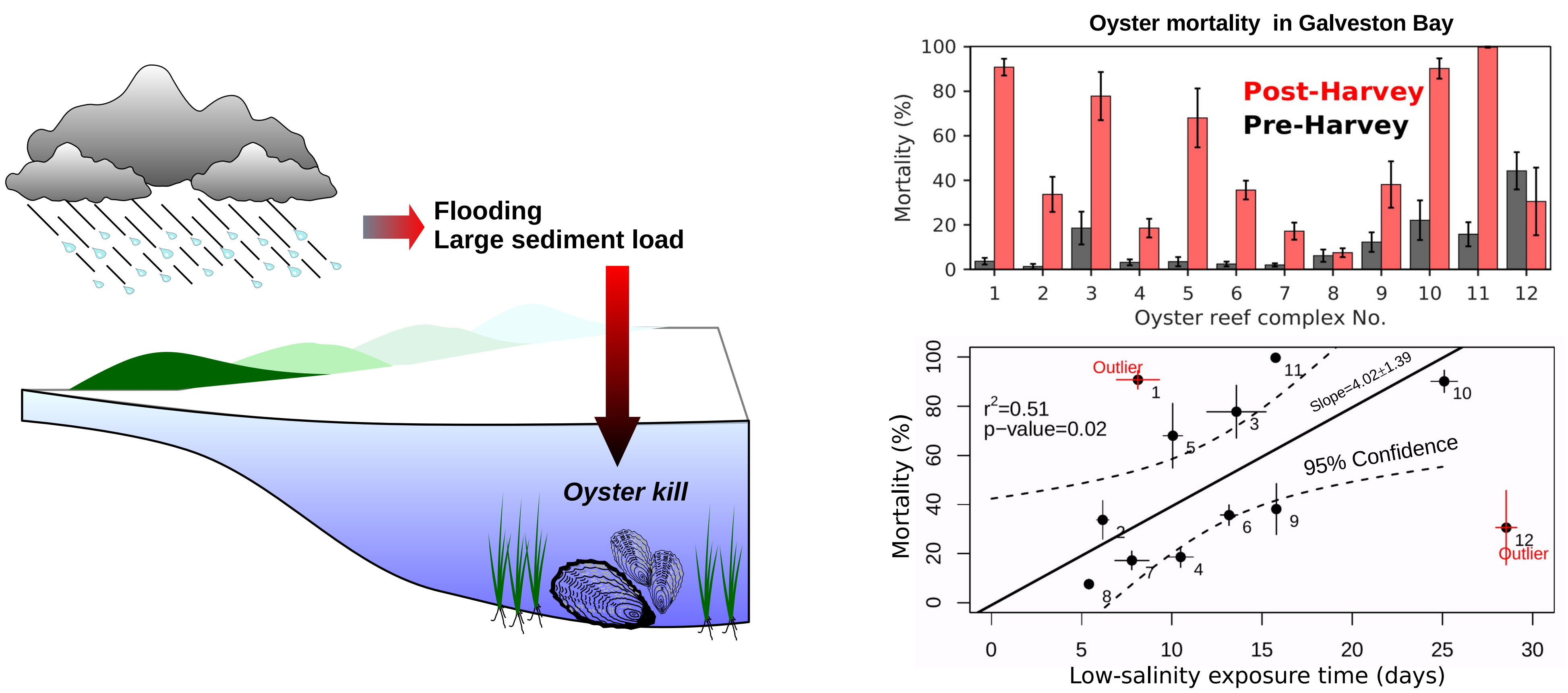

(a)
Oyster mortality (%)
Shell Only
76-100
51-75
26-50
0-25
Houston Ship Channel
1
2
3
4
5
6
7
8
9
10
11
12
29.7N
29.6N
29.5N
94.9W
94.8W
94.7W
94.6W
(b)
Post-Harvey
Pre-Harvey
Mortality (%)
0
20
40
60
80
100
Oyster reef complex No.


(a)
29.8N
29.6N
29.4N
29.2N
29N
95.2W
95W
94.8W
94.6W
94.4W
T_{E5} (days)
0
10
20
30
(b)
Texas City Dike
Storm deposit (cm)
0
10
20
30
40
(c)
Outlier
r^2=0.51
p−value=0.02
Slope=4.02±1.39
95% Confidence
Outlier
Mortality (%)
T_{E5} (days)
(d)
r^2=0.08
p−value=0.37
Mortality (%)
Storm deposit (cm)


TE5 (days)
0 5 10 15 20 25 30
ΔQ = 14×10^9 m^3
Area (TE5>7d)
Area (TE5>14d)
29.8N
29.4N
29.0N
95.0W
94.6W
(a) 0.0×ΔQ
(b) 0.1×ΔQ
(c) 0.2×ΔQ
(d) 0.3×ΔQ
(e) 0.4×ΔQ
(f) 0.5×ΔQ
(g) 1.0×ΔQ
(h) 2.0×ΔQ
(i)
×km^2
1200
1000
800
600
400
200
0
0
1
2×ΔQ



80°N
40°N
0°
40°S
80°S
180°
120°W
60°W
0°
60°E
120°E
180°
Bannow Bay, Ireland
Morlaix Bay, France
Thau Lagoon, France
Puget Sound, US
San Francisco Bay
Tomales Bay, US
Mission–Aransas Estuary
Breton Sound, US
Mississippi Sound, US
Northern Gulf of Mexico, US
Delaware Bay, US
Apalachiocola Bay, US
Matsushima Bay, Japan
Port Stephens, Australia
Moreton Bay, Australia
Wonboyn Lake, Australia
Tasmania, Australia
Oyster reef condition
Good
Fair
Poor
Functionally extinct


Flooding
Large sediment load
Oyster kill
Oyster mortality in Galveston Bay
Post-Harvey
Pre-Harvey
Mortality (%)
Oyster reef complex No.
Outlier
r²=0.51
p−value=0.02
Slope=4.02±1.39
95% Confidence
Outlier
Mortality (%)
Low-salinity exposure time (days)