Mass mortality of eastern oysters (*Crassostrea virginica*) in the western Mississippi Sound following unprecedented Mississippi River flooding in 2019

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Abstract

Globally, precipitation is expected to increase along with the rise of temperatures due to climate change, increasing the likelihood of freshwater intrusion into coastal ecosystems. In the spring and summer of 2019, heavy rainfall and snowmelt in the midwestern United States caused historic flooding of the Mississippi River, warranting two openings of the Bonnet Carré Spillway (BCS) to reduce pressure on levees in New Orleans, Louisiana. These openings released an unprecedented volume of freshwater into Lake Pontchartrain, and subsequently into the Mississippi Sound. This study investigated the impacts of these freshwater releases on eastern oyster (*Crassostrea virginica*) populations and water quality in the western Mississippi Sound and the Bay of St. Louis. Platforms housing oysters and water quality sensors that measured dissolved oxygen, salinity, and temperature, were deployed at oyster reef sites. At each reef, native oyster populations were assessed via dredge sampling to determine oyster survival. After 13 days, deployed oysters suffered 100% mortality at all sites except Henderson Point Reef and Kittiwake Reef, the sites farthest east of the BCS. On 27 September 2019, 62 days following the BCS closing, dredge sampling revealed no live native adult oysters or spat, even at sites where living oysters were collected earlier in the summer. If BCS openings increase in frequency or duration due to elevated precipitation, oyster populations in Mississippi could remain unsustainable for harvesting unless future freshwater intrusions are incorporated into management planning.

Introduction

Disturbances to coastal ecosystems due to climate change, such as elevated temperature, ocean acidification, sea level rise and frequency and/or severity of storms, are predicted to increase dramatically over the next several decades (Hoegh-Guldberg & Bruno 2010, Fischer et al. 2014, Wong et al. 2014). Due to their proximity to land and natural sources of freshwater influx, estuaries often experience high fluctuations in environmental conditions, such as dissolved oxygen (DO), temperature, and salinity, and these interact with local anthropogenic stressors, such as biological invasions, habitat disturbance, eutrophication and pollution, to affect survival of marine organisms in estuarine environments (Lenihan & Peterson 1998, Ko et al. 2014, Tweedley et al. 2015, Cheng et al. 2017, Pusack et al. 2019). As global temperatures rise, both storm intensities and precipitation rates associated with tropical cyclones are predicted to increase, which will affect estuarine environments adversely (Knutson et al. 2010, Sobel et al. 2016, Liu et al. 2019). Independent of tropical cyclones, heavy precipitation events have also increased as a result of a warming climate (Peterson et al. 2008, Lehmann et al. 2015). As storms grow in strength, frequency, and produce more rain, their potential to cause human fatalities and severe economic losses due to flooding, also increases (Pielke et al. 2008, Rappaport 2014).

In 2019, the Mississippi River basin experienced one of the wettest years in recorded history (Frederick 2019, NOAA National Centers for Environmental Information 2019), resulting in severe flooding. In Greenville, Mississippi, the Mississippi River remained at flood stage for a record-breaking five months, finally subsiding on 21 July 2019 (Erdman 2019). At Red River Landing, Louisiana, flood stage lasted for 226 days from 28 December 2018 to 10 August 2019 (National Weather Service 2019). In May 2019, a total of 68 river gauges in the Mississippi River Basin recorded their highest levels ever (Erdman 2019). The 2019 flood broke records set only by the ‘Great Mississippi Flood of 1927’, which inundated roughly 27,000 square miles with approximately 30 feet of water (Risk Management Solutions 2007).

In 1931, in response to the flood of 1927, the U.S. Army Corps of Engineers constructed the Bonnet Carré Spillway (BCS), a flood control structure at the southern end of the Mississippi River system that reduces the threat of flooding in the New Orleans area by diverting a portion of Mississippi River flow into Lake Pontchartrain (Lane et al. 2001). Prior to 2008, the BCS had been opened only eight times during high water events, but the openings have become more frequent as increased precipitation and subsequent flooding has threatened the areas surrounding the lower Mississippi River. More recently, the U.S. Army Corps of Engineers has opened the BCS during spring or summer months in 2008 (31 days), 2011 (42 days), 2016 (22 days), and 2018 (30 days) (US Army Corps of Engineers, New Orleans District 2019: Table 1). On 27 February 2019, Mississippi River water levels reached heights sufficient to warrant opening the BCS for 44 days, with a maximum flow rate of 213,000 ft^3/s, finally closing on 11 April 2019. Approximately one month later, the Mississippi River again reached dangerous heights, warranting a second spillway opening on 10 May 2019. This second opening lasted 79 days, with a maximum flow rate of 161,000 ft^3/s, finally closing on 27 July 2019 (US Army Corps of Engineers, New Orleans District 2019). The BCS openings in 2019 represent the first time in history that the spillway was opened in two consecutive years (2018 and 2019), and twice in the same year (2019).

As a result of this extreme flooding event, an unprecedented volume of freshwater from the Mississippi River was released through the BCS into Lake Pontchartrain and subsequently into the Mississippi Sound. While there are clear policy rationales for diverting flooding away from residential areas in Louisiana, these freshwater intrusions can have devastating impacts on coastal ecosystems. Studies of Mississippi coastal water quality following the 2008 and 2011 openings of the BCS found frequent development of bottom water hypoxia, which is known to impact marine organisms negatively (Ho et al. 2019). In addition to hypoxia, increased abundances of *Vibrio cholerae*, a potentially deadly human pathogen endemic to coastal waters that favors low salinity, were confirmed in Mississippi waters following the 2011 opening of the BCS (Griffitt & Grimes 2013). According to economic assessments and recovery models, commercial oyster harvest landings in Mississippi were estimated to have suffered $21.8 – 46 million in losses following the 2011 BCS opening (Posadas & Posadas 2017).

Extended freshwater intrusion events into estuarine systems clearly have negative impacts on both water quality and estuarine life (NOAA Fisheries 2019, Spraggins 2019), not only due to the low salinity itself, but also due to an influx of excess nutrients and other pollutants from agricultural and urban runoff (Turner et al. 2002, Bargu et al. 2011). Excess nutrients can cause harmful algal blooms (HAB) which can impact estuarine organisms, human health, commercial fishing, and tourism due to beach closures (Ansari et al. 2011, Mississippi Department of Environmental Quality 2019). Following the 1997 opening of the BCS, an expansive HAB of *Anabaena circinalis* and *Microcystis aeruginosa* persisted for approximately two months in Lake Pontchartrain after the closing of the spillway, and resulted in extensive fish kills and subsequent decomposition-induced hypoxia (Lane et al. 2001).

The eastern oyster (*Crassostrea virginica*) is an estuarine species that provides numerous ecosystem services, including enhancement of biodiversity, water quality improvement, shoreline stabilization, and is an important economic resource to coastal economies (Cressman et al. 2003, Peterson et al. 2003, Grabowski et al. 2012). On the Louisiana Gulf Coast, oyster landings have an inverse relationship with Mississippi River discharge (Turner 2006). Variability in salinity can impact oyster reproduction, larval recruitment and settlement, feeding ability, and susceptibility to parasitism and predation (La Peyre et al. 2003, Pollack et al. 2011, Pusack et al.

2019). The threat of extended freshwater events could ultimately result in the loss of important oyster reef ecosystem services that are vital to healthy and productive estuarine ecosystems.

The focus of this study was to investigate how the 2019 openings of the BCS impacted oyster populations in the western Mississippi Sound by assessing mortality of deployed and native oysters at sites representing an easterly distance gradient from the BCS over time. In addition to oyster mortality, *in situ* water quality parameters such as salinity, temperature, and DO were also measured at these sites during and following the freshwater intrusion event.

Materials and Methods

Oyster collection and maintenance

Oysters (*C. virginica*) were obtained from the Auburn University Shellfish Laboratory in Bayou La Batré (Dauphin Island, AL) in early April 2019. Oysters were transported to the Gulf Coast Research Laboratory (Ocean Springs, MS) and placed in a flow-through holding tank supplied with water from Davis Bayou, where salinity and temperature were similar to their previous holding conditions. Oysters were held overnight in the tank before being placed into sensor platforms and deployed in the field on 23 April 2019.

Field deployment and water quality measurements

Field deployment began on 23 April 2019 (T-0), following the first 2019 opening of the BCS, continued through the entire second opening of the year and for two months beyond, for a total of 157 days. Twenty oysters were selected randomly from holding tanks and placed in each of 12 oyster sensor platforms (Bell 2019). Sensor platforms were equipped with water quality sensors (HOBOware® loggers; Onset Computer, Bourne, MA, USA) that measured DO (U26-001), conductivity (U24-002-C), and temperature (measured by both the DO and conductivity loggers) for the duration of the deployment, and housed oysters on trays enclosed within crates on each platform, with holes to allow adequate water flow (Fig. 1). Two platforms were deployed at each of six field sites (Fig. 2) along the Mississippi Gulf Coast from 23 April – 6 May 2019 (T-1): a site with no oyster reef in the back of Bay St. Louis (Back Bay St. Louis: 30°21'03.6"N, 89°21'16.8"W), The Nature Conservancy (TNC) Bay St. Louis Reef (30°20'42.2"N, 89°17'41.5"W), St. Stanislaus Reef (30°18'02.7"N, 89°19'10.7"W), Waveland Reef (30°16'22.7"N, 89°22'12.9"W), Henderson Point Reef (30°17'33.5"N, 89°16'16.1"W), and Kittiwake Reef (30°19'56.8"N, 89°09'54.7"W). Following T-1, sensor platforms at Back Bay St. Louis and St. Stanislaus Reef were relocated temporarily for a separate study. On 24 May 2019 (T-2), after the 31 days of oyster deployment, ten sensor platforms were moved to the TNC Bay St. Louis Reef to record water quality for the remainder of the freshwater event, and a pH sensor (HOBOware® MX2501) was attached to one of the sensor platforms. The sensor platforms were recovered on 27 September 2019 (T-3).

In addition to the *in situ* sensors on the platforms, a YSI™ Professional Plus Handheld Multiparameter meter (6050000, Xylem Inc., Yellow Springs, OH, USA) was used to measure water quality at each site on every sampling day. Unless otherwise indicated, two measurements were taken, one at the surface for which the probe was submerged just below the surface of the water and one at the bottom. Parameters measured included: temperature, conductivity, dissolved oxygen, salinity, and pH (Table 2). Data from the *in situ* conductivity logger were extracted as specific conductance and converted to salinity using calibration points collected from the multimeter data in Table 2. To evaluate the spatial and temporal scale of freshwater intrusion across the broader Mississippi Gulf Coast during the study period, *in situ* salinity data were extracted from United States Geological Survey (USGS) monitoring sites (USGS National Water Information System 2019).

Deployed and native oyster mortality

Deployed oyster mortality in each platform was recorded after 13 days (6 May 2019: T-1) and 31 days (24 May 2019: T-2) of *in situ* exposure in each platform. To assess survival in native oyster populations, three dredge transects were conducted at each field site except for Henderson Point Reef, where six dredge transects were conducted due to its larger size. Each transect was 305 m long x 0.61 m wide (186.05 m^2). Following each dredge pull, the numbers of live and dead adult and juvenile (spat) oysters were counted. Oysters that were gaping, had both valves attached, and would not close their valves were counted as dead. Results are reported in percent living adults or spat per square meter.

Results

Water quality measurements

Back Bay St. Louis, TNC Bay St. Louis Reef, St. Stanislaus Reef, and Waveland Reef all experienced salinities of < 1 from 23 April to 24 May 2019 (Table 2). The two reef sites farthest east of the spillway, Henderson Point Reef and Kittiwake Reef, had salinities of 3.14 and 4.21, respectively, on 23 April 2019. Throughout the deployment, even these easternmost reefs showed a steady decrease in salinity, reaching salinities as low as 0.18 and 0.48, respectively, by 31 days post-deployment (24 May 2019). Measurements obtained on 27 September 2019, 63 days following the second closing of the spillway, showed recovery of salinity to 15 – 21 at all sites (Table 2). Salinity data from *in situ* sensors were in concordance with YSI™ multimeter measurements. From 23 April – 24 May 2019, *in situ* sensors measuring salinity at TNC Bay St.

Louis Reef recorded extremely low salinities of ≤ 2, which was sustained for approximately three months. These sensors captured a temporary peak in salinity when Hurricane Barry made landfall in Mississippi on 13 July 2019, but salinity quickly (3 d) returned to the prior low levels. Following the second closing of the BCS on 27 July 2019, salinity increased gradually to normal concentrations over ~60 days (Fig. 3). Similarly, USGS sensors at Rigolets and St. Joseph Island Light, the two sites closest to the BCS (Fig. 4a), recorded a prolonged period of low salinity (< 5), comparable to data from the oyster sensor platforms (Fig. 4b). In contrast, at Biloxi Bay and Gulfport Light, the easternmost sites, salinity dropped to < 5 for only a few weeks at the beginning of the second BCS opening (Fig. 4c).

Deployed and native oyster mortality

Percent mortality of the 20 deployed oysters deployed in each of the 12 oyster sensor platforms was calculated for each site at T-1 and T-2. There was 100% mortality after 13 days of deployment (25 days following the first closing of the BCS) at all sites except Henderson Point Reef (62.5% mortality) and Kittiwake Reef (30% mortality), the two most distant reefs from the BCS. At T-1, all live oysters remaining in the sensor platforms at Henderson Point Reef were collected for another study. At T-3 (14 days following the second opening of the BCS), the remaining oysters at Kittiwake Reef suffered an additional 14.3% mortality, resulting in an overall loss of 35% over the 31 days at that site.

Dredge sampling on 24 May 2019 (T-2) revealed the largest proportions of dead adult and spat oysters at Waveland Reef and TNC Bay St. Louis Reef (Fig. 5a). Of oysters sampled at Waveland Reef, the site closest to the spillway, 98% of adult oysters and 86.4% of spat collected were dead. At St. Stanislaus Reef, despite 100% mortality of deployed oysters, dredge sampling revealed 77% dead adult oysters and 32.9% dead spat. At TNC Bay St. Louis Reef, 100% of adult oysters and 77.8% of spat collected were dead. The greatest number of live native oysters at T-2 was at Henderson Point Reef, where nearly 80 live adults (9.6% dead) and > 200 live spat (7.5% dead) were collected in dredges (Fig. 5a). More dredge pulls (n = 6) were performed at this site due to its large size, but when standardized by area, the live oyster population was still highest at this site, with St. Stanislaus Reef having the second highest calculated average density of both adults and spat. Surprisingly, there were no live native oysters collected by dredging at Kittiwake Reef at T-2. Dredge data from 24 May 2019 are reported as population density and percent live and dead oysters (Fig. 5).

Due to a HAB and associated water contact warnings issued for the Mississippi Gulf Coast from July 2019 through the summer, as a result of the BCS openings, it was not possible to return to these field sites until 27 September 2019 (T-3), two months following the second closing of the BCS. At T-3, follow-up dredge sampling yielded no live native oysters at any of the five reef sites, despite the recovery of salinity to ≥ 15.

Discussion

Spring and summer of 2019 marked first time that the BCS was opened twice in one year, as well as the first time that the spillway was opened in two consecutive years. These openings of the BCS resulted in detrimental impacts on marine habitats of the Mississippi Gulf Coast, causing the declaration of an Unusual Mortality Event of dolphins (NOAA Fisheries 2019), a HAB that represented a risk to human health both through recreational and seafood consumption exposure (Mississippi Department of Environmental Quality 2019), and local testimonies of decimated oyster populations (e.g., Lee 2019, Spraggins 2019).

In typical years, the Mississippi Sound is a well-mixed estuary fringed with brackish salt marshes with various natural freshwater inputs and salinities ranging from 5 – 20 in nearshore areas heavily influenced by local rivers, and 20 – 25 in offshore areas with greater exposure to Gulf of Mexico (GoM) waters (Orlando et al. 1993, Griffitt & Grimes 2013). Oysters can tolerate a wide range of salinities, from roughly 5 to 40, with an optimal range of 14 to 28 (Galtsoff 1964). Oysters have their greatest potential for growth and reproduction in typical Gulf Coast estuarine salinities within this range (Shumway 1996). During the 2019 freshwater intrusion event, salinities dropped well below this range of oyster tolerance, to as low as 0.18 to 4.21. Because of the low salinity, deployed oysters experienced 100% mortality by 13 days of deployment (25 days after the first closing of the BCS) at the four sites closest to the BCS. In contrast, at T–1, there was 37.5 – 70% survival of deployed oysters at the two easternmost sites, where salinities measured 1 – 3. Although all remaining live deployed oysters at Henderson Point Reef were harvested at T-1, live oysters remained in the sensor platforms at Kittiwake Reef at 31 days of deployment (T-2; 14 days after the second opening of the BCS).

Generally, oysters are resilient in the face of large salinity fluctuations due to their ability to osmoconform, and can tolerate stressful salinity conditions for short periods of time by closing their valves. Extended periods of valve closure, however, results in mortality either from hypoxia and acidosis of the hemolymph or from starvation (La Peyre et al. 2013, Lavaud et al. 2017). Deployed oyster survival at Kittiwake Reef may have been higher due to the more gradual decline in salinity relative to sites closer to the BCS. When exposed to a rapid decline in salinity to < 1, oysters were not able to acclimate, as seen by the 100% mortality of deployed oysters at all other field sites. In a laboratory study in which salinity was gradually reduced to < 1 over a period of 48 hr, oysters in the low salinity treatments showed no significant difference in mortality when compared to controls following three weeks of exposure to freshwater (La Peyre et al. 2003).

Historically, oyster reefs in the western Mississippi Sound were among the most productive reefs in the GoM. In spite of declining oyster landings over the past several decades (Posadas 2015), between 2006 and 2012, Mississippi Department of Marine Resource oyster sampling recorded an average of 74 oysters (shell size > 25mm) per square meter across several subtidal reefs (Mississippi Department of Environmental Quality, National Fish and Wildlife Foundation 2016), a density two orders of magnitude greater than in this study (Fig. 5). Although these reefs have been impacted severely by stressful environmental conditions, recovery of the native oyster populations is vital in order to regain the benefits of the valuable ecosystem services they provide (e.g., Peterson et al. 2003).

Eastern oyster recruitment generally occurs in spring and summer, when temperatures reach ≥ 25°C and salinities range from 10-30 (Dekshenieks et al. 1993); however, warmer temperatures, combined with low salinity, can be lethal to oysters. Extended periods of low salinity (< 5) during warmer summer months (> 25°C) has caused significant negative impacts on oyster spawning, settlement, growth, and survival in the northern GoM (La Peyre et al., 2013). In the same study, La Peyre et al. (2013) found that at temperatures < 25°C in the spring and early summer, low salinity conditions still affected recruitment negatively, while mortality and growth were less impacted. Temperatures over the course of the monitoring dates ranged between 24 and 29°C (Table 2), suggesting that the high mortality suffered by native oyster populations could have been exacerbated by the combination of extremely low salinity and warm temperatures. Furthermore, oysters were unlikely to spawn in these conditions (Shumway 1996).

Despite 100% mortality of native oyster populations at all five reef sites in this study, the hard substrate produced by their shells remains. If oyster larvae encounter these reefs, they could settle upon the remaining dead oyster shells, providing an opportunity for natural recovery. Spawning and settlement are critical to ensuring the longevity and success of native oyster populations, and consequences of limited recruitment could affect the future availability of hard substrate for larval oysters to settle on, future population viability, and ultimately the availability of market-sized oysters for harvest and reproduction (Supan & Wilson 2001, Powell et al. 2009). Additionally, if restoration efforts are successful in other locations in the GoM, larval recruitment could increase through connectivity to the Mississippi Sound (e.g., Reeb & Avise 1990).

Because hypoxia and extended freshwater intrusion have been demonstrated to impact oyster reefs negatively (Turner 2006, Jeppesen et al. 2018), long-term *in situ* water quality monitoring is essential to identify areas suitable for restoration. This study clearly demonstrates the decimation of oyster reefs caused by the extended freshwater release flowing east from the BCS at least as far as Kittiwake Reef (approximately 120 km from the BCS). Further, the Gulf Coast Research Laboratory recorded that the freshwater intrusion extended to their easternmost station, approximately 180 km from the BCS, near Pascagoula, MS in July 2019 (Gulf Coast Research Laboratory 2019). Oceanographic data collected by the USGS indicate that sites farther east in the Mississippi Sound exhibited less dramatic declines in salinity and for shorter durations, with more rapid recovery than sites in the western Mississippi Sound (Fig. 4, USGS National Water Information System 2019).

Historically, oyster populations in Mississippi have been able to recover from naturally occurring environmental stressors, but have been less resilient to anthropogenic stressors. For example, oyster landings declined after Hurricane Katrina in 2005, but returned to pre-storm levels within three years (Mississippi Department of Marine Resources 2019). After the Deepwater Horizon Oil Spill in 2010, oyster harvest was halted due to the potential for oil contamination. Since then, harvests have remained at < 80,000 sacks per year, a > 75% decline from 2009, and the threats of overharvesting and climate change are only increasing (Mississippi Department of Marine Resources 2019). Heavy rainfall events have increased in the past several decades, with the twelve months preceding February 2019 recorded as the wettest period in 124 years over the upper Midwestern U.S. (Kunkel et al. 2003, Groisman et al. 2004, Frederick 2019), ultimately resulting in the unprecedented dual openings of the BCS in 2019. Models predict that most of the globe will experience a 16-24% increase in heavy precipitation intensity by 2100 due to climate change (Sun et al. 2007, Fischer et al. 2014). Therefore, the frequency of the BCS openings could increase in the future. An abrupt spike in salinity was observed when Hurricane Barry made landfall on the Mississippi Gulf Coast on 13 July 2019 (Fig. 3), but salinity quickly returned to extreme lows the following week. This increase in salinity suggests some potential for hurricanes to alleviate salinity stress temporarily in estuaries due to wind-induced mixing. Still, hurricanes can bring heavy rainfall and enhance erosion of coastlines and river basins, likely increasing particulate matter and contaminant runoff into coastal areas (Bianucci et al. 2018) which could impact resident oyster populations negatively.

The results of this study clearly demonstrate the widespread decimation of oyster reefs in the western Mississippi Sound due to the unprecedented freshwater release from the 2019 BCS openings. Whereas these openings were unique to date, BCS openings should be expected to increase in frequency under climate change scenarios that predict increasing extreme flooding events. Water quality in the eastern Mississippi Sound is impacted less heavily by freshwater intrusion from BCS openings than in the western region. Thus, oyster management on the Mississippi Gulf Coast should focus oyster reef restoration efforts in locations less impacted by low salinity stress. For oyster reef management to be successful, restoration of natural populations may need to focus on areas farther east, or on more western coastlines, such as Louisiana and Texas, that are “upstream” of the Mississippi River discharge into the GoM. In addition, in-water aquaculture efforts should be established farther offshore (e.g., near the barrier islands of Mississippi) where salinity is more stable. It is vital to understand how these freshwater events impact native populations of oysters and other commercially important species in the Mississippi Sound. Without careful consideration of future conditions, oyster reef habitat could continue to diminish on the Mississippi Gulf Coast.

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Conflicts of interest

The authors have no conflict of interests.

Compliance with ethical standards

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Availability of data and material

Data from this study are hosted at https://data.gulfresearchinitiative.org/ and can be accessed using doi.org/10.7266/J420QN15.

References

Ansari, A. A., S. S. Gill, G. R. Lanza, & W. Rast. 2011. Eutrophication: causes, consequences and control. Springer, Dordrecht. 394 pp.

Bargu, S., J. R. White, C. Li, J. Czubakowski, & R. W. Fulweiler. 2011. Effects of freshwater input on nutrient loading, phytoplankton biomass, and cyanotoxin production in an oligohaline estuarine lake. Hydrobiol. 661:377–389.

Bell, J. 2019. Evaluating the effects of water influx on the Mississippi Sound: Current vs. Historical Relationships. Thesis, The University of Mississippi.

Bianucci, L., K. Balaguru, R. W. Smith, L. R. Leung, & J. M. Moriarty. 2018. Contribution of hurricane-induced sediment resuspension to coastal oxygen dynamics. Sci. Rep. 8:1–10.

Cheng, B. S., L. M. Komoroske, & E. D. Grosholz. 2017. Trophic sensitivity of invasive predator and native prey interactions: integrating environmental context and climate change. Funct. Ecol. 31:642–652.

Cressman, K. A., M. H. Posey, M. A. Mallin, L. A. Leonard, & T. D. Alphin. 2003. Effects of oyster reefs on water quality in tidal creek estuary. J. Shellfish Res. 22:753–762.

Dekshenieks, M. M., E. E. Hofmann, & E. N. Powell. 1993. Environmental effects on the growth and development of eastern oyster, *Crassostrea virginica* (Gmelin, 1791) larvae: A modeling study. J. Shellfish Res. 12:241–254.

Erdman, J. 2019. The record-long Mississippi River flood of 2019 is finally ending, but one big concern remains. https://weather.com/safety/floods/news/2019-07-29-record-long-mississippi-river-flood-ends. Accessed December 4, 2019.

Fischer, E. M., J. Sedlacek, E. Hawkins, & R. Knutti. 2014. Models agree on forced response pattern of precipitation and temperature extremes. Geophys. Res. Lett. 41:8554-8562.

Frederick, B. 2019. Precipitation trends in the Mississippi River watershed. U.S. Army Corps of Engineers, Mississippi Valley Division. https://www.mvd.usace.army.mil/Portals/52/docs/Precipitation%20Trends.pdf. Accessed 7 November 2019.

Galtsoff, E. 1964. The American Oyster *Crassostrea virginica* Gmelin. US Fisheries Bull. 64:1–480.

Grabowski, J., R. D. Brumbaugh, R. F. Conrad, A. G. Keeler, J. J. Opaluch, C. H. Peterson, M. F. Piehler, S. P. Powers, & A. R. Smyth. 2012. Economic valuation of ecoystem services provided by oyster reefs. BioScience 62:900-909.

Griffitt, K. J. & D. J. Grimes. 2013. Abundance and distribution of *Vibrio cholerae*, *V. parahaemolyticus*, and *V. vulnificus* following a major freshwater intrusion into the Mississippi Sound. Microb. Ecol. 65:578–583.

Groisman, P.Y., R. W. Knight, T. R. Karl, D. R. Easterling, B. Sun, & J. H. Lawrimore. 2004. Contemporary changes of the hydrological cycle over the contiguous United States: Trends derived from *in situ* observations. J. Hydrometeorol. 5:64–85.

Gulf Coast Research Laboratory. 2019. Bonnet Carré Spillway Monitoring Update: August 2, 2019. https://gcrl.usm.edu/bonny.carre.spillway/2019%20Bonnet%20Carre%20Spillway%20Overview%20-%20August%202,%202019%20-%20Final.pdf. Accessed 17 January 2020.

Ho, P., M. J. Shim, S. D. Howden, & A. M. Shiller. 2019. Temporal and spatial distributions of nutrients and trace elements (Ba, Cs, Cr, Fe, Mn, Mo, U, V and Re) in Mississippi coastal waters: Influence of hypoxia, submarine groundwater discharge, and episodic events. Cont.

Shelf Res. 175:53–69.

Hoegh-Guldberg, O. & J. F. Bruno. 2010. The impact of climate change on the world's marine ecosystems. Science 328:1523-1528.

Jeppesen, R., M. Rodriguez, J. Rinde, J. Haskins, B. Hughes, L. Mehner, & K. Wasson. 2018. Effects of hypoxia on fish survival and oyster growth in a highly eutrophic estuary. Estuar. Coasts 41:89–98.

Knutson, T. R., J. L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J. P. Kossin, A. K. Srivastava, & M. Sugi. 2010. Tropical cyclones and climate change. Nat. Geosci. 3:157-163.

Ko, G. W. K., R. Dineshram, C. Campanati, V. B. S. Chan, J. Havenhand, & V. Thiyagarajan 2014. Interactive effects of ocean acidification, elevated temperature, and reduced salinity on early-life stages of the Pacific oyster. Environ. Sci. Technol. 48:10079–10088.

Kunkel, K. E., D. R. Easterling, K. Redmond, & K. Hubbard. 2003. Temporal variations of extreme precipitation events in the United States: 1895-2000. Geophys. Res. Lett. 30:1–4.

La Peyre, M. K., B. S. Eberline, T. M. Soniat, & J. F. La Peyre. 2013. Differences in extreme low salinity timing and duration differentially affect eastern oyster (*Crassostrea virginica*) size class growth and mortality in Breton Sound, LA. Estuar. Coast. Shelf Sci. 135:146–157.

La Peyre, M. K., A. D. Nickens, A. K.Volety, G. S. Tolley, & J. F. La Peyre. 2003. Environmental significance of freshets in reducing *Perkinsus marinus* infection in eastern oysters *Crassostrea virginica*: Potential management applications. Mar. Ecol. Prog. Ser. 248:165–176.

Lane, R. R., J. W. Day, G. P. Kemp, & D. K. Demcheck. 2001. The 1994 experimental opening of the Bonnet Carre Spillway to divert Mississippi River water into Lake Pontchartrain, Louisiana. Ecol. Engineer. 17:411–422.

Lavaud, R., M. K. La Peyre, S. M. Casas, C. Bacher, & J. F. La Peyre. 2017. Integrating the effects of salinity on the physiology of the eastern oyster, *Crassostrea virginica*, in the northern Gulf of Mexico through a Dynamic Energy Budget model. Ecol. Model. 363:221–233.

Lee, A. 2019. The power to open Bonnet Carré spillway rests 200 miles from 'struggling' Gulf Coast. The Sun Herald, Biloxi, MS. https://www.sunherald.com/news/local/counties/Harrison-county/article231398673.html. Accessed 7 November 2019.

Lehmann, J., D. Coumou, & K. Frieler. 2015. Increased record-breaking precipitation events under global warming. Climatic Change 132:501-515.

Lenihan, H. S. & C. H. Peterson. 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecol. Appl. 8:128-140

Liu, M., G. A. Vecchi, J. A. Smith, & T. R. Knutson. 2019. Causes of large projected increases in hurricane precipitation rates with global warming. NPJ Climate Atmospher. Sci. 2:1–5.

Mississippi Department of Environmental Quality, National Fish and Wildlife Foundation. 2016. The Mississippi Gulf Coast restoration plan: A pathway toward sustainable ecosystem restoration. https://www.mdeq.ms.gov/wp-content/uploads/2017/09/2016-Addendum-FINAL-10.31.2016.pdf. Accessed 4 February 2020.

Mississippi Department of Environmental Quality. 2019. MDEQ Issues Additional Water Contact Warnings. 6 August 2019. https://www.mdeq.ms.gov/mdeq-issues-additional-water-contact-warnings/. Accessed November 8, 2019.

Mississippi Department of Marine Resources. 2019. Harvest Landing Totals, Shellfish Bureau. https://dmr.ms.gov/shellfish/. Accessed September 2019.

National Weather Service. 2019. Mississippi River flood history 1543-present. https://www.weather.gov/lix/ms_flood_history. Accessed 30 January 2020.

NOAA Fisheries. 2019. Frequent questions: 2019 bottlenose dolphin unusual mortality event along the Northern Gulf of Mexico. https://www.fisheries.noaa.gov/southeast/marine-life-distress/frequent-questions-2019-bottlenose-dolphin-unusual-mortality-event. Accessed 1 November 2019.

NOAA National Centers for Environmental Information. 2019. Statewide precipitation ranks January-June 2019. https://www.ncdc.noaa.gov/monitoring-content/sotc/national/statewidepcpnrank/statewidepcpnrank-201901-201906.png. Accessed 30 January 2020.

Orlando, S. P. J., L. P. Rozas, G. H. Ward, & C. J. Klein. 1993. Salinity characteristics of Gulf of Mexico estuaries. National Oceanic and Atmospheric Administration, Office of Ocean Resources Conservation and Assessment, Silver Spring, MD. 209 pp.

Peterson, C. H., J. H. Grabowski, & S. P. Powers. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar. Ecol. Prog. Ser. 264:249–264.

Peterson, T. C., X. Zhang, M. Brunet-India, & J. L. Vazquez-Aguirre. 2008. Changes in North American extremes derived from daily weather data. J. Geophys. Res. 113:1-9.

Pielke, R. A., J. Gratz, C. W. Landsea, D. Collins, M. A. Saunders, & R. Musulin. 2008. Normalized hurricane damage in the United States: 1900-2005. Nat. Hazards Rev. 9:29–42.

Pollack, J. B., H. C. Kim, E. K. Morgan, & P. A. Montagna. 2011. Role of flood disturbance in natural oyster (*Crassostrea virginica*) population maintenance in an estuary in south Texas, USA. Estuar. Coasts 34:187–197.

Posadas, B. 2015. Long-term Mississippi oyster landings. https://hortmarine.wordpress.com/2015/02/09/long-term-mississippi-oyster-landings/. Accessed 4 February 2020.

Posadas, B. & B. K. Posadas. 2017. Economic impacts of the opening of the Bonnet Carre Spillway to the Mississippi oyster fishery. J. Food Distrib. Res. 48:42–45.

Powell, E. N., J. M. Klinck, K. A. Ashton-Alcox, & J. N. Kraeuter. 2009. Multiple stable reference points in oyster populations: Implications for reference point-based management. Fish. Bull. 107:133–147.

Pusack, T. J., D. L. Kimbro, J. W. White, & C. D. Stallings. 2019. Predation on oysters is inhibited by intense or chronically mild, low salinity events. Limnol. Oceanogr. 64:81–92.

Rappaport, E. N. 2014. Fatalities in the United States from Atlantic tropical cyclones: New data and interpretation. Bull. Amer. Meteorol. Soc. 95:341–346.

Reeb, C. A. & J. C. Avise. 1990. A genetic discontinuity in a continuously distributed species: mitochondrial DNA in the American oyster, *Crassostrea virginica*. Genetics 124:397-406.

Risk Management Solutions. 2007. The 1927 Great Mississippi Flood: 80-year retrospective. https://web.archive.org/web/20131029204950/https://support.rms.com/publications/1927_MississippiFlood.pdf. Accessed 30 January 2020.

Shumway, S. E. 1996. Natural environmental factors. In: Kennedy VS, Newell RIE, Eble AF (eds) The Eastern Oyster, *Crassostrea virginica.* Maryland Sea Grant, pp. 467–513.

Sobel, A. H., S. J. Camargo, T. M. Hall, C.-Y. Lee, M. K. Tippett, & A. A. Wing. 2016. Human influence on tropical cyclone intensity. Science 353:242-246.

Spraggins, J. 2019. Bonnet Carré Testimony for Senate Commerce Committee. Mississippi Department of Marine Resources. https://www.commerce.senate.gov/services/files/07A1FD3E-0CF3-420D-AD72-C5C38BCF29F9. Accessed 7 November 2019.

Sun, Y., S. Solomon, A. Dai, R. & W. Portmann. 2007. How often will it rain? J. Climate 20:4801–4818.

Supan, J. E. & C. A. Wilson. 2001. Analyses of gonadal cycling by oyster broodstock, *Crassostrea virginica* (Gmelin) in Louisiana. J. Shellfish Res. 20:215-220.

Turner, R. E. 2006. Will lowering estuarine salinity increase Gulf of Mexico oyster landings? Estuar. Coasts 29:345–352.

Turner, R. E., Q. Dortch, D. Justic', E. M. Swenson. 2002. Nitrogen loading into an urban estuary: Lake Pontchartrain (Louisiana, U.S.A.). Hydrobiol. 487:137–152.

Tweedley, J. R., R. M. Warwick, I. C. Potter. 2015. Can biotic indicators distinguish between natural and anthropogenic environmental stress in estuaries? J. Sea Res. 102:10–21.

US Army Corps of Engineers, New Orleans District (2019) Bonnet Carré Spillway Overview. https://www.mvn.usace.army.mil/Missions/Mississippi-River-Flood-Control/Bonnet-Carre-Spillway-Overview/Spillway-Operation-Information/. Accessed 30 January 2020.

USGS National Water Information System. 2019. https://waterdata.usgs.gov/nwis. Accessed 21 January 2020.

Wong, P. P., I. J. Losada, J.-P. Gattuso, J. Hinkel, A. Khattabi, K. L. McInnes, Y. Saito, & Sallenger. 2014. Coastal systems and low-lying areas. In: C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (eds) Climate change 2014: impacts, adaptation and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, pp 361-409.

Table 1. Duration and maximum daily flow rates for Bonnet Carré Spillway openings from 2008-2019 (data from U.S. Army Corps of Engineers, New Orleans District 2019)

Year	**Days Open**	**Maximum Flow Rate ($ft^3\ s^{-1}$)**
2008	31	114,286
2011	42	235,714
2016	22	203,000
2018	30	196,000
2019(1)	44	213,000
2019(2)	79	161,000

Table 2. Oceanographic data collected via handheld YSI multimeter at each field site in the Mississippi Sound on all sampling days.

Units: salinity (ppt), temperature (°C), dissolved oxygen (mg l^{-1}). NM = not measured

		T-0 23-Apr-19		T-1 6-May-19		T-2 24-May-19		T-3 27-Sep-19	
Site/Depth	**Parameter**	**Surface**	**Bottom**	**Surface**	**Bottom**	**Surface**	**Bottom**	**Surface**	**Bottom**
Back Bay St. Louis 1.34 m	Salinity	0.67	NM	0.4	.39	0.18	0.18	NM	
	Temperature	21.7	21.5	24.4	24.3	27.2	27.2		
	Dissolved Oxygen	9.84	10.03	7.66	7.2	7.14	7.04		
	pH	7.4	NM	7.49	7.33	7.28	7.12		
TNC Bay St. Louis Reef 1.49 m	Salinity	0.54	NM	0.64	0.64	0.14	0.19	15.3	15.3
	Temperature	22	21.5	24.7	24.6	27.4	27.4	28.3	28.4
	Dissolved Oxygen	10.71	10.03	7.5	7.41	7.36	7.23	8.55	7.9
	pH	8.5	NM	7.61	7.6	7.07	6.94	7.7	7.8
St. Stanislaus Reef 1.89 m	Salinity	0.4	NM	0.33	0.35	0.24	0.19	16.8	16.88
	Temperature	21.2	21	24.7	24.1	29.4	28.6	28.9	28.6
	Dissolved Oxygen	9.71	9.6	7.92	7.1	9.29	8.15	9.1	7.16
	pH	8.5	7.98	7.72	7.58	8.18	7.91	7.92	7.66
Waveland Reef 2.56 m	Salinity	0.32	NM	0.25	0.33	0.18	0.19	16.39	16.34
	Temperature	21.2	21.1	24.8	24.5	29.7	28.9	30.6	28.6
	Dissolved Oxygen	9.54	9.42	7.55	7.08	9.21	7.76	10.2	6.88
	pH	7.4	7.68	7.56	7.52	8.14	7.51	8.16	7.93
Henderson Point Reef 3.05 m	Salinity	3.14	NM	1.24	1.3	0.18	0.18	17.2	17.3
	Temperature	21.1	21.7	15	24.9	28.5	28.1	29.7	28.7
	Dissolved Oxygen	12.5	9.7	8.17	7.96	7.38	7.57	12.25	8.3
	pH	8.8	8.8	7.89	8	7.6	7.59	8.21	8.07
Kittiwake Reef 2.26 m	Salinity	4.21	NM	2.31	2.45	0.48	0.48	18.9	21.06
	Temperature	22.1	21.7	26	25.8	28.3	28.2	29.4	28.5
	Dissolved Oxygen	12.75	11.6	8.11	7.9	8.29	7.76	11.23	4.19
	pH	8.88	8.74	8.45	8.42	7.72	7.73	8.11	7.74

Figure Legends

Figure 1. Oyster sensor platform (a) exterior and (b) interior. Platforms were equipped with HOBOware® water quality sensors that measured dissolved oxygen, conductivity, temperature and pH for the duration of the deployment. Oysters were housed oysters on trays enclosed within crates on each platform, with holes to allow adequate water flow.

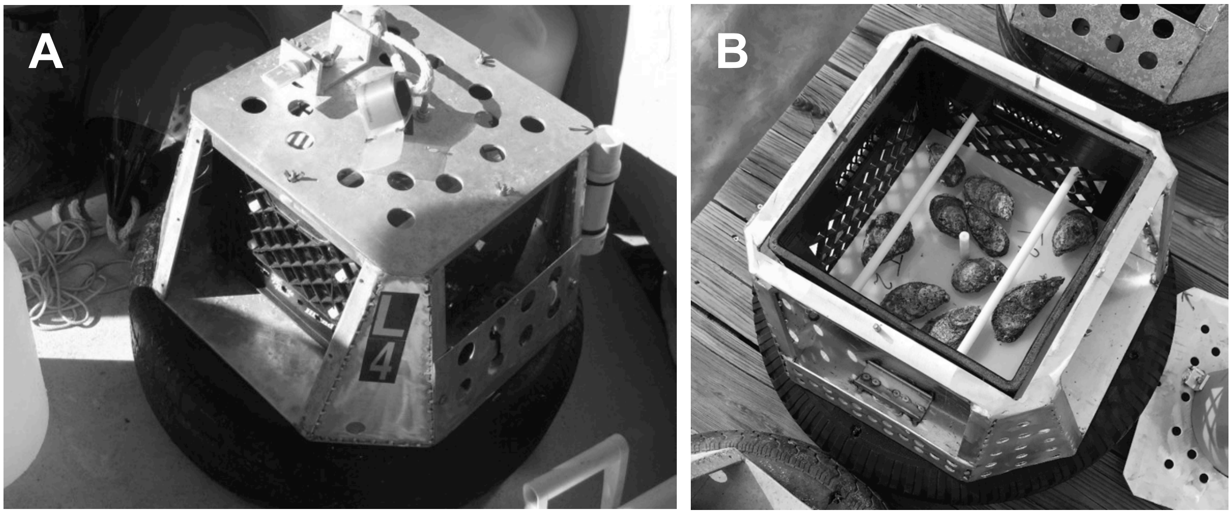
Figure 2. (a) Map of the Mississippi/Louisiana Gulf Coast. Black arrows depict the direction of freshwater flow from the BCS. (b) Map of sites where sensor platforms were deployed. (c) Timeline of sensor platform deployment in relation to the 2019 BCS openings.

Figure 3. *In situ* salinity measurements from sensors deployed at TNC Bay St. Louis Reef from 23 April 2019 to 27 September 2019. Highlighted period depicts spike in salinity due to Hurricane Barry, which made landfall on 13 July 2019.

Figure 4. (a) Map of USGS monitoring sites east from the BCS across the Mississippi Sound. *In situ* salinity at (b) three sites nearer the BCS (Rigolets, St. Joseph Island Light, Grand Pass), and (c) two farther sites (Gulfport Light, Biloxi Bay at Point Cadet Harbor). Highlighted areas show BCS openings (27 Feb – 11 April and 10 May – 27 July 2019). Data from USGS National Water Information System 2019.

Figure 5. (a) Population density of adult and spat oysters at the reefs where live native oysters were found on 24 May 2019. Bars represent mean population density ± SEM (n = 3-6 dredge pulls per site). (b) Cumulative percentage of live (white) and dead (black) adult and spat oysters

collected by dredge pulls on 24 May 2019. Number above each bar represents the total number of oysters collected. Back Bay St. Louis is not an oyster reef site, and Kittiwake Reef yielded no live native oysters.



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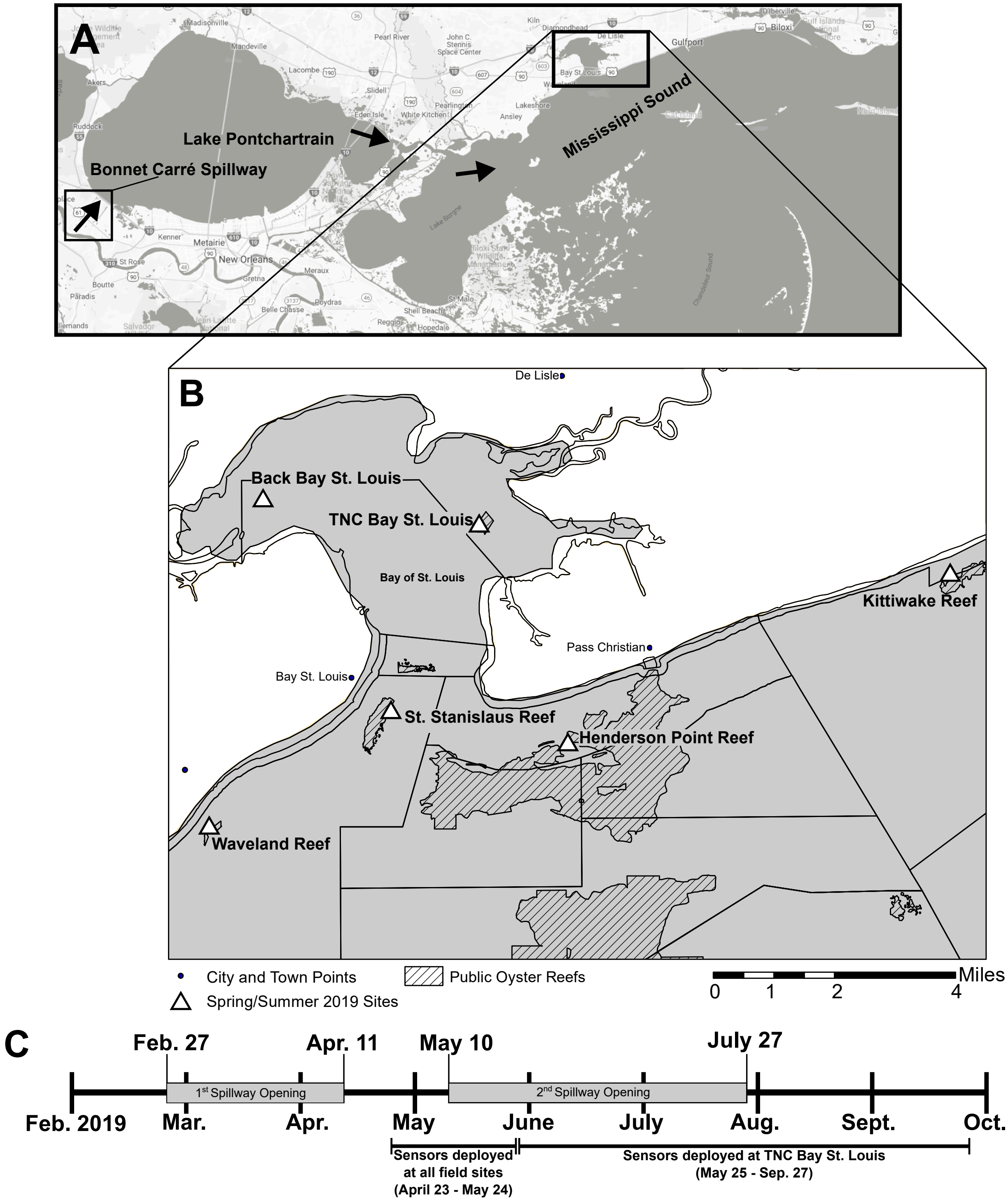

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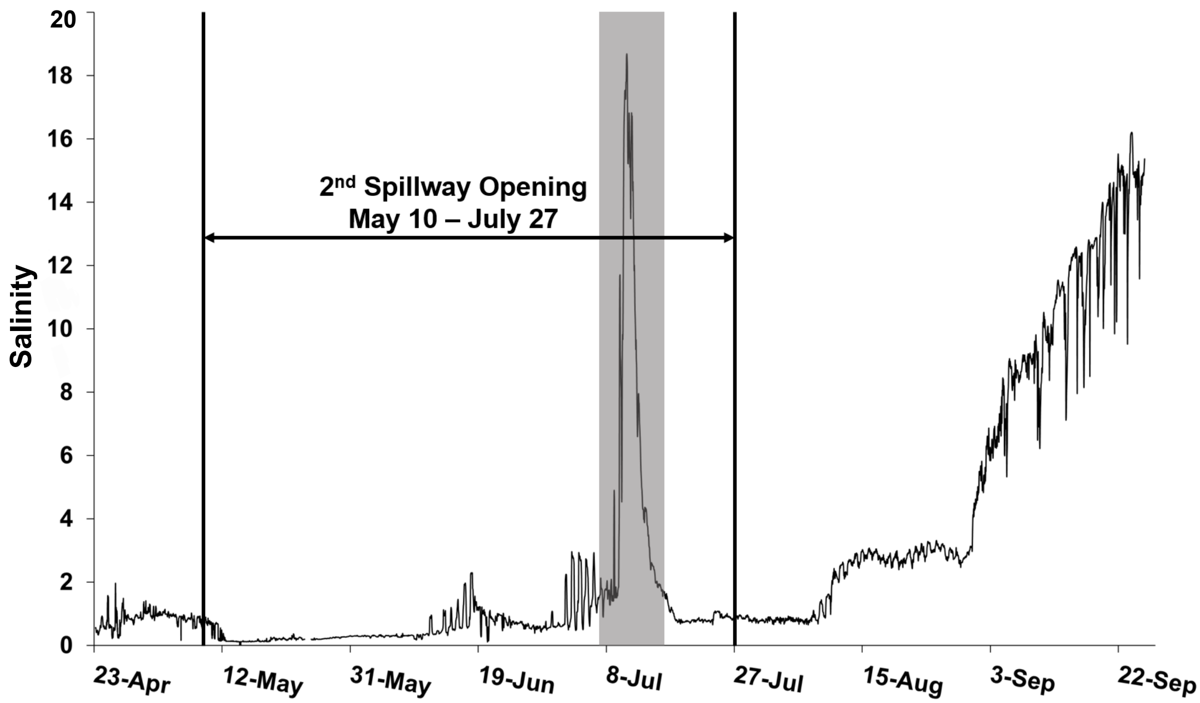

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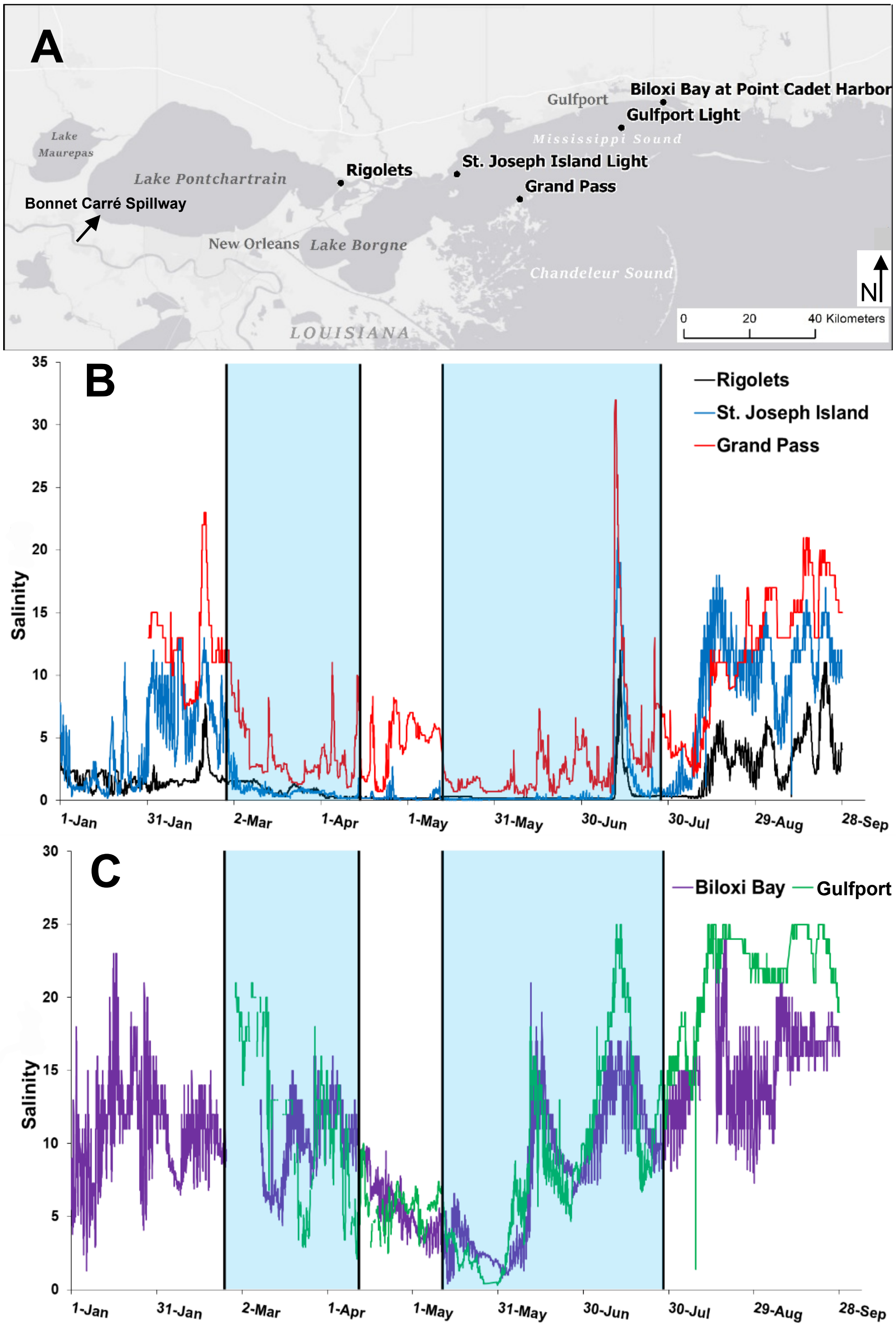

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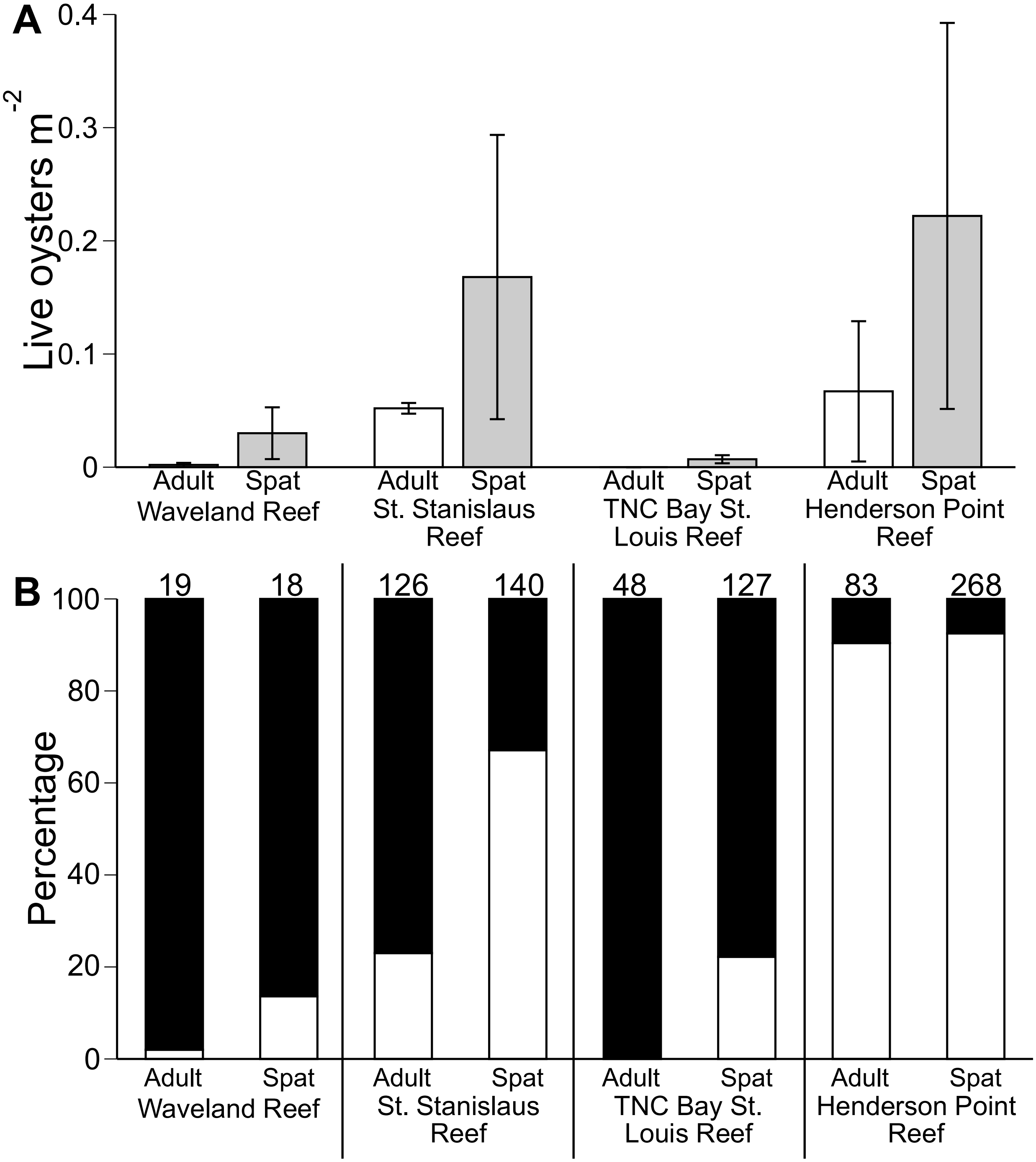

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