



Consequences of large-scale salinity alteration during the *Deepwater Horizon* oil spill on subtidal oyster populations

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ABSTRACT: Response actions associated with oil spills often have significant impacts on ecological communities. During the 87 d long *Deepwater Horizon* oil spill, the State of Louisiana (USA) released vast quantities of Mississippi River water into 2 estuarine basins (Barataria Bay and Black Bay/Breton Sound) in response to the approach of oil. We assessed the impact on subtidal oyster populations of this novel oil spill response action using 3 independent methods: (1) comparison of fisheries-independent post-spill densities to a pre-spill temporal baseline; (2) comparison of oyster density collected during natural resource damage assessment sampling between the area of maximal freshwater impact and reference areas in the 2 basins; and (3) estimation from a dose-response model derived from an analysis of an *in situ* mark and recapture study conducted in 2010 to assess the relationship between salinity and oyster mortality. A substantial portion of both basins (483 km² of Barataria Bay and 362 km² of Black Bay/Breton Sound) experienced prolonged periods of very low (<5 ppt) salinity in 2010 that lasted at least 1 mo longer than the average duration of low salinity between 2006 and 2009. The 3 approaches all indicate that dramatic losses occurred in the number of market-sized (>75 mm) oysters as a result of a system-wide lowering of salinities, with an estimated 1.16 to 3.29 billion market-equivalent oysters lost. The efficacy of the large-scale response action of altering hydrographic conditions during the summer oyster growth period should be examined in light of the major perturbation to oyster communities.

KEY WORDS: Estuary · Oil spill response · Natural resources damage assessment · Oyster reefs · Gulf of Mexico · *Crassostrea virginica* · Hydrography

INTRODUCTION

Eastern oysters *Crassostrea virginica* are a critical component of many estuarine ecosystems, particularly those along the US Gulf and mid-Atlantic coasts (Beck et al. 2011), and are the quintessential estuarine-dependent species, spending their entire life cycle within estuaries. Although eastern oysters have been

observed across a large range of salinities (3–36 ppt), they generally thrive in the narrow band of mesohaline water in an estuary (Melancon et al. 1998). This 'green band' of water formed by the interface between the sediment-laden, brown freshwater entering from riverine systems and runoff and the blue marine water ingression from the oceanic realm is a constantly fluctuating hydrographic zone of estuaries.

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Too much freshwater reduces local salinity to levels where survivorship, growth, or reproduction of oysters is impaired, whereas too much ocean water generally elevates salinities and is associated with higher levels of predators (e.g. the oyster drill *Stramonita haemastoma*) or disease (e.g. the protozoan parasite *Perkinsus marinus*) that leads to reduced survivorship (e.g. Gunter 1955, Davis 1958, 1979, Chatry et al. 1983, Brown & Richardson 1988, Soniat & Brody 1988, Fodrie et al. 2008, La Peyre et al. 2009, 2013, Soniat et al. 2013). Although the specific thresholds of these triggers varied from study to study, the general pattern of oysters thriving in waters whose average annual salinities fall between 8 and 22 ppt with frequent brief pulses of freshwater input is well established and accepted by oyster biologists. Because settlement of oysters is gregarious on existing oyster shells, sustainable populations of oysters require that the position of this green zone of water stays relatively fixed over time. A substantial perturbation of this salinity zone away from areas of existing oyster shell cover, particularly at a time of increased water temperatures, can both hamper reproduction and result in oyster mortality that can have lasting impacts on the oyster fishery as well as affecting the ecological benefits that accrue from healthy oyster reefs.

On 20 April 2010, the *Deepwater Horizon* (DWH) exploded and set off an unprecedented chain of environmental perturbations in the northern Gulf of Mexico (GoM). Hundreds of millions of liters of oil were spilled into the GoM, resulting in the oiling of at least 2000 km of estuarine and coastal shorelines. In addition to the contaminant release, response actions taken by state and federal resource agencies to mitigate the environmental disaster also introduced potential environmental perturbations. The State of Louisiana, in response to the potential damage from the compromised well head, took the unprecedented action of releasing large quantities of freshwater through diversion structures along the Louisiana coastline to prevent the ingress of oil and to flush contaminants from where oil was likely to come ashore (Martínez et al. 2012). The Davis Pond and Caernarvon diversions were the 2 major diversion structures opened; these structures allow freshwater from the Mississippi River to flow into Barataria Bay and Black Bay/Breton

Sound, respectively. The Davis Pond diversion is located on the southwestern bank of the Mississippi River in St. Charles Parish, approximately 24 km (15 miles) upstream of New Orleans (US ACE, New Orleans District; www.mvn.usace.army.mil/About/Projects/DavisPondFreshwaterDiversion.aspx), while the Caernarvon diversion is situated on the east bank of the Mississippi River in Plaquemines Parish, downstream of New Orleans (LDNR 2003). The Caernarvon diversion was opened in response to the DWH spill on 23 April 2010 and remained open through the first 2 wk of August at or near maximum capacity ($\sim 225 \text{ m}^3 \text{ s}^{-1}$; Fig. 1). Davis Pond remained open from 8 May through 10 September 2010, with flow ranging from 200 to $275 \text{ m}^3 \text{ s}^{-1}$.

Large-scale manipulation of hydrographic features is not a typical response to an oil spill; however, the scale of the DWH oil spill challenged conventional response activities both in the open ocean as well as in estuarine waters. Freshwater diversions are used to divert water from the Mississippi River to help enhance wetland vegetation and re-nourish marsh ecosystems (DeLaune et al. 2003). Normally, large quantities of freshwater are allowed to flow through the structures during the cooler winter and early spring months of each year because of potential impacts to oysters and other fisheries that would result from exposure to lower-salinity waters during the warmer summer months (Turner 2006, La Peyre et al. 2013, Rose et al. 2014). In 2010, these diversions remained opened for significantly longer and at a higher flow rate than in previous years.

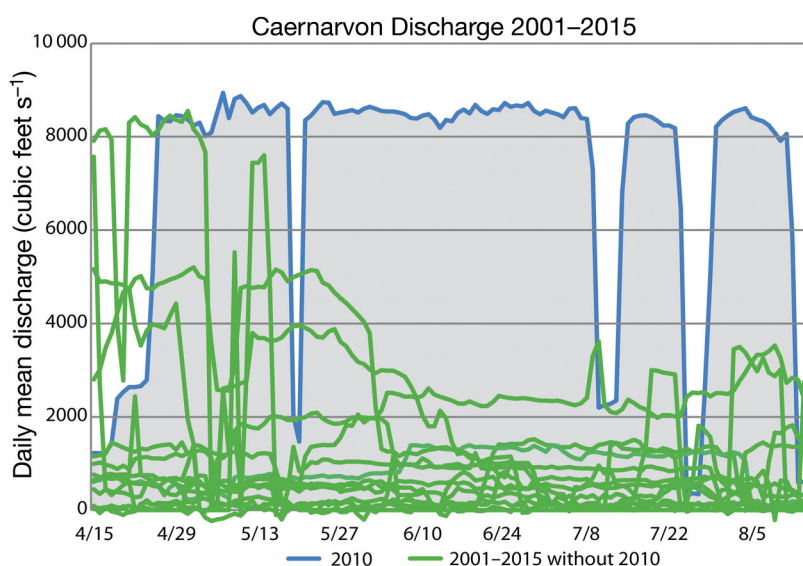


Fig. 1. Discharge of Mississippi River water from the Caernarvon freshwater discharge structure from 2001 to 2015. Dates are given as month/day; 1 cubic foot = 0.028 m^3

The introduction of substantial quantities of freshwater into an estuarine system, (e.g. due to a major storm event) would be expected to have substantive, albeit short-term (1–2 yr), consequences on oyster fishery resources in the 2 basins. In addition to their role in supporting a valuable US fishery, oysters are essential components of healthy estuarine ecosystems. Hence, changes in the abundance of oysters or the areal extent of oyster reef can have substantial ecological consequences. The suspension-feeding activity of oysters enhances benthic pelagic coupling and removes particulates from the water column, potentially increasing water clarity (see Coen et al. 2007 and Grabowski et al. 2012 for a complete list of ecological services). Reefs formed by the gregarious settlement of oysters provide ecological services including provision of habitat for fish and mobile invertebrates (Peterson et al. 2003), enhanced biogeochemical cycling (Piehler & Smyth 2011), and shoreline stabilization (Scyphers et al. 2011).

As part of the DWH oil spill natural resources damage assessment (DWH NRDA), we performed an extensive assessment of the potential impacts of the large-scale introduction of freshwater on oyster resources in coastal Louisiana. Because the diversions were open as part of the DWH oil spill response activities, damages resulting from the diversion openings would be a legitimate component of the damage assessment, and US federal regulations require the public to be compensated for the damages. We conducted a multi-pronged assessment of the impact of these freshwater diversions on subtidal oyster populations in the northern GoM. Multiple analyses using both state fisheries-independent data and data collected as part of the DWH NRDA showed substantial impacts of the freshwater diversion releases on oyster populations in Barataria Bay and Black Bay/Breton Sound.

MATERIALS AND METHODS

We estimated injury by comparing oyster density (abundance m^{-2}) in areas exposed to the 2010 Davis Pond and Caernarvon diversion openings against baseline oyster densities, where baseline is defined either as historical, pre-spill densities or as densities in post-spill areas unaffected by the diversions or other aspects of the DWH incident. We estimated injury in 2 basins: Barataria Bay basin to the west of the Mississippi River, which receives the outfall from the Davis Pond diversion, and Black Bay/Breton Sound basin to the east, which receives the outfall

from the Caernarvon diversion. We assessed differences in post-spill and baseline densities using multiple methods and datasets to test the robustness and bracket the uncertainty of our injury results. Specifically, we applied 3 approaches to quantify subtidal oyster injury. The first approach compared post-spill densities measured by the Louisiana Department of Wildlife and Fisheries (LDWF) to a pre-spill temporal baseline ('fisheries temporal'). The second approach ('NRDA spatial') employed a spatial definition of baseline conditions, based on modeled estimates of exposure to low salinities in each basin. It assessed oyster density differences between the area of maximal freshwater impact and baseline areas in these basins, using data collected as part of the DWH NRDA in 2010. The third approach ('Nestier tray/NRDA') defined injured and baseline locations using historical modeled salinity conditions and a dose-response model of freshwater impacts on mortality derived from analysis of annual Louisiana Nestier tray studies in the affected basins (Table 1).

Data sources

Louisiana fisheries-independent density data

We obtained oyster densities from diver-collected quadrat samples collected in June and/or July of each year from 2006 to 2010 from the LDWF annual oyster stock assessment program. The sampling program consisted of 8 sites in Barataria Bay and 32 sites in Black Bay/Breton Sound within known reef areas of the public oyster seed grounds (Fig. 2). From 2006 to 2009, site density was characterized using two 1.0 m^2 quadrats, except at cultch plant sites, where teams collected five 0.25 m^2 quadrats (LDWF 2006, 2007, 2008, 2009, 2010). All density results from 0.25 m^2 quadrats were scaled to 1.0 m^2 . Beginning in 2010, density was characterized using five 1.0 m^2 quadrats at all sites. Samples were collected in July of each year at approximately the same location, with LDWF teams randomly placing quadrats after poling at site coordinates to ensure sampling occurred on oyster habitat. We compiled LDWF density data into 3 size categories: spat (<25 mm), seed (25–75 mm), and market (>75 mm).

DWH NRDA density data

As part of the DWH NRDA efforts, oyster density data were collected from July to October 2010. Sam-

Table 1. Summary of injury calculation inputs for the 3 approaches used in this study. NRDA: natural resources damage assessment, LDWF: Louisiana Department of Wildlife and Fisheries

Method	Key data	Year(s) data collected	Baseline	Injury area	Injury calculation
Fisheries temporal	LDWF fisheries abundance data (oysters m ⁻²)	2006–2009, 2010	Based on historical data: avg. oyster densities 2006–2009	Area where oysters are likely to occur	Avg. difference between density in 2010 and historical-baseline × basin area
NRDA spatial	NRDA abundance data (oysters m ⁻²)	2010	Avg. densities of sites outside of freshwater polygon 2006–2009	FW polygons defined by areas with >30 additional consecutive days with salinity <5 ppt in 2010 compared to historical time periods	Survival difference between avg. density in vs. out of freshwater polygon
	Predicted salinity	2006–2009, 2010			
Nestier NRDA	Louisiana state Nestier tray dataset	2010	Back-calculated NRDA densities using calculated survival rates at NRDA site locations	Areas that indicated a decrease in survival in 2010 compared to historic periods based on the Nestier dose-response curve	Avg. survival difference × avg. baseline density
	Predicted salinity	2007–2009, 2010			
	NRDA densities (oysters m ⁻²)	2010			

pling consisted of up to 8 diver-collected quadrats at 200 m² study sites in Barataria Bay (8 sites) and Black Bay/Breton Sound (8 sites; Fig. 2). Because this study focused on subtidal oyster injury, sites where oyster habitat typical of nearshore or intertidal oysters was observed were excluded (<5%). The NRDA sample sites included some of the regularly sampled LDWF stock assessment sites plus additional Barataria Bay sites periodically sampled by LDWF. NRDA quadrat sampling locations were randomly generated from oyster habitat areas identified at these sites following side-scan sonar surveys of each site. Field teams used both 0.25 and 1.0 m² quadrats, with the larger size used where oyster habitat was less contiguous. Quadrat samples were enumerated by size class for spat-, seed-, and market-sized oysters using the same definitions applied to the LDWF data. Density results from 0.25 m² quadrats were scaled to estimate density per 1.0 m².

Louisiana Nestier tray data

We obtained data from annual oyster Nestier tray survival studies conducted by LDWF for the years 2007 to 2012. These studies measured the survival of oysters experiencing various salinity regimes. In January of each year, LDWF deployed 70 × 70 × 7.6 cm Nestier trays on the seafloor at a range of distances from the Davis Pond and Caernarvon freshwater diversion outfalls (Fig. 3). Each tray included 20 seed-sized (25–74 mm shell height) oysters collected from the basin where the tray was deployed. Oysters were affixed to the tray in a grid. After deployment, LDWF examined the oysters on each tray during monthly site visits and recorded data on individual oyster sta-

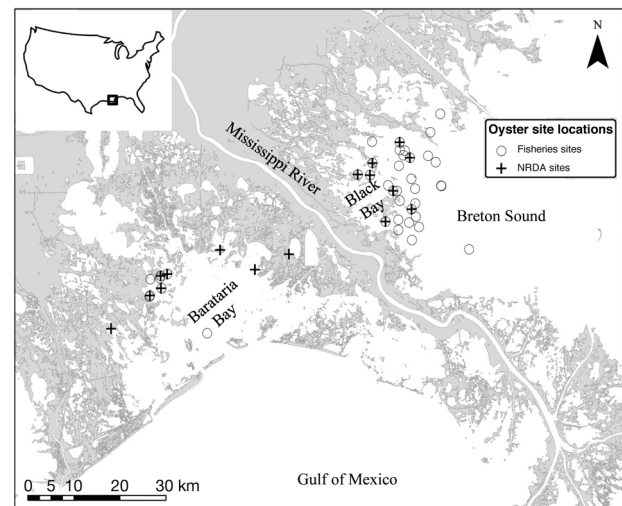


Fig. 2. Oyster sampling locations for the Louisiana Department of Wildlife and Fisheries (LDWF) fisheries data and the natural resources damage assessment (NRDA) studies

tus (alive, dead, or missing; the latter was excluded from our calculations), oyster growth, bottom salinity, and water temperature (P. Banks pers. comm.).

Predicted daily salinity

Daily average salinities and temperatures for 2006 through 2012 were estimated on a 200 × 200 m grid-cell basis using a spatio-temporal kriging model (Szpiro et al. 2009, Lindstrom et al. 2011) fit to an extensive database of water quality observations in Barataria Bay and Black Bay/Breton Sound (McDonald et al. 2015). The model employed both continuous (hourly or daily) monitoring data as well as discrete

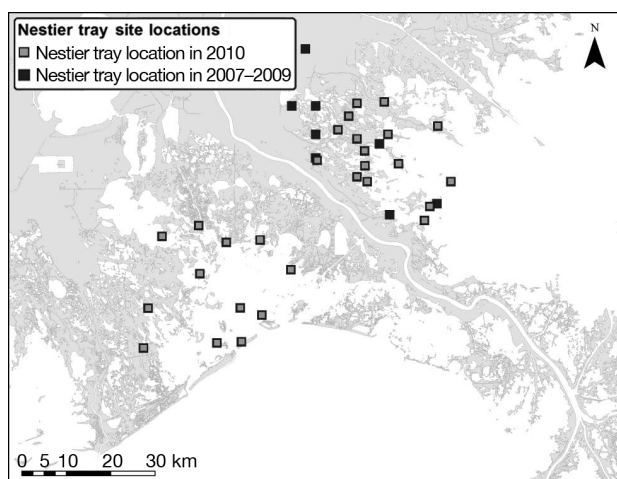


Fig. 3. Geographic extent of sites used in the Nestier tray/natural resources damage assessment (NRDA) approach. The majority of sites display 2010 (light grey) sample locations co-occurring with some 2007–2009 (black) sample locations. See Fig. 2 for further details

(sporadically collected) measurements of water quality from 2006 through 2010, including measurements recorded during DWH NRDA oyster sampling. The model included data collected by LDWF, Louisiana Coastal Protection and Restoration Authority, Louisiana Department of Health and Hospitals, Louisiana Department of Environmental Quality, Mississippi Department of Environmental Quality, and United States Geological Survey (Fig. 4).

Percent cover

Percent cover of oyster habitat was estimated for 2 strata within our study area (Fig. 5). One stratum covers 'known/likely oyster habitat,' which includes habitat previously mapped by Louisiana and habitat recommended by state biologists as highly likely to contain productive habitat based on historical harvest activity. The other represents 'possible oyster habitat,' where characteristics such as depth and salinity are sufficient to support oyster habitat, but where no *a priori* evidence of oyster habitat existed. Two sources provided percent cover estimates in the first stratum: 2010 LDWF side-scan sonar mapping in a portion of Black Bay/Breton Sound ('LDWF' stratum), and 2011 DWH NRDA oyster

habitat mapping using poling at randomly selected 200 m² sites in both Barataria Bay and Black Bay/Breton Sound (Roman & Stahl 2015). For areas in the possible oyster habitat stratum, percent cover estimates were generated from 2014 side scan sonar surveys conducted by DWH NRDA teams at randomly selected 200 m² sites within both basins. For this stratum, percent cover was further stratified based on the presence or absence of oyster leases in the mapping area. Louisiana has an extensive system of leasing sea floor bottom for cultivation of oysters. Lease holders often relay cultch material with oyster spat from high-salinity areas to lease areas for oyster grow out.

Injury calculation

The injury calculation approaches we employed require 4 basic steps: (1) establishing baseline conditions of oysters unaffected by the freshwater diversion openings; (2) identifying the areas exposed to freshwater from the 2010 diversion openings; (3) comparing post-spill densities against baseline densities; and (4) scaling spill-related density changes across all oyster habitat in the exposed areas (Table 1).

Fisheries temporal assessment

The fisheries temporal approach estimated oyster injury by comparing oyster densities in 2010 in

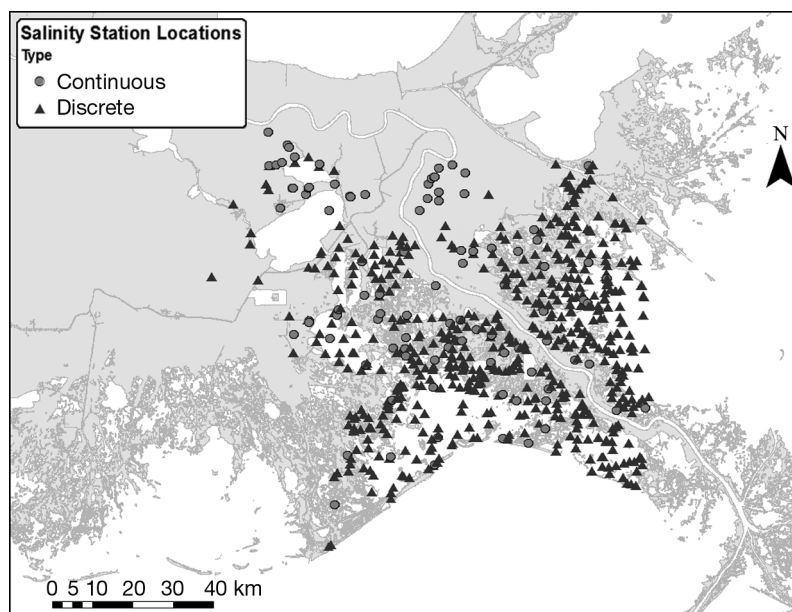


Fig. 4. Salinity sampling and monitoring stations in the study area. See Fig. 2 for further details

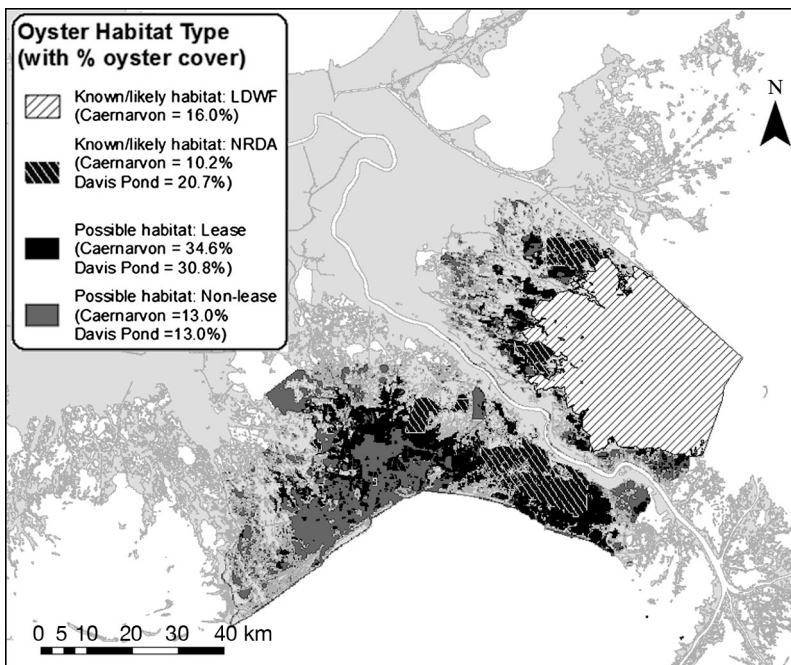


Fig. 5. Geographic extent of oyster strata and estimated reef percent cover.
See Fig. 2 for further details

the affected basins to historical (pre-spill) average baseline densities in those basins from 2006 through 2009. Both the 2010 and baseline oyster densities were derived from the LDWF fisheries independent annual monitoring data; the baseline starting year of 2006 was selected so that the baseline would accurately reflect oyster densities following Hurricane Katrina, which could have disrupted or relocated oyster habitat.

The baseline data set for each basin included average densities derived from individual measurements from all LDWF sites in that basin reporting density data in at least 2 of the pre-spill years (6 sites in Barataria Bay and 29 sites in Black Bay/Breton Sound). Differences in densities for spat-, seed-, and market-sized oysters were calculated for each basin separately, scaled to the corresponding injury area, and then summed. Oyster losses were scaled by first estimating the area of oyster habitat in m^2 in each basin and then multiplying that habitat area by the average density loss in oysters m^{-2} . The area of oyster habitat is estimated by multiplying the area of each sampling stratum shown in Fig. 5 by the corresponding percentage of area in that stratum covered by oyster habitat and then summing across strata. The general formula for this calculation was:

$$\text{Oyster loss} = (\text{Density}_{(2006-2009)} - \text{Density}_{2010}) \times \sum \text{Area}_{\text{stratum}} \times \% \text{cover}_{\text{stratum}} \quad (1)$$

This calculation was performed for each size class. We also calculated an overall number of 'market equivalent' oysters, by assuming 56% of the lost seed oysters and 30% of the lost spat would have survived to market size, based on mortality functions derived from data in Soniat et al. (2012, 2014) and Duke (2008). We then added those losses to the lost market oysters to obtain a total market equivalent oyster loss. As a lower bound on this type of analysis, we also estimated the fisheries temporal-based injury using only the fisheries-independent sites that fell within the low-salinity impact polygon described in the NRDA spatial assessment approach below.

NRDA spatial assessment

The NRDA spatial assessment approach delineated the exposed and baseline areas based on the modeled average daily salinity estimates described above. The injury was estimated by comparing densities observed during NRDA sampling events within and outside of the low-salinity exposure areas in each basin in 2010. Both baseline and injured area densities were measured as part of the DWH NRDA in 2010.

We used the results of the spatio-temporal salinity model to delineate polygons in both Barataria Bay and Black Bay/Breton Sound that describe areas of substantial freshwater impact in 2010 relative to historical conditions. Exposures were determined based on interpolated average daily salinities between 27 April and 15 September. This is when the freshwater from the diversions would have reached the study area, and is therefore considered the 'critical time' period. For each 200 m^2 grid cell in the salinity model, the maximum number of consecutive days below 5 ppt during the critical time period was calculated for each year between 2006 and 2010. Brief periods when average daily salinities were above 5 ppt for less than 3 d were ignored in the computation of maximum number of consecutive days; such events were not common in the data set. For each grid cell, the maximum number of consecutive days was averaged for the years 2006 to 2009 as the 'historical condition.' If the difference between the historical condition and the 2010 average was more than 30 d, the grid cell was considered affected. Thus, the

polygon of all affected grid cells represents the area with a significant increase in prolonged low-salinity exposure in 2010. The difference of 30 d was selected to maximize the difference between average salinities inside and outside the polygon in 2010, thereby representing the greatest low-salinity impact.

For each size class in 2010, we calculated the difference in oyster densities between areas inside (exposed) and outside (baseline) of the impact polygons described above. The seed-size oyster density in Barataria Bay was higher inside the freshwater-impact polygon than outside. This value was considered as 'no injury' and treated as a 0 in the subsequent injury analysis. Oyster loss was scaled by adjusting the injured area for percent cover of oyster habitat. We employed the following general equation:

$$\text{Oyster loss} = (\text{Density}_{\text{out}} - \text{Density}_{\text{in}}) \times \sum \text{Injured area}_{\text{stratum}} \times \% \text{ cover}_{\text{stratum}} \quad (2)$$

Seed and spat losses were scaled to market equivalents as described in the fisheries temporal approach and summed with the lost market oysters.

Nestier tray/NRDA assessment

Data from annual oyster Nestier tray studies conducted by LDWF were used to develop dose-response curves linking oyster survival with freshwater exposures during the months of April to September for Nestier tray locations in both Barataria Bay and Breton Sound basins. Doses were measured as the maximum number of consecutive days of salinity below 5 ppt over the April to September time period at each Nestier tray location. This was computed using the year-specific spatial-temporal model results for the grid cell closest to each Nestier tray location.

We limited dose-response modeling to Nestier tray sites with at least 50 % oyster survival as of the April status assessment in each given year to avoid including sites with high mortality due to factors other than summer freshwater exposure. In addition, 4 Barataria Bay Nestier sites classified as marine (~10 % of sites) were excluded, as these sites may have experienced increased mortality resulting from enhanced predation or increased disease due to their more saline waters (Gunter 1955). We developed dose-response curves for the period from 2007 through 2012, (excluding 2010), as well as for 2010 only. In the curve-fitting process, we set the dose-response

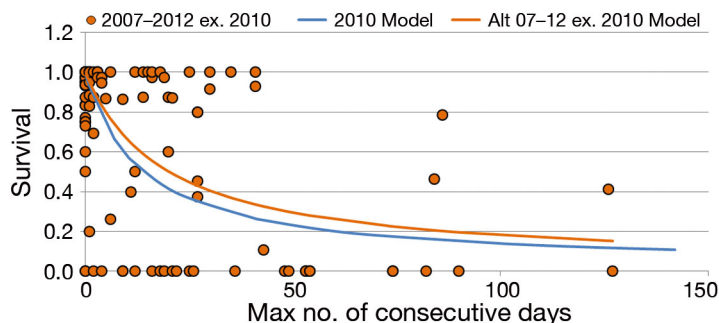


Fig. 6. Dose-response curve demonstrating the relationship between oyster survivorship and number of days below 5 ppt salinity. ex.: excluding

curves to 100 % survival at the 0 consecutive days of low salinity. We found little difference between the fitted dose-response curves developed for specific years; thus, our analysis uses the 2010 curves, since those represent relationships between salinity and survival in the year of interest (Fig. 6).

Using the 2010 dose-response curves and results from the salinity model, the decrease in the oyster survival rate in each 200 m² grid cell due to the 2010 freshwater diversion exposures was calculated as the difference between survival rate based on the maximum number of consecutive low-salinity days in 2010 and the survival rate based on the average historical (2006–2009) maximum of consecutive low-salinity days in the same cell. Grids with higher predicted survival in 2010 than prior years were assumed to have a 0 decrease in survival. Declines in the survival rate were then averaged across all grid cells within each basin and oyster habitat stratum.

Baseline oyster density values were derived from NRDA quadrat oyster density results collected in 2010. The survival difference (Δ Survival) for each NRDA quadrat location was calculated from the dose-response curves as described above. The pre-spill density values for each NRDA quadrat location were estimated using the following equation:

$$\text{Density}_{\text{pre-spill}} = \frac{\text{Density}_{2010}}{1 - \Delta \text{Survival}} \quad (3)$$

Baseline oyster densities were then computed as the average estimated pre-spill density per basin.

The number of oysters lost per m² was determined as the product of the average change in the survival rate in 2010, the area of oyster habitat experiencing decreases in survival in 2010, and the average baseline density estimated from the NRDA sites. We used the following general equation to calculate the oyster loss:

$$\text{Loss} = \Delta\text{Survival} \times \text{Density}_{\text{baseline}} \times \sum (\text{Impacted area}_{\text{stratum}} \times \% \text{ cover}_{\text{stratum}}) \quad (4)$$

Losses were estimated by size class and converted to market equivalent oysters in the same manner described above.

RESULTS

Salinity area of impact

Major changes in the hydrographic regime of both the Barataria and the Back Bay/Breton Sound basins were observed during the summer of 2010. The change in the number of consecutive days where mean salinity fell below 5 ppt was dramatic: on average, locations in the study area averaged 20.3 additional consecutive days of very low salinity (<5 ppt)

in 2010, compared to average historical values, with a maximum of 138 d. The vast majority of the meso-haline areas of both basins experienced extended periods (>30 d) of salinity <5 ppt. The extent of the area of freshwater impact, defined as areas experiencing more than 30 consecutive days of salinities <5 ppt in 2010 when compared to historical baseline salinities, covered 483 km² in Barataria Bay and 362 km² in Black Bay/Breton Sound. When exposure is measured in terms of total days <5 ppt (i.e. not necessarily consecutive), the area of influence expands to 528 km² in Barataria and 424 km² in Black Bay/Breton Sound.

Oyster losses

All 3 approaches to estimating oyster injury found substantial losses of oyster populations in the sub-

Table 2. Affected area, reef percent cover, and oyster densities by approach and basin. FW: freshwater, FID: fisheries-independent data, OH: oyster habitat, LDWF: Louisiana Department of Wildlife and Fisheries, NRDA: natural resources damage assessment

Quantification approach (5 ppt threshold)	Basin	Stratum	Affected area (km ²)	% oyster cover	Baseline density (oysters m ⁻²)			Post-spill density (oysters m ⁻²)			Decrease in density due to FW impact (oysters m ⁻²)		
					Spat	Seed	Market	Spat	Seed	Market	Spat	Seed	Market
Nestier tray	Black Bay/ Breton Sound	Known/likely OH	44.4	10	0	17.0	8.8	0	11.8	6.1	0	5.2	2.7
		Possible OH (lease)	90.3	35				0	13.2	6.9	0	3.8	2.0
		Possible OH (non-lease)	94.8	13				0	14.3	7.4	0	2.7	1.4
		LDWF	361.4	31				0	13.9	7.2	0	3.1	1.6
		Outside OH	108.8	0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
	Barataria Bay	Known/likely OH	184.0	21	5.8	41.7	32.0	4.8	34.7	26.7	1.0	7.0	5.4
		Possible OH (lease)	302.9	31				4.4	32.0	24.5	1.4	9.8	7.5
		Possible OH (non-lease)	279.6	13				4.4	31.4	24.1	1.4	10.3	7.9
		Outside OH	659.1	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
FID	Black Bay/ Breton Sound	Known/likely OH	75.2	10	9.9	8.8	1.5	0.4	1.7	0.3	9.5	7.0	1.2
		Possible OH (lease)	107.6	35									
		Possible OH (non-lease)	135.4	13									
		LDWF	953.1	16									
	Barataria Bay	Known/likely OH	189.6	21	7.9	11.4	1.4	1.0	2.4	2.0	6.9	9.0	-0.6
		Possible OH (lease)	363.6	31									
		Possible OH (non-lease)	547.6	13									
NRDA	Black Bay/ Breton Sound	Known/likely OH	31.4	10	0	19.8	9.5	0.0	3.7	3.1	0.0	16.1	6.4
		Possible OH (lease)	81.0	35									
		Possible OH (non-lease)	76.7	13									
		LDWF	91.3	25									
		Outside OH	81.2	0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Barataria Bay	Known/likely OH	16.4	21	5.7	27.0	24.3	3.2	31.2	20.6	2.5	0 ^a	3.7
		Possible OH (lease)	78.3	31									
		Possible OH (non-lease)	104.5	13									
		Outside OH	284.0	0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

^aThe seed-size oyster density in Barataria Bay increased, according to the NRDA sample data. This value was considered as 'no injury' and treated as a 0 in the injury analysis

Table 3. Estimates of oysters killed as a result of lowered salinities during summer of 2010 by approach and oyster size class. NRDA: natural resources damage assessment, FW: freshwater

Consecutive days approach	FW	Oyster losses in 2010 (10^6 oysters)				
		Market + seed	Market	Seed	Spat	Market equivalent
Fisheries temporal assessment	—	3642	130	3512	3573	3169
NRDA spatial assessment	5 ppt	1431	560	1025	101	1164
Fisheries in freshwater polygon	5 ppt	1164	142	1022	1389	1131
Nestier tray/NRDA	5 ppt	3543	1465	2078	216	2694

tidal freshwater impact zone in 2010 (Tables 2 & 3). The simplest approach, fisheries temporal, demonstrated a substantial decline in oysters in 2010 compared to pre-spill years. Compared to baseline values derived from the measured average densities in summer quadrat surveys from 2006 to 2009, oyster densities decreased in 2010 by 70 % (market) to 100 % (seed and spat) in Black Bay/Breton Sound (Table 2). Similar density declines were seen for spat and seed in Barataria Bay; however, market-sized oysters increased slightly ($+0.6$ oyster m^{-2}). These changes in density over the large area of likely oyster habitat (mapped reefs, lease areas, and non-lease areas outside mapped resource) in Barataria Bay (1101 km^2) and Black Bay (1271 km^2) resulted in the loss of an estimated 3.2×10^9 market equivalent oysters (Table 3), where market equivalent oysters are the sum of market-sized oysters lost plus the lost spat and seed that would be expected to survive to market size over the next 1 or 2 yr. Restricting our extrapolation of injury to the portions of the 2 basins that lie within

the 5 ppt injury polygons resulted in smaller injured areas (483 km^2 for Barataria Bay and 362 km^2 for Black Bay/Breton Sound). The resulting lower bound injury estimate in market equivalent oysters was 1.1×10^9 market equivalent oysters (see 'Fisheries in freshwater polygon' in Table 3).

The results for the NRDA spatial approach reflect the oyster abundance differences between NRDA sampling sites located inside and outside the modeled freshwater impact polygons (Fig. 7). Overall, they show an extensive decline in oyster populations across all size classes and in both assessed basins. Within these polygons, densities of seed and market-sized oysters decreased in Black Bay/Breton Sound, and densities of spat and market-sized oysters decreased in Barataria Bay (Table 2). The decline extended over a large area of likely oyster habitat in Black Bay/Breton Sound (280 km^2) and Barataria Bay (199 km^2) and resulted in a total market equivalent loss of 1.19×10^9 oysters across the freshwater impacted areas. Spat densities remained unchanged in

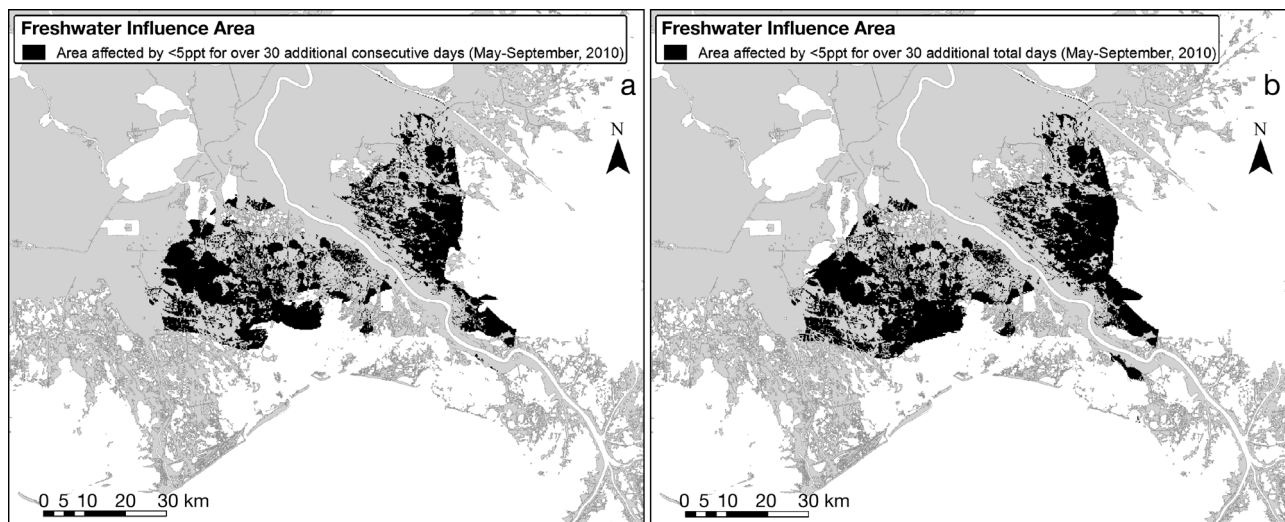


Fig. 7. Areas experiencing more than 30 additional days of salinities <5 ppt from May to September 2010, compared to the average number of days <5 ppt over the same period between 2006 and 2009. Areas of maximum freshwater influence estimated using (a) consecutive days of salinity <5 ppt and (b) total days of salinity <5 ppt

Black Bay/Breton Sound (0 m^{-2}). Seed densities increased slightly in Barataria Bay (Table 2). This small increase was considered as a case of 'no injury' and treated as a 0 in our injury calculations.

The Nestier tray/NRDA method also showed clear declines in oysters across all size classes. Predicted post-spill densities were lower for each size class (except oyster spat in Black Bay/Breton Sound, which were 0 before and after). The largest losses were seen in seed-sized oysters in both basins (Table 2), although decreases in market-sized individuals were also notable. These density declines would be expected to occur across large areas in Barataria Bay (766 km^2) and Black Bay/Breton Sound (591 km^2) based on the 5 ppt freshwater injury polygon. Unlike the previous injury estimates, we were able to create more spatially explicit injury estimates in each of the known and likely oyster habitats by predicting survival based on estimated salinities in each 200 m^2 grid. This approach yielded a loss of 2.78×10^9 market equivalent oysters.

DISCUSSION

Nearshore ecosystems often act as repositories for contaminants released into the open ocean and rivers. Key to mitigating the ecosystem damage caused by the deposition of oil and other contaminants is often a swift response. In many cases, post-spill assessments of injury have indicated large impacts from the response activities (e.g. high pressure washing of the rocky intertidal during the 'Exxon Valdez' oil spill cleanup, see Driskell et al. 2001). The geographic extent (1000s of km of potentially impacted beaches and marshes) and duration (87 d of oil release) of the DWH oil spill necessitated unprecedented response and clean-up activities. The responses included the widespread uses of vast quantities of dispersants at sea, digging and disposing of beach sands, burning of oil at sea and in the marsh, extensive flushing of marshes with estuarine water, and a host of novel large-scale manipulations of hydrography and geomorphology (Martínez et al. 2012, Park et al. 2014). The large-scale introduction of freshwater from diversion structures is a novel approach to mitigation and one that our analysis suggests should be more thoroughly examined for future oil spills.

All 3 estimates of injury indicated substantial losses (over 1 billion market equivalent-sized oysters) resulting from the late spring/summer release of large quantities of freshwater from diversion structures in

2010. Loss of oysters from the release of freshwater and consequent decreases in salinity is not a new phenomenon; extensive literature has documented negative impacts of low salinities on oysters (Chatry et al. 1983, Melancon et al. 1998, Turner 2006, La Peyre et al. 2009, Soniat et al. 2013). The extent of the loss in 2010, however, was highly unusual in its magnitude, which is a direct result of the release of high volumes of freshwater at a time of high water temperatures (La Peyre et al. 2013) and the need to keep the structures open for such a long time given the unexpectedly long duration of the spill event.

Vast areas of both basins experienced prolonged low salinity that would be expected to affect oyster survival. Our comparison of the 2010 salinity data to the baseline period of 2006–2009 demonstrated a vast spatial extent (100s of km^2) of unusually low-salinity waters resulting from the diversion discharges. The injury polygon used for the NRDA spatial analysis defined the area that would lead to loss of oysters due to salinities <5 ppt for more than 30 consecutive days. This level is consistent with literature findings that extended periods of low salinities result in extensive high oyster mortality. In our study, this threshold is also supported by the extensive Nestier tray data collected by the State of Louisiana.

Although we chose a threshold of 5 ppt for consecutive days, most of the oligohaline and mesohaline areas were near 1–3 ppt for the vast majority of the summer as a result of the continuous high discharge from the diversion structures. Our results are likely conservative because our decision to estimate exposure based on consecutive days of low salinity likely underestimates the full area impacted by decreased salinities in 2010 versus the historical baseline. The areas in the total days polygons are somewhat larger and hence would give a larger injury estimate.

Of the 3 approaches used, the fisheries temporal method is the simplest. This approach compared the average of baseline densities (2006–2009) to the average after the spill in 2010 at fixed stations. Changes in density were assumed to be a result of the unique conditions in 2010. This approach yielded the highest injury estimate of 3.2×10^9 market equivalent oysters lost. The before/after aspect of this analysis is used in many types of environmental assessment (see Schmitt & Osenberg 1996) and controls for spatial variability by holding sites fixed over time. The limitation of the design is the lack of control or reference areas to contrast to the area of impact. Restricting the fisheries temporal approach to the area within the 5 ppt freshwater impact area decreased the injury estimate by over 60% (3.2 vs.

1.1×10^9 market equivalent oysters). This substantial decrease in the injury estimate probably represents a separation of the zone of complete mortality from extreme low salinity from areas that were more marginally impacted. Evidence for this is the overall increase in market size oysters in Barataria Bay. Closer inspection of the site pattern revealed some locations where larger oysters were seemingly unaffected by the extreme low-salinity areas. Such areas may have experienced periodic refuges of salt water because of their closer proximity to inlets or deep-water channels.

Our second approach to injury assessment, the NRDA spatial analysis, benefits from a design that delineates reference and impact sites in the same year. Sampling areas inside the polygon experiencing 5 ppt for >30 consecutive days served as the impact sites and those outside the polygon (but within the affected basins) served as our references, allowing us to control for basin-wide effects in 2010. Decreases in densities were evident in all size classes of oysters, with the exception of seed-size oysters in Barataria Bay. Applying the change in density over the area of our impact polygon resulted in an injury estimate of 1.2×10^9 market equivalent oysters lost. The magnitude of this estimate agrees with the fisheries temporal approach when restricted only to the 5 ppt exposure polygon. Despite differences in site selection criteria between the LDWF sampling, which serve as the basis for the fisheries temporal assessment, and the NRDA sampling, both sampling protocols used diver-collected quadrats, which likely increases the compatibility of the comparison between studies. The strength of the before/after contrast with the fisheries temporal assessment coupled with the impact/control nature of the NRDA spatial design results in a relatively robust assessment that produces remarkably similar injury estimates and serves as validation for what we conclude is the minimum injury estimate owing to the freshwater-diversion response actions.

The fisheries temporal and the NRDA spatial assessment injury approaches both have limited spatial resolution; the change in oyster density is applied to the entire injury domain. Although both estimates adjust the injury to account for differences in percent cover of oysters in the different strata (mapped oyster reef, leased areas, likely oyster habitat), a universal delta density is applied to all strata. The Nestier tray/NRDA approach offers a spatially explicit injury estimate by using stratum-specific density changes as well as stratum-specific oyster percent cover estimates. The approach also uses the dose-response

curve generated from the LDWF Nestier tray study to predict pre-spill oyster densities.

While the results of the different approaches to estimating injury are consistent in direction and rough magnitude, uncertainty exists in all 3 approaches and confidence intervals over the different approaches. We believe that the range 1.1 to 3.2 billion oysters lost encompasses the range of uncertainty due to measurement and procedural errors. The estimate of 2.7×10^9 oysters from the Nestier tray injury approach is likely the most rigorous of our estimates because of its spatially explicit nature and its use of a detailed exposure-response relationship based on studies of freshwater impacts on oysters in the same basins where the injury occurred.

The design of the NRDA subtidal oyster studies was intended to evaluate abundance of oysters throughout the area where oil was observed on shorelines and surface waters. While toxicity studies have demonstrated that exposure to oil in water from the DWH spill could also have potentially harmed oysters, confirmation of such exposure is limited. In addition, in statistical analyses attempting to relate oyster densities to NRDA-collected data on oiling (measured in terms of co-located sediment tPAH) and oil-on-water (days, frequencies, and presence/absence), distance to heavily oiled shorelines did not support a discernable association between exposure to oil and subtidal oyster densities.

Besides oil and freshwater, several other factors known to affect oyster populations were examined during our study and were found not to offer compelling alternative explanations for the overall oyster decline observed across these 3 analyses. Competing hypotheses such as harvest pressure would not apply to 2010, since oysters were not harvested in the 2 basins as a result of public health concerns following the oil spill. Both the prevalence and severity of oyster disease (dermo) and oyster predators (such as oyster drills *Thais haemostoma*) would be expected to be substantively reduced by the reduction in salinities; furthermore, extensive NRDA oyster sampling and disease analysis in 2010 and 2011 showed very low prevalence of infection throughout our study area (<2 on a scale of 1 to 5, where scores of 3 indicate mortality potential). Temperature was typically either constant over the period of interest or exhibited a very slight decline and contributed minimally to variation within and outside of areas of freshwater exposure; thus it is unlikely to confound our results. In addition, precipitation in 2010 did not appear to be abnormal, based on an analysis of records from the US Historical Climatology Network daily dataset; potential impacts

from drought or from excessive rainfall lowering salinities in these basins are therefore unlikely.

Using a series of methods and multiple data sets, progressing from the simplest to more sophisticated approaches, we consistently found that post-spill densities were lower than both temporal and spatial baseline comparison density estimates. Results were robust to data sets and changes in approach. We are confident that the freshwater exposures from Louisiana diversions in 2010 produced substantial, widespread oyster mortality in both Barataria Bay and Black Bay/Breton Sound basins. Discharge records show an atypical pattern and unusually high magnitude of freshwater flow from Davis Pond and Caernarvon diversions in the late spring and summer 2010. The efficacy of releasing large quantities of freshwater in response to the approach of oil from offshore should be carefully examined given the injury to oysters that we documented in this study. Such an analysis should be holistic at the ecosystem level and include responses of other organisms and habitats within the estuary.

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