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A PAST, PRESENT, AND FUTURE OUTLOOK ON THE MISSISSIPPI OYSTER FISHERY

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ABSTRACT The eastern oyster (*Crassostrea virginica*) is an ecologically and economically important species that provides invaluable services for coastal communities. The oyster industry has a long history and tradition in the U.S. Gulf Coast states, but this fishery has declined dramatically in recent years following Hurricane Katrina, the *Deepwater Horizon* oil spill, and freshwater flooding events. Mississippi was once known as the "seafood capital of the world," but no commercial harvest from Mississippi oyster reefs has occurred since the 2018–2019 season. A review of the Mississippi oyster fishery was conducted to characterize historical conditions relative to a sustainable resource in this region, and how the oyster resource has changed over time due to environmental factors and nonbiological events. Since state management of the oyster fishery began in 1902, oyster landings have fluctuated dramatically over time due to complex interactions between man-made and natural disasters, variability in salinity regimes, and alterations in management authority and approaches. Prior to 2010, Mississippi oyster populations eventually recovered from mass mortality events due to improved environmental conditions coupled with large cultch planting efforts. Significant resources have been invested to restore wild oyster populations in the northern Gulf of Mexico, but these efforts have faced many obstacles, and the baseline to assess restoration progress is not well defined. Present-day challenges hindering oyster recovery efforts in Mississippi were also examined to improve understanding of key abiotic and biotic factors that influence oyster reef health and resilience. At present, adult populations are severely diminished and appear to be more recruitment-limited than during previous historical collapses. Climate change-related precipitation events in the past decade have altered water quality in the Mississippi Sound and have further hampered critical early life history recruitment processes, as well as overall reef resilience. Successful restoration and persistence of sustainable oyster reefs in Mississippi under current and future conditions will require substantial investment in management practices that provide suitable substrate for larval settlement, as well as enhancement of existing stock to promote increased larval supply.

KEY WORDS: oyster fishery, management history, *Crassostrea virginica*, restoration, environmental disturbances, anthropogenic stressors, overfishing

INTRODUCTION

The eastern oyster (*Crassostrea virginica*) was one of the most valuable fisheries in the United States, but by the early 1900s, many natural oyster reefs were depleted or disappeared entirely (Churchill 1920, MacKenzie 1996, Kirby 2004). States responded by enacting laws and management regimes regulating oyster extraction and reef cultivation activities, such as shell and seed plantings (Galtsoff 1943, Kirby 2004), yet this fishery has been difficult to sustain because harvesting simultaneously removes both the animal and the habitat necessary for subsequent recruitment and population renewal (Johnson et al. 2022). Declines in oyster landings from the traditional Northeast and Chesapeake Bay fisheries due to overharvesting led to increased production from the Gulf states by the 1950s (Vanderkooy 2012). The northern Gulf of Mexico contains the largest remaining wild oyster fishery in the world (Beck et al. 2011) and supplies more than half of the U.S. commercial oyster landings (National Marine Fisheries Service 2021), but oyster reef habitat and biomass have declined from historic levels in this region as well (Zu Ermgassen et al. 2012).

Oysters are ecosystem engineers that provide valuable services beyond food provision (Dame 1996, Shumway 2011, Grabowski et al. 2012). Oyster reef habitats support diverse communities of fish and invertebrate species that have commercial and recreational importance (Wells 1961, Peterson et al. 2003, La Peyre et al. 2019). As filter feeders, oysters improve water clarity and remove excess nutrients in estuaries (Newell 2004, Kellogg et al. 2013). These biogenic reefs also protect shorelines from erosion by reducing wave energy (Meyer et al. 1997, Scyphers et al. 2011). The estimated value of the nonharvest ecosystem services ranges between $5,500 and $99,000 per hectare per year (Grabowski et al. 2012). Large-scale oyster reef restoration projects have been increasing in recent decades, focused both on fishery enhancement and ecosystem services restoration (Blomberg et al. 2018, Bersoza Hernández et al. 2018).

The oyster industry in Mississippi has a long and important history, but harvests have fluctuated dramatically over time due to natural and man-made disturbances and significant environmental variability (Fig. 1). Mississippi contributed 5%–15% of all Gulf of Mexico oyster landings between 1960 and 2008 (Vanderkooy 2012), but following several 21st century disasters, there has been no commercial harvest in the state since 2018 (Fig. 1). In 2015, the Mississippi Governor created the Governor's Oyster Restoration and Resiliency Council in

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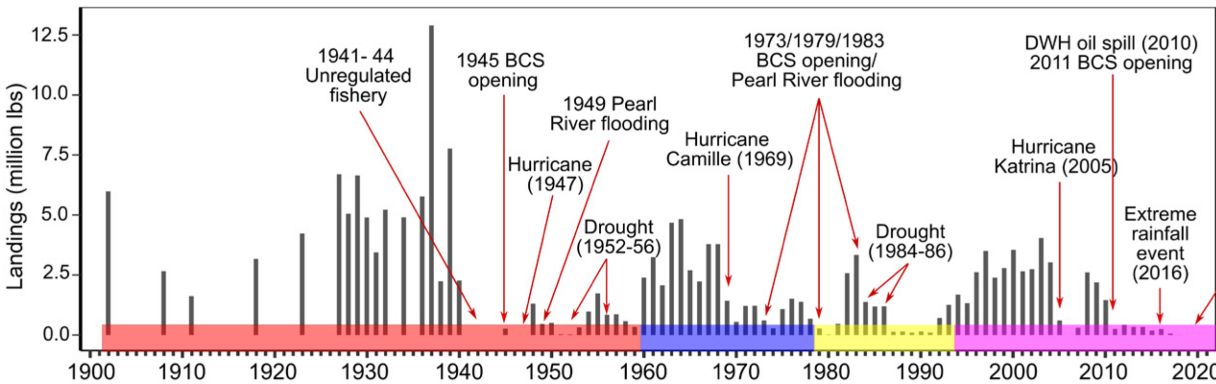

Figure 1. Annual oyster landings (million pounds of meat) in Mississippi (MS) with major fishery disaster events (red arrows) and timeline of state oyster fishery management agencies (1902–1959 = MS Seafood Commission, 1960–1978 = MS Marine Conservation Commission, 1979–1993 = MS Bureau of Marine Resources, 1994–present = MS Department of Marine Resources). Gaps in years prior to 1950 due to lack of available landing data (Lyles 1967, NOAA Fisheries Office of Science and Technology 2022).

response to the decline in landings after Hurricane Katrina, the *Deepwater Horizon* (DWH) oil spill, and the 2011 Bonnet Carré Spillway opening to guide restoration and revitalization of oyster reefs in the state for harvest and ecological benefits (Mississippi Oyster Council 2015). More than $60 million of DWH settlement funds have been awarded to fund projects focused on oysters in Mississippi (Brooke & Alfasso 2022), and there are significant plans for future restoration projects coordinated by state management agencies (MDMR 2021a). This review of the Mississippi oyster fishery characterizes the historical conditions relative to a sustainable resource in this region and how the oyster resource has changed over time due to environmental factors and nonbiological events. Furthermore, present-day challenges hindering oyster recovery efforts in Mississippi were examined to better understand the abiotic and biotic factors that influence oyster reef health and resilience.

HISTORY OF THE MISSISSIPPI OYSTER FISHERY

Official records of oyster production in Mississippi began in 1880, but harvesting had been occurring for centuries prior by Indigenous people and European colonists (Gunter 1975). Oysters have been harvested from reefs by hand, tongs, or dredge. Oyster tonging uses two rakes on long poles operated like scissors to scoop oysters off the bottom (Fig. 2A). Dredging involves the use of an oyster dredge, which is a metal-toothed frame with an attached bag, that is dragged by boat along the bottom to scrape up oysters (Fig. 2B). The first oyster law on record in the state of Mississippi attempted to prohibit dredging in 1860 but was later repealed by the state legislature due to stakeholder pushback in 1865 (Stephens 2021). There are limited historical mapping records and quantitative assessments of oyster density and extent for Mississippi reefs (Moore 1913, Christmas 1973). Overall, the locations of harvestable oyster reefs in Mississippi do not appear to have changed over time, but the reef extent and area have declined (Table 1, Fig. 3). The western Mississippi Sound contains the largest and majority of oyster reefs in Mississippi, with the most extensive reefs occurring within 3–11 km offshore south of Pass Christian. Smaller patch reefs occur nearshore at the opening of St. Louis Bay and to the south at St. Joe Reef. Oyster reefs are also found in Biloxi Bay, near the mouth of the Pascagoula River, and within Graveline Bayou.

The Mississippi Sound is a shallow water estuary (3–4 m) highly influenced by freshwater influxes that impact the salinity regime (Eleuterius 1977). The optimal salinities and temperature for oyster growth and survival in the northern Gulf of Mexico are salinity of 10–20 and 20°C–30°C, respectively (Butler 1954, La Peyre et al. 2021). Salinity levels less than 2 for several weeks can lead to adult mortality, especially when in conjunction with higher temperatures (Cake 1983). Oyster spawning typically occurs between April and October, with peaks in late May/early June as water temperatures increase to 25°C, and in September as water temperatures cool (Butler 1954, Cake 1983). The Pearl River in the west and Pascagoula River in the east are the major freshwater sources, with higher discharges in the spring and lower discharges in the summer and fall months (Orlando et al. 1993). The minor rivers of Jourdan, Wolf, Biloxi, and Tchoutacabouffa, as well as localized runoff, are also important freshwater contributors. Total rainfall and major river discharge can greatly vary from year to year (Fig. 4A, B). In addition, the Bonnet Carré Spillway (BCS) diverts flood waters from the Mississippi River through Lake Pontchartrain and Lake Borgne into the western Mississippi Sound (Fig. 3). The BCS was built by the U.S. Army Corps of Engineers in response to the Great Mississippi Flood of 1927 and has been opened 15 times since construction finished in 1931 for varying durations at different times of the year to reduce the risk of flooding to New Orleans during threatening flood stages of the Mississippi River (Table 2, Fig. 4C).

Coastal Mississippi county control of oyster reefs was established in 1896 but withdrawn in 1902 when the Board of Oyster Commissioners was appointed by the Mississippi governor to maintain and replenish the oyster reefs in the state using public funds (Vanderkooy 2012). The Mississippi Oyster Commission, later renamed Seafood Commission, conducted regular oyster shell plantings on public oyster reefs and moved seed oysters from Pascagoula reefs to reefs in Biloxi Bay and the western Mississippi Sound. In 1904, the first year of shell planting by the Commission, over 14,500 m^3 of oyster shells were planted on Biloxi, Pass Christian, and Pascagoula reefs (Mississippi Oyster Commission 1906). A mapping survey of the location and condition of Mississippi oyster reefs east of Biloxi was performed in 1911 and reported about 1,708 acres of natural reefs with 475 acres containing scattered to dense populations of harvest-sized

Figure 2. (A) Oyster tongers in Biloxi Bay pre1900s. (B) Oyster schooners were first used to tow dredges for oyster harvest during the late 1800s and early 1900s. (C) Oyster shuckers for the canning industry around 1905. (D) A pile of shells outside an oyster canning factory in the 1930s. All photos are courtesy of the Mississippi Department of Archives and History.

TABLE 1.

Oyster reef size (in acres) across time at locations in the Mississippi Sound (see Fig. 3).

Location	1911*	1966†	2015‡
St. Joe Reef	Not surveyed	740	473
St. Louis Bay Reefs	Not surveyed	252	103
Pass Christian Reefs	Not surveyed	7,680	5,166
Biloxi Bay Reef	582	534	30
Pascagoula Reefs	1,126	540	337

*Moore (1913).
†Christmas (1973).
‡MDMR (2018b).

oysters (approximately 3 to >7 oysters per m^2) (Table 1; Moore 1913). Biloxi surpassed Baltimore, MD, in the quantity of oysters canned in the early 1900s and earned the town the nickname "seafood capital of the world" (Fig. 2C, D; MacKenzie 1996, Stephens 2021). Approximately 5,000 people were used in the Mississippi oyster industry during the 1914–1915 seasons (Mississippi Oyster Commission 1916). An average of about five million pounds (approximately 2.3 million kg) of oyster meat were landed annually between 1902 and 1940 (Fig. 1), but there were many gaps in yearly landing data due to insufficient federal funding to collect fishery statistics (Gunter 1948).

During 1941 and 1944, oyster reefs in Mississippi were unregulated and reported to have been overfished with shells not returned to the reefs during World War II (Fig. 1; Gunter 1975). In 1945, the BCS was opened for the second time since of construction, and oyster reefs in the western Mississippi Sound experienced 50%–100% mortality (Table 2; Engle 1948, Butler 1949). In 1948, Congress authorized the U.S. Fish and Wildlife Service to appropriate $3 million (approximately $37 million in 2024 dollars) to the states of Mississippi and Louisiana as reimbursement for the damage caused to the fishery by the opening of the spillway (Butler 1949). A Category 3 hurricane made landfall on the Mississippi coast in 1947 and inflicted heavy oyster losses on nearshore reefs in the western Mississippi Sound, hindering recovery from the 1945 BCS opening (Engle 1948).

High discharge from the Pearl River in 1949 caused additional oyster mortality and reduced growth on reefs already suffering (Fig. 4B; Butler 1949). Oyster landings remained depressed in the 1950s due to high salinities from below-average rainfall and river discharge (Fig. 4A, B). These conditions allowed populations of the oyster drill (*Stramonita haemastoma*), a voracious oyster predator, to flourish (Chapman 1958). The protozoan parasite *Dermocystidium marinum*, presently known as *Perkinsus marinus* or more commonly Dermo, was also identified during this time period in oysters from the Gulf of Mexico (Mackin et al. 1950). Intense Dermo infections were associated with increased oyster mortality under conditions of

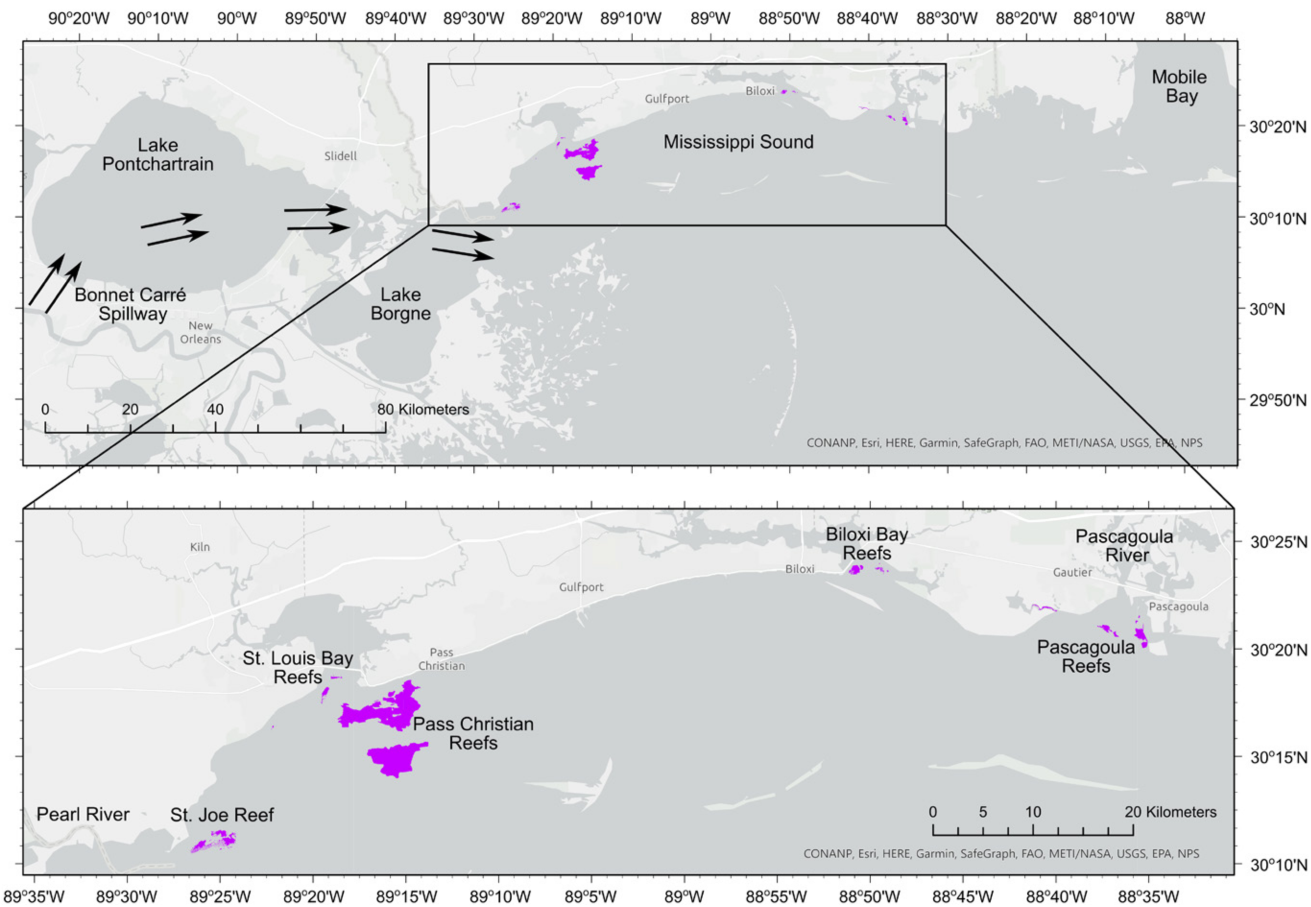

Figure 3. Map of Mississippi oyster reefs (MDMR 2018b).

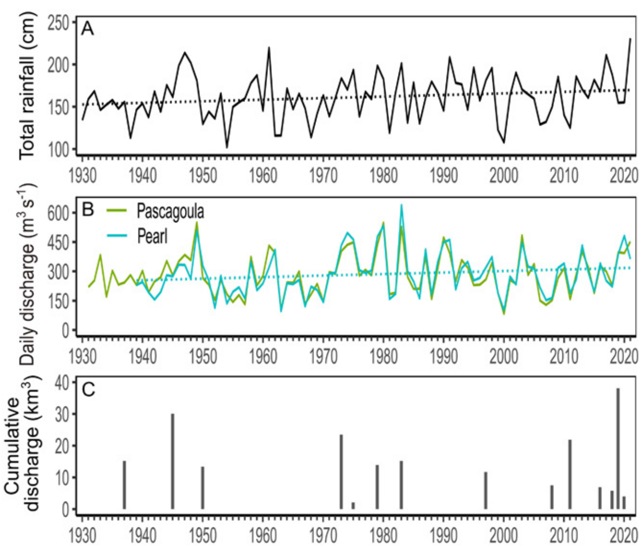

Figure 4. (A) Total annual rainfall in cm for MS coastal division (NOAA National Centers for Environmental Information 2022). (B) Average daily discharge (m^3/s) at USGS streamflow gage stations in Pearl River near Bogalusa, LA (station id: 2489500) and Pascagoula River at Merrill, MS (station id: 2479000) (data available at https://waterdata.usgs.gov/nwis). (C) Estimated cumulative discharge (km^3) during Bonnet Carré Spillway openings (Table 2). Dashed lines are general linear trends in rainfall and Pearl River discharge.

TABLE 2.

Bonnet Carré Spillway opening dates and discharge amounts (data from Parra et al. 2020, U.S. Army Corps of Engineers 2020).

Year	Dates of opening	No. of days	Estimated cumulative discharge (km^3)
1937	28 Jan–16 Mar	48	15.2
1945	23 Mar–18 May	57	30.1
1950	10 Feb–19 Mar	38	13.4
1973	8 Apr–21 Jun	75	23.5
1975	14 Apr–26 Apr	13	2.11
1979	17 Apr–31 May	45	13.9
1983	20 May–23 Jun	35	15.2
1997	17 Mar–17 Apr	32	11.7
2008	11 Apr–8 May	28	7.5
2011	9 May–20 Jun	43	21.9
2016	10 Jan–1 Feb	23	6.9
2018	8 Mar–30 Mar	23	5.8
2019	27 Feb–11 Apr	44	15.1
	10 May–27 Jul	79	23.0
2020	3 Apr–30 Apr	29	4.0

high temperature and high salinity (Mackin 1951, Ray 1954). An average of approximately 630,000 pounds (approximately 290,000 kg) of oyster meat were landed annually between 1945 and 1959 (Fig. 1).

The Mississippi Seafood Commission was abolished in 1960 and a new commission was established with an entirely new membership, including William J. Demoran, a marine biologist, serving as the advisor. The Mississippi Marine Conservation Commission implemented an oyster bottom improvement program that included oyster bottom surveys, shell and seed plantings, and oyster reef cultivation by raking reefs with dredges in the spring to expose clean shell surface for oyster larval settlement in the summer (Gunter 1975, MacKenzie 1977). Average annual landings of oyster meat between 1960 and 1969 were almost four times higher, about three million pounds (approximately 1.4 million kg) per year, than the previous 15 y (Fig. 1).

Harvest closures due to sewage discharge from the growing population and industry on the Mississippi coast also became a prominent issue in the 1960s. Pascagoula Bay reefs were closed entirely in 1961 after a hepatitis A outbreak (Mason & Mclean 1962). Those reefs had also decreased more than 50% in size between the 1911 survey and 1966 (Table 1). Biloxi Bay reef closures began in 1945 in the Back Bay and extended southward until the entire bay was closed in 1967 (Lyles 1976, Broutman & Leonard 1988).

Hurricane Camille struck the Mississippi coast as a Category 5 hurricane in 1969, physically damaging oyster reefs and destroying fishing vessels and processing factories (Gunter 1975, Lyles 1976). As reefs were beginning to recover, flooding from the Pearl River and the 1973 BCS opening (Fig. 4B, C) depressed salinities in the western Mississippi Sound and devastated oyster populations (Lyles 1976, MacKenzie 1977). Federal funding was received after Hurricane Camille and the flood of 1973 for reef rehabilitation, and extensive shell plantings occurred on public reefs after these events (Fig. 5; Leard et al. 1999).

Oyster landings averaged about 950,000 pounds (approximately 430,000 kg) of meat between 1970 and 1978 (Fig. 1). In an effort to boost the oyster industry during this period, a Mississippi state law was passed in 1977 to allow leaseholders to relay oysters from reefs permanently closed due to pollution to private leases in approved waters. Over 50 leases were approved by 1979, but reefs in closed areas were depleted of marketable oysters by 1980 and private relaying and the interest in leasing declined (Berrigan et al. 1991, Leard et al. 1999).

In 1978, the Mississippi Department of Wildlife Conservation was established, which created the Bureau of Marine Resources. The Bureau took over management of the oyster fishery in 1979

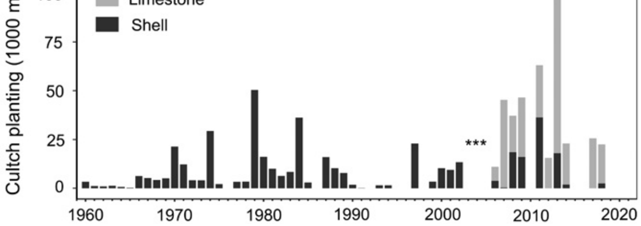

Figure 5. Amount of shell and/or limestone cultch material planted on Mississippi public oyster reefs per year (Gulf States Marine Fisheries Commission 1999, 2001, 2002, 2003, 2004, Leard et al. 1999, MDMR 2020). Asterisks denote a record of plantings for each year between 2003 and 2005 but no available data on the amount of material.

and initiated an Oyster Reef Rehabilitation Program between 1979 and 1980 using federal disaster funds to revitalize oyster reefs severely damaged by floodwaters released from the 1979 BCS opening (Deegan et al. 1981). Over 66,000 m^3 of clamshell cultch material was planted on reefs in the western Mississippi Sound (Fig. 5) and most of the oysters harvested in the 1981–1982 season were from spat that had developed on shell material from these plantings (Deegan et al. 1981, Gulf States Marine Fisheries Commission 1983). High mortality occurred on public oyster reefs again in 1983 due to another BCS opening and high discharge from the Pearl River (Gulf States Marine Fisheries Commission 1985). Another large shell planting occurred in 1984 (47,407 m^3 of clamshell cultch, Fig. 5), but drought conditions creating high salinities and promoting oyster drill populations prevented reefs from recovering (Leard et al. 1999, Vanderkooy 2012). By the end of the 1980s, fishing efforts had decreased due to unpredictable landings coupled with water quality issues and pollution closures, and only about 125,000 pounds (approximately 60,000) of oyster meat were harvested annually between 1987 and 1991 (Fig. 1; Posadas et al. 1993, Vanderkooy 2012).

Oyster management shifted once again in 1994 with the creation of the Mississippi Commission on Marine Resources and the Mississippi Department of Marine Resources (MDMR) (MDMR 2020). MDMR was given the power to manage oyster resources under the jurisdiction of the Mississippi Commission of Marine Resources and maintains this responsibility as of 2023. This change in regulatory authorities brought about a renewed interest in enhancing marine fisheries for the state. By 2000, the Mississippi oyster industry, including the harvesting, processing, and restaurant sectors, generated almost $72 million in total sales and supported 1,594 jobs (Posadas 2003). Annual oyster landings averaged about 2.7 million pounds (approximately 1.2 million kg) of oyster meat during the first 10 y of MDMR management between 1994 and 2004 (Fig. 1).

CHALLENGES FOR 21ST CENTURY MISSISSIPPI OYSTER REEFS

Hurricane Katrina made landfall in Mississippi on 29 August 2005, severely damaging or completely destroying coastal communities from Louisiana to Alabama (Abbott-Jamieson & Ingles 2015). Ninety percent of oyster reefs in Mississippi were damaged after Hurricane Katrina, and reefs were closed to harvesting for the subsequent 2 y (Vanderkooy 2012). Federal funds, made available from the 2006 Emergency Disaster Recovery Program for oyster restoration, were used by the state to perform extensive cultch planting (Fig. 5) and oyster relaying from Biloxi Bay and Pascagoula Reefs to the more severely damaged reefs in the western Mississippi Sound (Vanderkooy 2012, Posadas & Posadas 2017). By 2008, dredge survey data from MDMR indicated more than 200% rebound in legal-sized (>75 mm) oysters on public oyster reefs in the western Mississippi Sound (Fig. 6). Oyster landings recovered between 2008 and 2010 and averaged about 2.1 million pounds (approximately 950,000 kg) of oyster meat annually (Fig. 1). In 2009, the oyster industry contributed $23.7 million to the economy of Mississippi and generated 562 jobs (Posadas 2014).

On 20 April 2010, the *Deepwater Horizon (DWH)* oil rig exploded and released hundreds of millions of liters of crude oil for

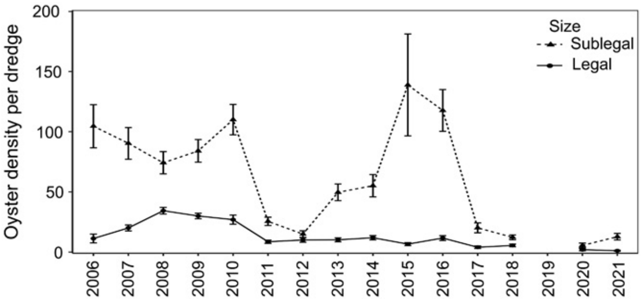

Figure 6. Density (mean ± SE) of sublegal (<75 mm shell height) and legal (≥75 mm) harvest-sized oysters on Mississippi public oyster reefs from 1-min dredge tow surveys provided by MDMR. No MDMR sampling data was given for 2019.

87 days into the northern Gulf of Mexico, resulting in the oiling of at least 2,000 km of estuarine and coastal shorelines. Most of the oil impacted Louisiana, but over 250 km of the Mississippi shoreline experienced oil exposure (Nixon et al. 2016, Rouhani et al. 2017). Nearshore and subtidal oyster populations sustained major losses in the central portion of the northern Gulf of Mexico due to the oil spill itself and the disaster response of opening freshwater diversions in southeastern Louisiana. Combined, these resulted in an absence of spat recruitment in Louisiana and Mississippi waters in 2011 (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016, Grabowski et al. 2017, Powers et al. 2017). Mississippi public reefs were opened for harvest between 8 November 2010 and 30 April 2011, but only for tonging, and a total of 41,253 sacks (approximately 300,000 lbs or approximately 130,000 kg) were harvested (MDMR 2011). The BCS opening in May 2011 inflicted further heavy mortality on the few remaining oysters in the western Mississippi Sound and only 65 sacks were harvested in the 2011–2012 season (Fig. 1; MDMR 2012, Posadas & Posadas 2017). Oyster densities across all size classes were severely reduced on Mississippi public reefs in 2011 and 2012 (Fig. 6).

Between 2012 and 2014, over 187,000 m^3 of oyster shell and limestone were deployed across 1,430 acres of existing oyster reefs in the western Mississippi Sound as part of the early restoration phase from the DWH Natural Resource Damage Assessment trustees (Fig. 5; MDMR 2021a). There were initially high levels of spat recruitment on the enhanced reefs (Deepwater Horizon Natural Resource Damage Assessment Trustees 2021, La Peyre et al. 2022), and by 2015, the densities of sublegal-sized oysters, which include spat (<25 mm) and seed (25–75 mm) size classes, had returned to preDWH levels on public oyster reefs in the western Mississippi Sound (Fig. 6). Reef area on western Mississippi Sound reefs in 2015, however, had declined by more than 33% since the last extensive survey in 1966 (Table 1).

A mass oyster mortality event occurred in the late summer of 2016 due to widespread low dissolved oxygen levels in the western Mississippi Sound (Pace et al. 2020, Deepwater Horizon Natural Resource Damage Assessment Trustees 2021). Seasonal hypoxia in the Mississippi Sound is commonly attributed to increased vertical stratification of the water column during summer months due to reduced wind mixing (Ho et al. 2019, Parra et al. 2020). Stratification leading to bottom water hypoxia may have been exacerbated by an extreme rainfall event that produced 20–30 cm of rainfall between 10 and 14 August 2016 (Brown et al. 2020). Spat and seed oyster densities declined sharply on the western Mississippi Sound oyster reefs in 2017 and remained low in 2018 (Fig. 6). Oyster landings averaged about 230,000 pounds (approximately 100,000 kg) of oyster meat annually between 2011 and 2018 (Fig. 1).

In 2019, the BCS was opened twice in the same year, for the first time ever, and cumulatively discharged the largest amount of freshwater on record during the combined 123-day openings (Table 2, Fig. 4C). Salinity levels were severely depressed, often reduced to near zero, between March and July on oyster reefs in the western Mississippi Sound (Gledhill et al. 2020, Pace et al. 2020). Dredge surveys revealed high levels of oyster mortality on reefs nearest the BCS beginning in May, and 100% mortality was found on all western Mississippi Sound reefs by June (Gledhill et al. 2020, Pace et al. 2020). Additionally, no spat settlement was observed during the 2019 spawning season on reefs in the western Mississippi Sound (Morgan & Rakocinski 2022, Pace et al. 2023). Beach water advisories were also issued for coastal Mississippi between June and October due to the presence of microcystin-producing cyanobacteria transported from blooms that formed in Lake Pontchartrain during and following the second BCS opening (Soto Ramos et al. 2023, Bargu et al. 2023). The Department of Commerce declared a fishery resource disaster for the oyster fisheries in Louisiana, MS, and Alabama for 2019 due to the extreme freshwater flooding event, and again for 2020 in Mississippi due to ongoing impacts from the 2019 BCS openings (NOAA Fisheries 2023).

By the end of 2021, oyster reefs in the western Mississippi Sound showed few signs of recovery (Fig. 6; Pace et al. 2023). No wild harvest has occurred on Mississippi oyster reefs since the 2019 BCS openings due to the lack of oysters (Fig. 1). Recent larval transport models have demonstrated that oyster reefs in Louisiana and the eastern Mississippi Sound may serve as sources of oyster larvae for western Mississippi oyster reefs (Milroy et al. 2020, Powers et al. 2023), but these populations have experienced significant losses as well (Fig. 7). For example, Drum Bay cultch plant in Louisiana completed in 2013 during the DWH Natural Resource Damage Assessment early restoration phase was identified as a potential source reef for Pass Christian reefs (Cambazoglu et al. 2020, Milroy et al. 2020). Oyster recruitment and survival were initially high at the restored Drum Bay site in 2015, but seed and sack oyster densities decreased dramatically by 2021 to only approximately one oyster of each size class per m^2 (Fig. 7). Larvae from oyster reefs in the eastern Mississippi Sound, such as in Pascagoula Bay, may similarly contribute to western Mississippi oyster reefs (Powers et al. 2023), but they also suffered about an 85% decline in seed and sack oyster densities from 2015 to 2021 (Fig. 7).

FUTURE OF OYSTER RECOVERY IN MISSISSIPPI

Current wild oyster spawning stocks across the Mississippi Sound are severely reduced and larval supply is not sufficient for sustainable oyster recovery (Morgan & Rakocinski 2022, Pace et al. 2023). Restoration efforts in Mississippi focused on improving recruitment by rebuilding adult populations in addition to habitat enhancement may best promote recovery. A common restoration technique in recruitment-limited systems is to

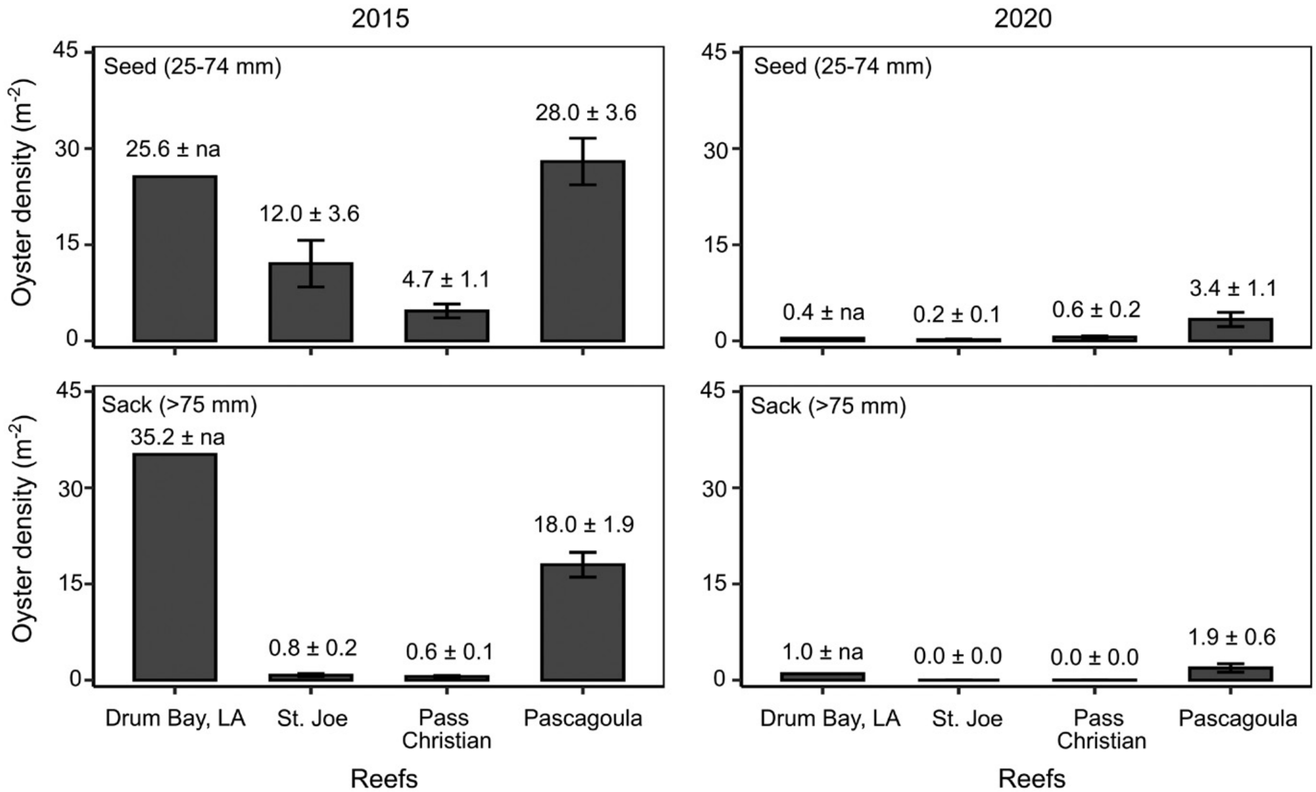

Figure 7. Oyster density (mean ± SE) of seed (25–74 mm shell height, top) and sack (≥75 mm, bottom) sized oysters at Louisiana's Drum Bay cultch plant and on Mississippi public oyster reefs (Fig. 3) from quadrat sampling in 2015 (left) and 2021 (right) provided by MDMR and from Louisiana Department of Wildlife & Fisheries annual stock assessment reports (LDWF 2017, 2023).

allow larvae to settle on shell material under controlled settings and then deploy the resulting "spat-on-shell" onto natural or restored reefs (Brumbaugh & Coen 2009, Geraldi et al. 2013). In 2021, MDMR remotely set approximately 11 million spat on oyster shell and deployed more than 35 m^3 of this spat-on-shell onto a restored reef in Biloxi Bay (MDMR 2021b). Recently settled oysters are highly vulnerable to environmental stressors and predation (Knights et al. 2012, Pruett et al. 2022), and restoration projects that use deployed juvenile bivalves have had mixed success (Geraldi et al. 2013, Grizzle et al. 2021). Oyster gardening programs are a restoration strategy to enhance oyster survival during the vulnerable spat stage by using individuals or organizations to grow spat-on-shell off docks in cages or floats prior to planting in restoration areas (Brumbaugh & Coen 2009, Fitzsimons et al. 2020). The Mississippi Oyster Gardening Program was established using DWH settlement funds in 2016 and has over 50 gardening sites that care for hatchery-produced spat-on-shell until they reach a size that can be planted onto restored reefs in the Mississippi Sound (Mississippi Oyster Gardening Program 2023). Designating restored reefs as sanctuary reefs or no-take reserves that are protected from harvesting can further promote the establishment and maintenance of spawning stock (Brumbaugh & Coen 2009). Over $35 million of DWH settlement funds have been dedicated to creating a network of spawner sanctuaries across the Gulf of Mexico, including a reef in Mississippi (Deepwater Horizon Oil Spill Regionwide Trustee Implementation Group 2021). These spawner sanctuaries can benefit areas open to harvest by serving as sources of oyster larvae (Schulte et al. 2009, Peters et al. 2017).

Hatchery-produced oysters can also contribute to oyster reef restoration efforts by reducing harvest pressure on wild broodstock while providing jobs and income for the oyster industry (Bendick et al. 2018). In addition to supplementing commercial production, in-water oyster aquaculture provides many of the same ecosystem services as natural or restored reefs, such as improved water clarity, nutrient removal, and habitat provision (Shumway et al. 2003, Van Der Schatte Olivier et al. 2020). Across the Gulf states, interest and investment in off-bottom aquaculture, which grows hatchery-produced seed in enclosed gear above the substrate, has increased since it was introduced commercially in 2009 (Walton & Swann 2021). In 2018, MDMR permitted a zone for off-bottom aquaculture outside of Biloxi Bay and established a training program to support and develop oyster farmers. By 2021, over 450 acres were available to lease for oyster farming at the Deer Island Aquaculture Park and more than 800,000 oysters were sold by Mississippi oyster farmers between 2018 and 2021 (Posadas 2022). DWH settlement funds have also been invested toward the construction of an oyster hatchery and research center at The University of Southern Mississippi to provide oysters for aquaculture and restoration, and conduct research on oyster husbandry and rearing techniques (Brooke & Alfasso 2022). The hatchery utilizes a closed recirculating system with artificial seawater so larvae and spat can be produced during periods of naturally low production due to poor water quality in the Mississippi

Sound. A selective breeding program has also been established involving multiple hatcheries across the Gulf of Mexico aimed at producing oysters with beneficial traits for oyster fitness, such as disease resistance and tolerance to extreme environmental stress, and developing a germplasm repository to preserve genetic resources (Yang et al. 2021).

Stressors that have historically triggered significant fluctuations in oyster populations are now being exacerbated due to climate change, increasingly threatening restoration efforts and future oyster populations. Hurricanes have caused several extensive oyster mortality events in Mississippi, as a result of physical damage from high wave energy, reduced salinities from increased freshwater input, and/or burial by sediment (Engle 1948, Gunter 1975, Vanderkooy 2012). Tropical storms and hurricanes are also a major concern for off-bottom aquaculture due to oyster mortality and the loss of gear and equipment (Sturmer et al. 2020). The frequency of stronger, more intense, hurricanes is predicted to rise with warming global temperatures and changes in atmospheric circulation patterns (Emanuel 2005, Knutson et al. 2020). Between 2017 and 2021, one or more named storms impacted the Mississippi coast each year, with 2020 being the most active Atlantic hurricane season on record, especially within the Gulf of Mexico (National Hurricane Center 2022). In the face of increased severe storm events, healthy oyster reefs can provide coastal protection by attenuating wave energy and buffering against storm surge, but resilient and self-sustaining reefs are required for these benefits to persist (Chowdhury et al. 2021).

Heavy rainfall events have also increased in recent decades and alterations in precipitation patterns are projected to continue with climate change (Coumou & Rahmstorf 2012, Powell & Keim 2015, Collins et al. 2019). Coastal Mississippi experienced the wettest year on record in 2021, and reduced salinity levels were observed across the Mississippi Sound (Fig. 4A; Pruett et al. 2022). Seven of the total 15 BCS openings since its completion in 1931 have occurred in the 21st century (Table 2). Wetter winters and more frequent extreme precipitation events are expected in the future for the Mississippi River Basin region, which may lead to continued recurrent BCS openings (Kunkel et al. 2013, Karmalkar & Bradley 2017, Turner 2022). Future BCS operations need to consider ways to avoid harm to Mississippi and Louisiana coastal resources and restoration investments. In the past, the most lethal BCS openings to oyster populations have been associated with larger volumes of freshwater discharge occurring in late spring (May–June) when water temperatures are higher and oysters are less able to cope with salinity stress (Loosanoff 1952, Rybovich et al. 2016). Recently developed circulation models (Wiggert et al. 2022) can be used to predict the impact of BCS openings or other future freshwater diversion structures on salinity and temperature conditions in the Mississippi Sound to inform the timing and discharge level of openings.

Changes to freshwater discharge due to climate-change mediated alterations in precipitation patterns and flood management practices will impact other water quality parameters that influence the health of Mississippi oyster reefs in addition to salinity. Coastal eutrophication from excess nutrient input during high river discharges stimulates algal bloom formation and can cause declines in dissolved oxygen levels and pH due to enhanced microbial respiration when algae dies and decays (Cai et al. 2011, Paerl et al. 2018). Algal blooms can produce harmful toxins that necessitate shellfishery closures, such as microcystin-producing cyanobacterial blooms associated with BCS openings (Bargu et al. 2011, 2023). The red tide (*Karenia brevis*) blooms that originate in Florida but are advected west across the Gulf also impact Mississippi oysters (Maier Brown et al. 2006, Soto et al. 2018). Hypoxia negatively impacts oyster growth and survival (Lenihan & Peterson 1998, Pace et al. 2020), and may intensify with future warming temperatures due to decreases in oxygen solubility, increases in biological respiration, and increases in stratification (Breitburg et al. 2018). Excess CO_2 from eutrophication-induced acidification can add to the absorbed atmospheric CO_2 from anthropogenic inputs (Cai et al. 2021) and exacerbate the potential adverse effects of ocean acidification on oyster growth and calcification rates (Lemasson et al. 2017). Additionally, river discharges are poorly buffered and typically more acidic than oceanic waters, thus increased freshwater inputs can cause changes in carbonate chemistry that lower the availability of calcium carbonate needed for oyster shell formation (Cai et al. 2021). Prior to and during the 2019 BCS openings, low calcium carbonate saturation states (Ω_{arag} <1) were recorded in waters on or near oyster reefs in the western Mississippi Sound, suggesting that Mississippi oyster populations may be vulnerable to current and future acidification conditions (Savoie et al. 2022, Sankar et al. 2023). Long-term water quality monitoring for the Mississippi Sound, especially for dissolved oxygen and carbonate chemistry, is severely lacking, but greatly needed to guide current and future oyster management and restoration.

Recent policy changes have also been enacted to facilitate the recovery of the Mississippi oyster fishery, along with the extensive oyster reef restoration efforts. In 2017, basket dredges, which use a rigid framed basket instead of a flexible bag made of iron or rope to scoop up oysters whereas dredging, were deemed destructive to oyster reefs by MDMR and banned for use in harvesting (MDMR 2018a). Regardless of gear type, harvesting reduces reef height and makes oysters more susceptible to hypoxia and burial by sedimentation (Lenihan & Peterson 2004, Colden et al. 2017). Harvested reefs will continue to degrade until reef extinction if no recruitment or shell replacement occurs, even if fishing pressure is removed (Colden et al. 2017, Soniat et al. 2022). Based on models of collapsed oyster fishery recovery, fishery moratoria, coupled with substantial habitat restoration, is recommended as the most rapid and sustainable way to rebuild oyster populations (Wilberg et al. 2013, Johnson et al. 2022). In 2023, the state of Mississippi passed new legislation opening over 24,000 acres of oyster-growing bottoms in the Mississippi Sound, including formerly public oyster reefs, to private on-bottom leasing (Mississippi Administrative Code 2023). MDMR has designated 20% of the area available for leasing as state-owned reefs to maintain for public harvest if adult populations recover. Since the early 1900s, private leasing has been an important component of oyster fisheries in many states, such as Louisiana and Virginia, (Mackenzie 1996, Schulte 2017), but has been relatively limited in Mississippi besides the brief period of popularity during the late 1970s when private relaying was legalized (Berrigan et al. 1991, Leard et al. 1999). Leaseholders are responsible for maintaining oyster production of on-bottom leases through cultivation using the deployment of cultch material or spat-on-shell. The state hopes that private industry can help renew oyster production and contribute to the long-term sustainability of the fishery (MDMR 2023).

CONCLUSIONS

Oyster landings in Mississippi have varied dramatically over time due to complex interactions between natural and man-made disasters, variability in salinity regimes, and alterations in management authority. Significant cultch plantings have aided in the recovery of Mississippi oyster populations in the past, when coinciding with optimal environmental conditions, but currently, there are not enough wild oysters in the Mississippi Sound to repopulate the reefs. Since 2010, reduced oyster reef resilience has been documented across the Gulf of Mexico due to multiple stressors (Soniat et al. 2022, Hintenlang et al. 2024), and many large-scale cultch plantings using DWH settlement funds have yet to demonstrate substantial recovery (La Peyre et al. 2022, Pine et al. 2023). Successful restoration and persistence of sustainable oyster reefs under current and future conditions will require significant investment in, and implementation of, management practices that provide not only suitable substrate for larval settlement but also enhance broodstock to promote increased larval supply. The growth and development of on-bottom and off-bottom aquaculture will likewise be necessary to rebuild and sustain the oyster industry for future generations.

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