

## Fish Assemblages in Louisiana Salt Marshes: Effects of the Macondo Oil Spill

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**Abstract** Marsh-resident fishes play important roles as both predators and prey in coastal systems, influence secondary production, and are important trophic links to adjacent coastal waters. As such, they also serve as sentinel species in efforts to understand the magnitude and

implications of anthropogenic habitat disturbance or degradation. An evaluation of the juvenile and adult marsh fish response to the Macondo oil spill in 2010 was conducted in 2012 and 2013 by sampling in both oiled and unoiled marshes in coastal Louisiana. To complement this analysis, we also examined marsh-fish assemblage structure across several subhabitats (marsh edge, creeks, ponds, depressions). The fauna, collected with traps, was dominated by cyprinodontiform fishes (*Fundulus grandis*, *Fundulus xenicus*) and complemented by others in this group (*Cyprinodon variegatus*, *Poecilia latipinna*, *Fundulus pulvereus*, *Fundulus jenkinsi*, *Fundulus similis*). Among the dominant species, abundance was often the highest in ponds and marsh surface depressions, with many fish species also commonly found in creeks, but few fish were collected along the marsh edge. Comparisons across representative oiled and unoiled sites from Caminada, Terrebonne, and Barataria Bays did not reflect any consistent differences in species composition, abundance, and size as a function of oiling 2–3 years after the oil spill reached Louisiana marshes. This interpretation may be confounded by multiple stressors, including natural events (e.g., oil redistribution by storms, and seasonal flooding of the marsh surface), and other man-made perturbations (e.g., freshwater discharge).

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### Introduction

Salt marshes in Louisiana are exposed to multiple stressors including marsh loss due to reduced sedimentation and increased subsidence (Reed 1989), sea level rise (Britsch and Dunbar 1993; Sasser et al. 1986; Boesch et al. 1994;

Couvillion and Beck 2013), hurricanes (Brock et al. 2013; Palaseanu-Lovejoy et al. 2013), and manipulations such as freshwater diversions (Chesney et al. 2000). The fate and effect of oil development and pollution on these marshes have received frequent attention in the literature (DeLaune et al. 1990; Smith et al. 1984; Mendelssohn et al. 1993; Ko and Day 2004; Roth and Baltz 2009; May 1977). The most recent event, and the one with perhaps the greatest potential to impact coastal marshes, was the Macondo oil spill in 2010. This spill resulted in the accumulation of crude oil on an estimated 15.6 % of Louisiana's marsh shoreline (Turner et al. 2014a) and a total of 1,773 km of shoreline along the Gulf of Mexico (Michel et al. 2013; Turner et al. 2014b). The earliest interpretations suggest that marsh shoreline erosion was enhanced (McClenachan et al. 2013) and that resident insects and other invertebrate populations were suppressed (McCall and Pennings 2012) or had slower growth (Rozas et al. 2014) in the immediate aftermath (<12 months) of the spill. Some evidence, however, suggests that these marshes and marsh residents are resilient to oil pollution and can recover from spill effects (Roth and Baltz 2009; DeLaune and Wright 2011; Silliman et al. 2012).

An evaluation of the marsh fish response is especially important because they are central to marsh systems as both predators and prey and thus influence secondary production (Hagan et al. 2007) and trophic transfers within marshes and adjacent estuaries (Subrahmanyam and Drake 1975; Tupper and Able 2000; Nemerson and Able 2004), including in Louisiana (Mendelssohn et al. 2012). Despite this qualitative understanding of the importance of these fishes, their role in Louisiana marshes remains poorly described at more quantitative levels. The exceptions are studies of food habits (Rozas and LaSalle 1990) and habitat use (Baltz et al. 1993; Rozas and Reed 1993; Peterson and Turner 1994) for the dominant Gulf killifish (*Fundulus grandis*). Specific studies that focused on the Macondo oil spill effects on this species have indicated that the genomics, physiology, and development were negatively impacted (Whitehead et al. 2012; Dubansky et al. 2013; Crowe et al. 2014).

Our objectives were to (1) determine the species composition, habitat use patterns (among marsh edge, marsh creek, marsh pond, and marsh surface depression), and size composition of the dominant salt marsh surface fishes at multiple locations in Caminada, Barataria, and Terrebonne Bays (Fig. 1) with a special emphasis on *F. grandis* and other cyprinodontiform fishes because of their potential as sentinel species (Vivian et al. 2012; Burnett et al. 2007); and (2) provide an initial analysis of the marsh fish assemblage response to the Macondo oil spill at oiled and unoiled sites.

## Methods and Materials

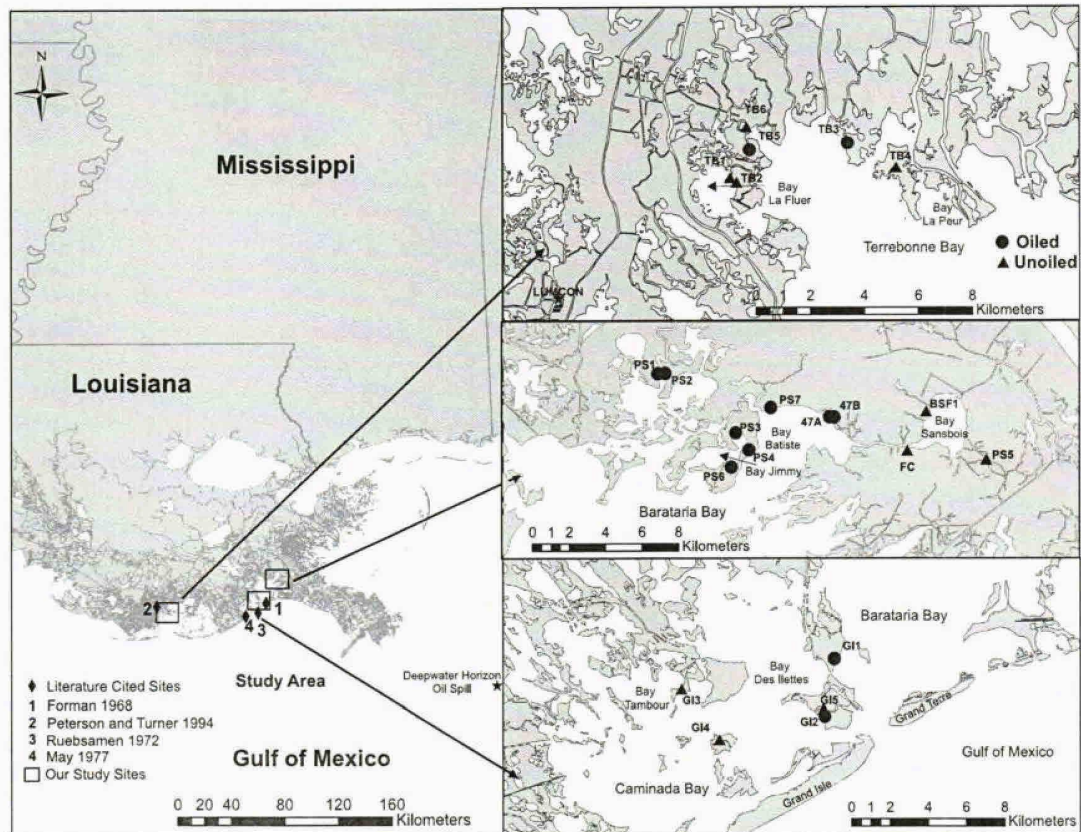
### Study Sites

The study sites span a range of 90 km along the LA coast including most of the Terrebonne and Barataria Bay systems (which have among the highest surface areas of wetland and open water habitats of any estuaries along the US Gulf Coast [Turner 2001]). The study sites also span most of the region between the Mississippi and Atchafalaya Rivers, which are the main conduits of water, sediments, and nutrients to Louisiana marshes. The Caminada, Barataria, and Terrebonne Bays that comprise the specific study sites are part of the Mississippi River Deltaic Plain (Baumann 1980, 1987; Deegan and Thompson 1985). Regionally, salt marshes are dominated by *Spartina alterniflora* with smaller contributions from *Distichlis spicata*, *Juncus roemerianus*, *Spartina patens*, and *Avicennia germinans* (Baumann 1980; Visser et al. 1998). Many of the marshes in the study area have a characteristic profile from a creek or bay edge with a natural levee of denser, taller vegetation on the marsh edge and sparser, shorter vegetation in the interior marsh with occasional ponds or marsh surface depressions as depicted in Peterson and Turner (1994). The distribution of the vegetation, sediments, fishes, and other mobile organisms is greatly influenced by the frequency and duration of flooding (Baumann 1980, 1987). Diurnal tides in Louisiana salt marshes have an average amplitude of 0.3 m, resulting in a low frequency of marsh inundation. Although these astronomical tides are important, the frequency and intensity of marsh flooding in coastal marshes are significantly affected by wind and larger-scale meteorological forcing. Seasonal flooding, as forced by dominant wind patterns, is frequently bimodal with peaks in spring and fall and with lowest water levels in the winter and summer (Baumann 1980, 1987; Turner 1991; Rozas 1995). Climatological forcing can also influence marsh flooding (Childers et al. 1990).

The selection of oiled and unoiled sites was based on a comparative survey (Shoreline Cleanup Assessment Technique [SCAT]) (Michel et al. 2013; Rozas et al. 2014) before the oil reached the marshes (early May 2010) and after the marshes were oiled in May–June 2010 (Whitehead et al. 2012; Lin and Mendelssohn 2012; Turner et al. 2014a) and characterized as oiled (presumably Macondo oil) or unoiled (Table 1).

### Fish Sampling Locations and Techniques

We sampled oiled and unoiled sites in Caminada, Terrebonne, and Barataria Bays with an emphasis on four marsh subhabitats during multiple 3-day sampling events: June 2012 (13 sites), May 2013 (17 sites), and October 2013 (12 sites) (Fig. 1 and Table 1). At each site, we collected fishes with baited (dry dog food) wire mesh traps (41 cm long, 22 cm



**Fig. 1** Study areas in Terrebonne, Caminada, and Barataria Bays in Louisiana with specific locations of oiled and un-oiled sites indicated in Table 1. Designations are based on SCAT categories. Other locations used for comparison are also indicated by *closed symbols*

wide with 3-mm mesh) with the openings of all traps standardized to a 3-cm diameter with a plastic cylinder. Subhabitats included marsh edge (marsh adjacent to open water), creeks (embedded within marshes), ponds (discrete bodies of water within the marsh surface), and depressions (on the marsh surface without discrete boundaries, typically shallower than ponds). Prior to comparisons of oiled and un-oiled marshes, we evaluated trap deployment duration (1 vs 24 h) effects on fish species composition and abundance (catch per unit effort [CPUE] and/or total) at two un-oiled marsh islands (0.2 km apart) at the Louisiana Universities Marine Consortium (LUMCON) (Fig. 1 and Table 1) between late June and early July, 2012. After retrieval, the individual traps were emptied and the contents placed in plastic bags on ice until they could be frozen at the end of each day. Sampling intensity at these sites varied as a function of availability of selected subhabitats at some locations and low water levels, which prevented fish from reaching the marsh surface on some dates and locations. Temperature and salinity at each site were measured with a portable Hach HQ40d meter (Hach Company, Colorado) (Table 1).

In the laboratory, samples were thawed and identified using meristics (Boschung and Mayden 2004; McEachran and

Fechhelm 1998; Lang et al. 2011). More specifically, we recognize the Louisiana populations as *Fundulus similis* (not *Fundulus majalis*), *Fundulus pulvereus* (not *Fundulus confluentus*), and *Adinia xenica* as *Fundulus xenicus* (Ghedotti and Davis 2013). Once identified, each individual fish was measured and total length was recorded to the nearest millimeter (mm TL).

#### Data Analysis

Comparisons of fish abundance (cyprinodontiforms only) at un-oiled and oiled sites in Caminada, Terrebonne, and Barataria Bays were based on average catch for the three or four traps deployed at each subhabitat type during each set. Data were summarized as mean  $\pm$  standard error of the mean (SEM). Mean catch per unit effort (CPUE; fish per trap per hour soak) values between un-oiled and oiled (light, moderate, or heavy oiling based on SCAT surveys; Table 1) sites and different subhabitats were compared using Kruskal-Wallis (rank sum) tests. This non-parametric method (normal distribution not assumed) was employed because the number of zero values in the data sets skewed the distributions. Fish sizes were compared using Kruskal-Wallis tests. In a further attempt

**Table 1** Description of sampling sites in Terrebonne, Caminada, and Barataria Bays in Louisiana in June 2012 and May and October 2013

Site	Sampling event	Degree of oiling (SCAT category)	Vegetation	Salinity range	Temperature range (°C)	Subhabitats
<b>Terrebonne Bay</b>						
LUMCON A and B	Jun-Jul 2012	No oil	S.a., J.r.	14.0–17.6	26.0–35.2	E, C, P, D
TB-1	Jun 2012, May 2013, Oct 2013	No oil	S.a., J.r.	9.4–16.4	25.0–30.8	E, C, P, D
TB-2	Jun 2012, May 2013	No oil	S.a., J.r.	10.0–18.2	24.0–27.9	E, C, P, D
TB-3	Jun 2012	Light/moderate	S.a., J.r.	20.0–22.0	26.0–26.6	E, C, P, D
TB-4	Jun 2012	No oil	S.a.	20.6–21.9	29.4–30.6	E, C, P, D
TB-5	May 2013, Oct 2013	Light	S.a.	9.7–13.1	26.3–30.6	E, C, P, D
TB-6	May 2013, Oct 2013	No oil	S.a.	10.1–12.6	27.2–30.6	E, C, P, D
<b>Caminada Bay</b>						
GI-1	Jun 2012, May 2013, Oct 2013	Moderate	S.a.	17.5–23.1	26.1–31.9	E, C, P, D
GI-2	Jun 2012, May 2013, Oct 2013	Light/moderate	S.a.	18.0–25.4	24.7–30.8	E, C, P
GI-3	Jun 2012, May 2013, Oct 2013	No oil	S.a., A.g., P.v.	12.9–23.6	27.5–28.7	E, C, P, D
GI-4	Jun 2012, May 2013, Oct 2013	No oil	S.a., A.g., P.v.	8.1–19.0	27.9–30.0	E, C, P, D
GI-5	Jun 2012, May 2013, Oct 2013	No oil	S.a., A.g., P.v.	18.0–25.0	25.0–32.3	E, C, P, D
<b>Barataria Bay</b>						
PS-1	Jun 2012	Light/moderate	S.a., J.r.	8.2	30.1	E, C, P
PS-2	Jun 2012	Light	S.a., J.r.	7.2	29.1	E, C, P
PS-3	Jun 2012, May 2013, Oct 2013	Light/heavy	S.a., J.r.	7.6–11.0	26.8–30.0	E, C, P, D
PS-4	Jun 2012	Moderate/heavy	S.a., J.r.	10	30	E, C, P, D
PS-5	May 2013, Oct 2013	No oil	S.a., J.r.	11.1–11.3	28.2–28.8	E, C, P, D
PS-6	May 2013, Oct 2013	Heavy	S.a., J.r., D.s.	10.4–13.7	25.8–27.0	E, C, P, D
PS-7	May 2013, Oct 2013	Heavy	S.a., J.r.	8.2–11.3	28.8–29.8	E, P, D
FC <sup>a</sup>	May 2013	No oil	na	9.1	28.0	E, C, D
BS-F1	May 2013	No oil	na	na	na	E, C, P, D
47A	May 2013	Moderate	na	8.3	30.2	E, C, D
47B <sup>a</sup>	May 2013	Moderate	na	8.4	30.9	E, C, D

The far right column indicates the subhabitats sampled at each site. Subhabitats include edge (E), creek (C), pond (P), and depression (D). Degree of oiling is based on the Shoreline Cleanup Assessment Technique (SCAT) from the Deepwater Gulf Response to the Macondo oil spill. Sites with light, moderate, or heavy oil were defined as “oiled” for statistical analyses. Vegetation types: S.a. = *Spartina alterniflora*, J.r. = *Juncus roemerianus*, D.s. = *Distichlis spicata*, A.g. = *Avicennia germinans*, P.v. = *Philoxyeris vermicularis*

na not available

<sup>a</sup> FC and 47B are overnight (16 h) samples and were not included in comparisons of habitat use

to place our sampling in perspective, we have summarized other fish sampling efforts in Louisiana that have focused on, or been appropriate for, sampling cyprinodontiform fishes in marshes (Fig. 1 and Table 2).

We used Primer v6 software to determine the extent to which habitat type and oiling influenced assemblage structure (Clarke 1993). Only species occurring in >10 % of samples were included in our analyses (Rozas et al. 2013). All data were log ( $x+1$ ) transformed and analyzed using the non-parametric two-way analysis of similarity (ANOSIM, Bray-Curtis similarity index) procedure. Each factor was graphically displayed using a non-metric multidimensional scaling plot to visually interpret patterns in assemblage composition. The similarity percentages (SIMPER) technique was then used to

determine which individual species varied in their contribution to the Bray-Curtis index.

We also evaluated the impact of trap deployment time by comparing catch rates of the most abundant species from 1- and 24-h sets at two sites on two dates (June and July 2012) at LUMCON (sites A and B) (Fig. 1) across the main subhabitat types (marsh edge, creek, pond, and depression) based on two traps per subhabitat. Differences among three treatments (subhabitats: creek, pond, and depression) and deployment times (1 vs 24 h) were analyzed using a nested analysis of variance (ANOVA; treatments were SUBHABITAT and sampling EVENT within each SUBHABITAT). The marsh edge subhabitat was dropped from the analysis because <1 % of the fish were collected within this habitat type (see the Results

**Table 2** Species composition of cyprinodontiform fishes in Louisiana salt marshes from this study and earlier studies, including two unpublished theses

Sampling Location	Percent species composition								Habitat sampled	Number of fish	Gear sampling	Source
	F.g.	F.x.	C.v.	F.p.	P.l.	L.p.	F.j.	F.s.				
LUMCON 24 h	55.8	12.9	1.4	7.1	22.6	0	0	0.1	E, C, P, D	3,061	Trap	This study
LUMCON 1 h	55.5	31.0	1.2	2.0	9.6	0	0.8	0	E, C, P, D	607	Trap	This study
Terrebonne Bay	57.9	36.8	2.0	0.7	0.6	0	0	1.9	E, C, P, D	687	Trap	This study
Caminada Bay	71.3	18.3	2.1	0	1.1	0	0	7.1	E, C, P, D	2,073	Trap	This study
Barataria Bay	11.5	31.8	25.2	3.9	27.3	0	0	0.3	E, C, P, D	2,733	Trap	This study
LUMCON area	33.7	22.9	5.9	17.1	8.6	6.7	5.2	0	Marsh surface	1,968	Flume	Peterson and Turner (1994)
LUMCON area	51.6	–	–	–	0.3	40.3	7.7	0	Edge	310	Seine	Peterson and Turner (1994)
Bayou Thunder	9.4	19.6	59.2	1.4	8.5	1.2	–	0.6	Pools	24,244	Trawl	Ruebsamen (1972)
Bayou Savin and Bayou Ferblanc (unoiled)	88.1	2.1	8.7	1.1	0	0	–	0.06	Pools	7,175	Trap	May (1977)
Leaville (oiled)	96.7	0.8	2.2	0.08	0	0	1	0.01	Pools	2,468	Trap	May (1977)

The oiled sites at Leaville were designated such based on chronic operational oil seepage at the Leaville Oil Field. Fish species: F.g. = *Fundulus grandis*, F.x. = *Fundulus xenicus*, C.v. = *Cyprinodon variegatus*, F.p. = *Fundulus pulvereus*, P.l. = *Poecilia latipinna*, L.p. = *Lucania parva*, F.j. = *Fundulus jenkinsi*, F.s. = *Fundulus similis*. Subhabitats for this study include edge (E), creek (C), pond (P), and depression (D)

section). We analyzed untransformed CPUE given that balanced ANOVA designs are robust to minor departures from normality (Quinn and Keough 2002).

## Results

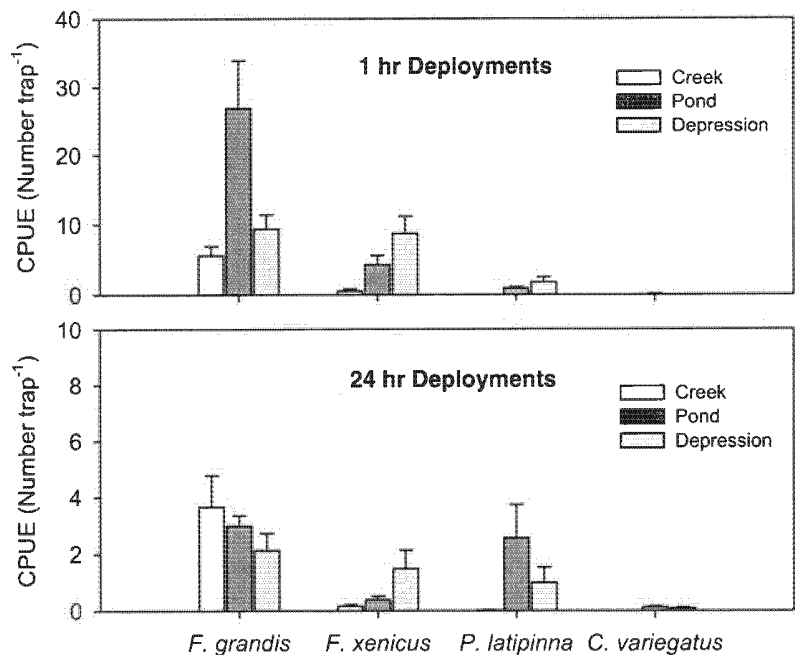
We sampled 22 sites with 549 individual trap sets while collecting seven cyprinodontiform fishes (Tables 1 and 2). Of these, 3,668 fishes were sampled in the trap duration experiments (also supporting our comparisons of marsh subhabitat utilization) while 5,422 fishes were captured in the oiled versus unoiled comparisons. Across all sampling, we collected fundulids (*F. grandis*, *F. pulvereus*, *F. similis*, *F. jenkinsi*, *F. xenicus*), a cyprinodontid (*Cyprinodon variegatus*), and a poeciliid (*Poecilia latipinna*). The comparison of trap sampling duration on two dates across similar habitats determined that the 24-h duration sets caught more total fish at both sites (LUMCON A and B of 629 and 2,432 individual fish of all species, respectively) than those at 1 h (LUMCON A and B of 134 and 473 individual fish of all species, respectively). The same pattern was not evident when abundance was expressed as catch per hour. Overall (LUMCON A and B combined), higher hourly catch rates were recorded in the 1-h sampling trials (mean $\pm$ SEM=19.0 $\pm$ 4.5,  $n=32$ ) than in the 24-h durations (mean $\pm$ SEM=4.0 $\pm$ 0.9,  $n=32$ ),  $p=0.012$  (Fig. 2). These comparisons were made at similar temperatures (26–33.5 °C) and salinities (14–17.6) across all subhabitats, and thus, these variables were unlikely to affect species composition. In general, a sampling duration

of 1 h was reasonably consistent with the 24-h sampling, across several measures, but offered the marked advantage of reduced sampling effort and, consequently, greater replication across our widely spaced sampling sites. As a result, we consistently employed 1-h sampling durations to compare oiled and unoiled marshes and subhabitats across the larger study area. We also averaged catch rates at each habitat type (subhabitat) during each set in an effort to reduce the variability introduced by inherent differences in catch rates among traps, as seen in the LUMCON comparisons between 1- and 24-h sampling durations (Table 3 and Fig. 2).

## Fish Species Composition and Abundance

Overall species composition was consistent among sites, but the relative dominance of species varied among bays (Table 2). *Fundulus grandis* followed by *F. xenicus* were the most abundant species at the Terrebonne and Caminada Bay sites with the two species accounting for 90 and 95 % of the total catch, respectively. However, at the lower salinity Barataria Bay sites, species composition was more balanced with four species (*F. xenicus*, *P. latipinna*, *C. variegatus*, and *F. grandis*) accounting for >95 % of the total catch and each species accounting for between 11 and 32 % of the total (31.8, 27.3, 25.2, and 11.5 %, respectively; Table 2). Fish abundance also varied among sampling events (June 2012,  $n=1588$ ; May 2013,  $n=513$ ; October 2013,  $n=3397$ ) (Table 2 and Fig. 4). *Fundulus grandis* and *F. xenicus* were the most abundant in June 2012 (46.8 and 44.3 %, respectively), but *F. grandis* ranked third (21.8 %) after *F. xenicus* (38.4 %) and *P. latipinna* (25.9 %) in May 2013. In October 2013,

**Fig. 2** Composite species abundance (CPUE = catch per hour, mean±SEM,  $n=8$ ) by subhabitat (creeks, ponds, and depressions) for the dominant species at 1- and 24-h deployments in LUMCON. The results of nested ANOVAs for each species indicate no significant differences in CPUE among treatments (subhabitats) (see Table 3). Note that the scale of the vertical axes in the two plots differ



*F. grandis* was the most abundant species (39.4 %). The remaining species were less abundant: *C. variegatus* (5.2 % in June 2012, 4.5 % in May 2013, 18.9 % in October 2013), *P. latipinna* (1.3 % in June 2012, 25.9 % in May 2013, 18.2 % in October 2013), *F. pulvereus* (1.2 % in June 2012, 7.0 % in May 2013, 1.7 % October 2013), and *F. similis* (1.1 % in June 2012, 2.3 % in May 2013, 4.2 % in October 2013).

Fish species composition varied little with regional environmental characteristics. Salinity was the most variable with the lowest values at Barataria Bay (7.2–13.7), the highest values at Caminada Bay (8.1–25.4), and intermediate values at Terrebonne Bay (9.4–22.0) (Table 1). Salinity did not appear to influence species composition except possibly that the sites with the highest and lowest values were dominated by *F. grandis* at Caminada Bay and *F. xenicus* at Barataria Bay sites (Table 2). Temperatures were high (24.0–32.3 °C) across all sites during the June (2012) and May (2013) collecting periods, but somewhat lower during the October (2013) sampling (24.7–28.8 °C) (Table 1).

#### Fish Subhabitat Use

Marsh fish species composition varied by subhabitat, but subhabitat availability was not uniform across sites. At most sites, available subhabitats included marsh edge, creek, pond, and depression. However, several sites lacked depressions (GI-2, PS-1, PS-2) or ponds (FC, 47A, 47B), and one site (PS-7) lacked creeks (Table 1). For all species across both years, very few individuals ( $n=2$ ) were caught in traps at the marsh edge during any deployment period. For the dominant

species, *F. grandis*, abundance was greatest in creeks (43 % and ponds (43 %). For the second most abundant species, *F. xenicus*, abundance was greatest in ponds (64 %) and depressions (28 %). The next most abundant species, *C. variegatus* and *P. latipinna*, were primarily collected in ponds (97 and 94 %, respectively).

These same patterns of subhabitat use were generally true at the LUMCON trap duration sites where high numbers of fishes were caught in ponds and depressions (1 h=52 and 39 %, 24 h=41 and 32 %, respectively). The greatest difference in catch between deployment durations occurred in creeks, where a higher percentage of fish were caught in 24-h deployments (26 %) than in the 1-h deployments (8 %). Very few fish (1 % for both 1- and 24-h deployments) were caught at the marsh edge. As in the Terrebonne, Caminada, and Barataria Bay sites, *F. grandis* at LUMCON was most abundant in creeks (37 %) and ponds (39 %) and *F. xenicus* was mostly found in depressions (68 %) and ponds (25 %). Both *P. latipinna* and *C. variegatus* were abundant in ponds (68 and 65 %, respectively) at LUMCON, but unlike in other bay sites, they were also common in depressions (31 and 35 %, respectively).

#### Fish Assemblage Responses in Oiled and Unoiled Marshes

The same species were dominant in oiled and unoiled sites, with *F. grandis* and *F. xenicus* among the most commonly captured species in both. For all four of the dominant species, catch rates were similar among available subhabitats (creek, pond, depression) in unoiled and oiled sites (Fig. 3). However,

**Table 3** Nested analysis of variance (ANOVA) tables for differences in fish abundance (CPUE) among treatments (subhabitats: creeks, ponds, and depressions) at 1- and 24-h deployments

Source of Variation	df	SS	MS	F	p
(1 h)					
<i>Fundulus grandis</i>					
Subhabitat	2	2,058.3	1,029.2	2.0	NS
Sampling event	9	4,602.1	511.3	371.9	<0.001
Residual (error)	12	16.5	1.4		
<i>Fundulus xenicus</i>					
Subhabitat	2	776.1	388.0	1.4	NS
Sampling event	9	2,433.4	270.4	721.0	<0.001
Residual (error)	12	4.5	0.4		
<i>Poecilia latipinna</i>					
Subhabitat	2	114.3	57.2	1.1	NS
Sampling event	9	450.0	50.0	54.5	<0.001
Residual (error)	12	11.0	0.9		
<i>Cyprinodon variegatus</i>					
Subhabitat	2	4.1	2.0	1.5	NS
Sampling event	9	12.8	1.4	6.6	0.02
Residual (error)	12	2.5	0.2		
(24 h)					
<i>Fundulus grandis</i>					
Subhabitat	2	9.4	4.7	0.3	NS
Sampling event	9	147.1	16.3	222.9	<0.001
Residual (error)	12	0.9	0.07		
<i>Fundulus xenicus</i>					
Subhabitat	2	7.8	3.9	0.9	NS
Sampling event	9	38.2	4.2	101.9	<0.001
Residual (error)	12	0.5	0.04		
<i>Poecilia latipinna</i>					
Subhabitat	2	0.5	0.2	3.1	NS
Sampling event	9	0.7	0.08	2.9	0.045
Residual (error)	12	0.3	0.03		
<i>Cyprinodon variegatus</i>					
Subhabitat	2	0.07	0.03	0.99	NS
Sampling event	9	0.32	0.03	1.8	NS
Residual (error)	12	0.24	0.02		

Tables for each species include degrees of freedom (df), sum of squares (SS), mean square (MS), *F*-statistic, and *p* value

NS not significant

the high temporal variability in fish abundance between sampling events (Fig. 4) may have limited our ability to detect subtle differences. Only in October 2013, more than 3 years after the Macondo oil reached Louisiana marshes, was *F. grandis* abundance at oiled sites ( $19.5 \pm 8.7$  fish caught per hour) significantly different (greater) ( $H=4.4$ ,  $n_{\text{unoiled}}=26$ ,  $n_{\text{oiled}}=21$ ,  $p=0.019$ ) than in unoiled sites ( $4.5 \pm 2.3$  fish caught per hour). Both *P. latipinna* and *C. variegatus* tended to be more abundant at unoiled sites in May and October 2013, but

these patterns were based on small overall sample sizes for each species (Fig. 4), and the difference was only significant for *P. latipinna* in May 2013 ( $H=5.5$ ,  $n_{\text{unoiled}}=15$ ,  $n_{\text{oiled}}=11$ ,  $p=0.036$ ).

The mean sizes of the two most frequently collected fishes, *F. grandis* and *F. xenicus*, were statistically different between oiled and unoiled sites across creeks, ponds, and depressions (Fig. 5). Larger individuals of both species were collected in depressions at oiled sites (means=43.8 and 28.2 mm TL, respectively) relative to those at unoiled sites (means=38.6 and 26.3 mm TL, respectively) ( $p=0.019$  and  $p=0.008$ , respectively). The opposite was true for fish of both species collected in ponds, where smaller *F. grandis* and *F. xenicus* were collected in oiled sites (means=38.5 and 25.2 mm TL, respectively) than in unoiled sites (means=52.8 and 30.6 mm TL, respectively) ( $p<0.001$  and  $p<0.001$ , respectively). Differences in sizes within creeks depended on the species, with *F. grandis* being slightly larger at oiled sites (mean=48.7 mm TL) than at unoiled sites (mean=47.7 mm TL,  $p=0.011$ ) and *F. xenicus* being smaller at oiled sites (mean=29.4 mm TL) than at unoiled sites (mean=33.6 mm TL,  $p<0.001$ ).

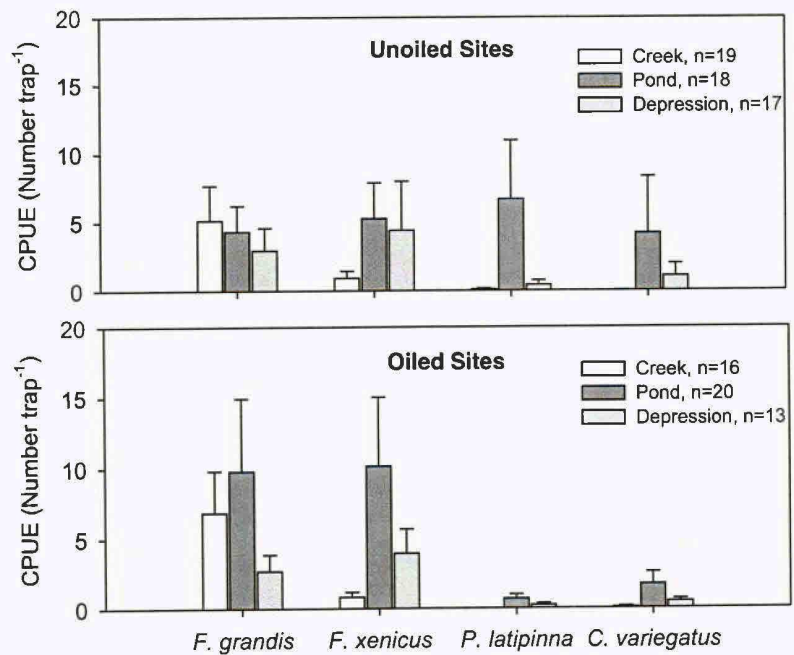
An initial test of the assemblage structure of fishes indicated no difference between sampling events (Global  $R=0.002$ ,  $p=0.296$ ) and, as a result, further analyses were combined across all sampling periods. Fish assemblage composition varied significantly among the subhabitats sampled (Fig. 6; ANOSIM Global  $R=0.171$ ,  $p=0.001$ ). Pairwise comparisons indicated that this difference was driven largely by the different fish abundances between marsh edge and other habitats (creek:  $R=0.231$ ,  $p=0.001$ ; ponds:  $R=0.33$ ,  $p=0.001$ ; and depressions:  $R=0.217$ ,  $p=0.001$ ). Creek assemblages were different from those in ponds ( $R=0.067$ ,  $p=0.003$ ) and depressions ( $R=0.03$ ,  $p=0.038$ ), but pond and depression assemblages were not distinct ( $R=0.019$ ,  $p=0.128$ ). We found no significant differences between the assemblages at oiled and unoiled sites (Fig. 6; ANOSIM Global  $R=0.01$ ,  $p=0.158$ ). Subsequent SIMPER analyses indicated that any differences in community composition were largely driven by shifts in abundance among three dominant species, *F. grandis*, *F. xenicus*, and *P. latipinna* (Table 4).

## Discussion

### Salt Marsh Fish Species Composition and Abundance

The dominant fishes we collected across a variety of marsh surface sites were representative of previous reports from Louisiana marshes (Peterson and Turner 1994; Rozas and Reed 1993). Among these are several unpublished theses (Ruebsamen 1972; May 1977) that focused on fundulids and cyprinodontids. An evaluation of fundulids and

**Fig. 3** Composite species abundance (CPUE = catch per hour, mean  $\pm$  SEM) by subhabitat (creeks, ponds, and depressions) for the dominant species at all sampling events at unoiled and oiled sites. The results of Kruskal-Wallis (rank sum) one-way analysis of variance (ANOVA) tests for each species indicate no significant differences ( $p > 0.05$ ) in CPUE among treatments (subhabitats)



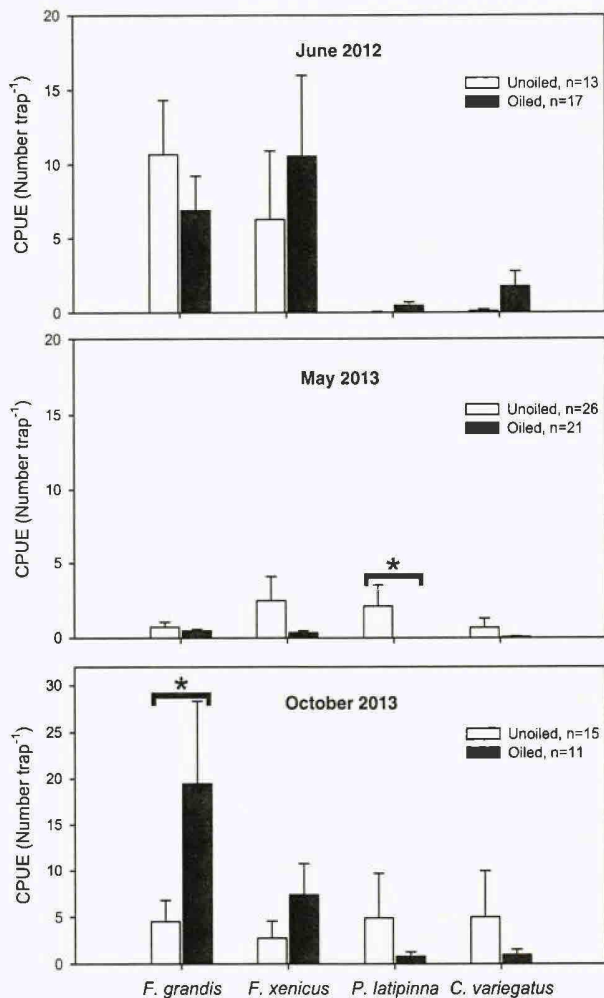
cyprinodontids in relatively unaltered marshes near Timbalier and Caminada Bays using similar baited traps to those used in our study found identical species composition, with the exception that *F. jenkinsi* was not reported (May 1977). The species were dominated by *F. grandis* (90 % of total fish) but also included *C. variegatus* (7 %), *F. xenicus* (2 %), *F. pulvereus* (1 %), and *F. similis* (rare). Six of the same species were collected in extensive sampling near Grand Terre, Louisiana (Forman 1968), but the relative proportions differed, apparently because of the subhabitats sampled. Most noticeably in the Grand Terre collections, *F. similis* was much more abundant (41.1 % of all fishes collected) at these higher salinities along sandy bay shores. *C. variegatus* was also abundant (40.9 %) near Grande Terre in creeks and marsh ponds but less well represented in our study. *Fundulus grandis* and *F. xenicus* were much less abundant (11.5 and 5.0 %, respectively) near Grand Terre as well. Many of the same species we collected occurred in small trawl samples in intertidal ponds and intertidal creeks near Grand Isle, Louisiana (Ruebsamen 1972).

Our results are generally similar to those from these previous sampling efforts, across multiple gears and multiple habitats. Together, these indicate that cyprinodontiform fishes are dominant forms in marshes but the patterns of habitat use vary among species. Our findings agree with those of Peterson and Turner (1994), who differentiated Interior Marsh Residents (*F. pulvereus*, *F. xenicus*, *C. variegatus*, *P. latipinna*), Interior Marsh Users (*F. grandis*, *Lucania parva*), Marsh Edge Users (*F. jenkinsi*), and Marsh Subtidal (none). These categories correspond to the subhabitats in which we determined use, with Interior Marsh ponds and depressions dominated by

*F. xenicus*, *F. pulvereus*, and *P. latipinna* and occasionally *C. variegatus*. *Fundulus grandis* was collected across these habitats and in creeks and thus fits the Interior Marsh User category. While relatively rare (Peterson et al. 2003), *F. jenkinsi* was a Marsh Edge User based on a few collections reported here and in other sampling by us. One limitation of the use of flumes (Peterson and Turner 1994) on the marsh surface is that small, recently hatched individuals that remain in shallow sheets of water on the marsh surface may go undetected. The use of this shallow standing water was verified when we used small mesh (1 mm) dip nets to collect one of the dominant species at very small sizes (*F. grandis*, range = 7–13 mm,  $n=25$ ). The reduced abundance of fishes at the marsh edge observed in our study (<0.5 % of total catch) was similar to results for cyprinodontiform fishes based on a drop sampler (Baltz et al. 1993). In that study, all of the same species occurred (along with *L. parva*), but those at the marsh edge only constituted <0.0002 % of the numerous fishes collected.

The use of these subhabitats and categories may be dynamic due to seasonal and episodic changes in marsh flooding frequency. In Louisiana, and throughout the northern Gulf of Mexico, there is seasonal variation in flooding frequency and duration (Baumann 1980, 1987; Sasser 1977; Turner 1991; Rozas 1995; Minello et al. 2012). Generally, the semi-annual rise and fall in water level cause a bimodal pattern of marsh flooding with the highest duration of flooding in the spring and fall and the lowest duration of flooding in the winter and to a lesser degree in mid-summer. This seasonal pattern can be further influenced by large-scale climatological events such as the El Niño-Southern Oscillation (Childers et al. 1990) and most drastically by hurricanes and tropical storm events. The





**Fig. 4** Species abundance (CPUE = catch per hour) of dominant cyprinodontiform fishes in oiled and unoiled marshes by sampling period in June 2012 and May and October 2013. The results of Kruskal-Wallis (rank sum) tests indicate no significant differences in CPUE among treatments (unoiled vs oiled), except for *P. latipinna* in May 2013 ( $p=0.036$ ) and *F. grandis* in October 2013 ( $p=0.019$ ), where statistical differences are indicated by asterisks

flooding of the marsh surface can drastically affect fish availability to sampling gear such as traps. When the marsh floods, fish from ponds, depressions, and creeks have access to the previously unflooded marsh surface and can disperse and are less likely to enter traps and be available to other gears because of the dense vegetation. Alternatively, all of these may be denied access to subhabitats and associated food, spawning sites, and access to nursery areas during periods of low water level.

The same species collected on the marsh surface in Louisiana are representative of other northern Gulf of Mexico marshes with some variation depending on habitat type. In Mississippi marshes, a variety of sampling techniques (e.g., Breder trap and kick seine) captured the same species with *F. grandis* being the most abundant, and also relatively

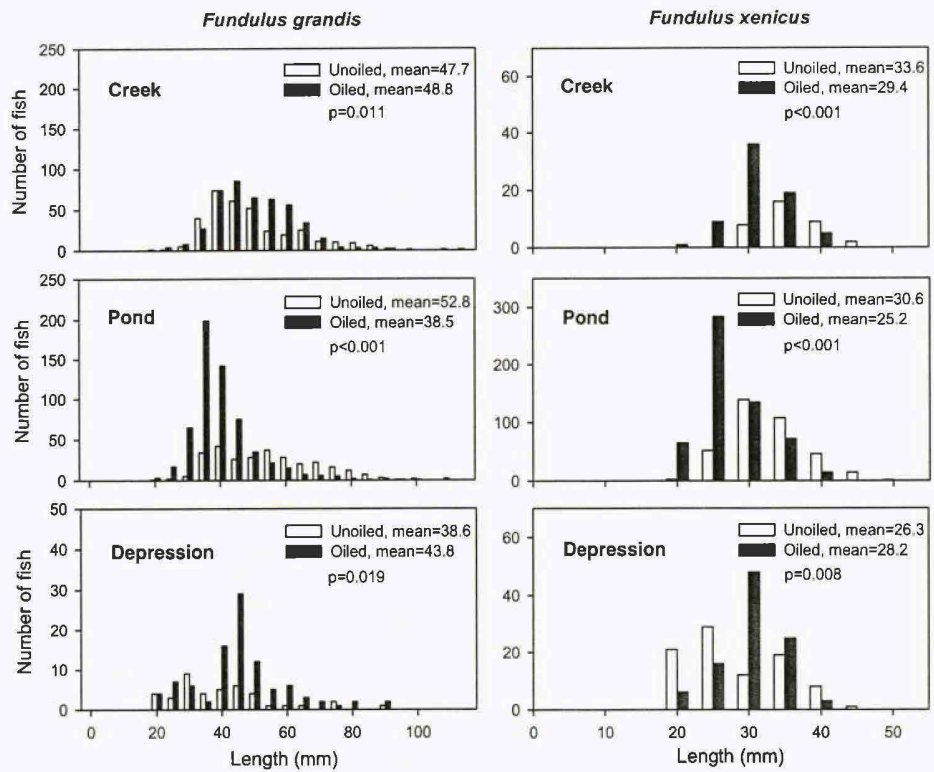
large numbers of *F. jenkinsi* and very few *F. similis* (listed as *F. majalis similis*) (Fulling et al. 1999). In Florida marshes, the same species or congeners (*F. confluentus* instead of *F. pulvereus*) occur in seine collections at the mouths of marsh creeks, with these dominated by *F. grandis* and *F. similis*, and including *C. variegatus*, *F. xenicus*, *P. latipinna*, and *L. parva* (Subrahmanyam and Drake 1975; Lipcius and Subrahmanyam 1986). In the same general area, seine collections found some of the same species as in our Terrebonne/Barataria/Caminada Bay sampling except that some of the species that were rare in our study were dominant along vegetated and unvegetated beaches (Naughton and Saloman 1978). In Texas marshes in Galveston Bay, some of the same cyprinodontids as in our study are dominant, including *F. grandis* and *C. variegatus* (Rozas and Zimmerman 2000). While sampling gear bias can readily influence observations of fish species composition (e.g., Able 1999), and the same is true for traps (Kneib and Craig 2001; Layman and Smith 2001; Dupuch et al. 2011), the consistent use of traps is supported as a useful technique, in part because of the consistency with which they have been used, the ease of sampling, and that their use does not require modification of the marsh (May 1977; Fulling et al. 1999; Paradis et al. 2012; Able et al. 2010).

Together, these observations indicate that the dominant cyprinodontiform fishes observed by our trap sampling over a wide spatial area in Terrebonne, Barataria, and Caminada Bays are representative of northern Gulf of Mexico marshes. Thus, this group is an appropriate focus for studies of disturbance impacts on the marsh surface, such as the Macondo oil spill. Further, cyprinodontiform fishes are ideal as sentinel species for detecting the effects of oil on marshes for several reasons; most of these are related to their high degree of residency. First, all cyprinodontiform fishes have demersal, attached eggs (Able 1984) and deposit them in vegetation, shells, or the substrate (Able and Hata 1984). Second, the larvae and small juveniles, at least for some species of *Fundulus*, *Lucania*, and *Cyprinodon*, are typically found on the marsh surface (Able and Hagan 2003; Teo and Able 2003; Able et al. 2005). Third, several species for which data are available (*Fundulus* and *Cyprinodon*) are known to exhibit a high degree of site fidelity over much of their life cycle (Chitty and Able. 2004; Able et al. 2006; Teo and Able 2003), including *F. grandis* in some of our Louisiana study sites (Jensen et al., unpublished data) and elsewhere in the Gulf of Mexico (Nelson et al. 2014). Fourth, their hardiness makes it unlikely that any negative responses are due to natural variation.

#### Fish Assemblage Responses in Oiled and Unoiled Marshes

The timeline for occurrence of oil in Louisiana marshes provides a baseline for understanding the fish response. The Macondo Well exploded on April 20, 2010, and the best

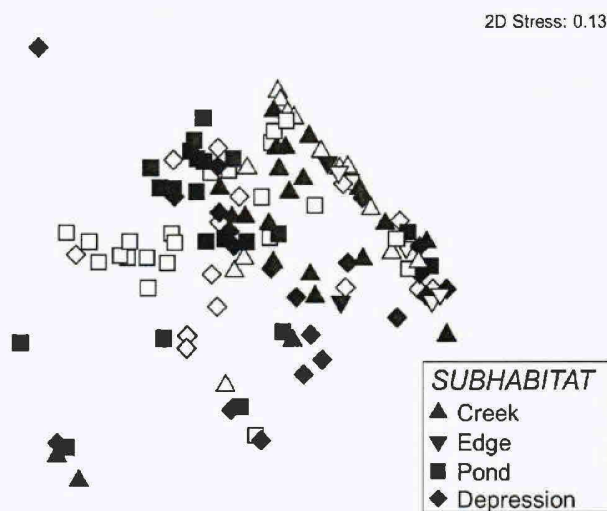
**Fig. 5** Size composition of *F. grandis* and *F. xenicus* by subhabitat type across all sampling events in oiled (black bars) and unoiled (white bars) marshes. *p* values are provided for each length frequency comparison



estimates suggest that this floating but weathered oil initially reached Louisiana marshes, and our specific study sites, during May and June of 2010. Because *F. grandis* spawns in the fall and spring (Waas and Strawn 1983; Greeley and MacGregor 1983; Lipcius and Subrahmanyam 1986), both young-of-the-year and age 1 individuals may have been

affected. Thus, the fish we collected in 2012 and 2013 potentially would have been exposed to oil in selected marshes for their entire lives, although we do not know definitively the age of *F. grandis* and the oil may have degraded over time (Rozas et al. 2014; Turner et al. 2014b) or been redistributed after storms (Turner et al. 2014a). Despite this exposure to oil, there were no overt signs of decreased abundance in these marshes because we captured representative species and sizes at all sites in both years. Some of our findings may be confounded by differences in marsh morphology. The lack of marsh surface standing water, either ponds or depressions, was more typical of higher elevation, sandier sites, such as some in Caminada Bay near Grand Isle (Fig. 1). In some instances, all the subhabitats were sampled but catches were very low or zero because the water levels were high and fish appeared to be spread over the entire marsh surface and not as susceptible to capture.

The finding of no obvious oil effects on numerous metrics (composition, abundance, size, and assemblage composition) is inconsistent with the deleterious genetic and physiological effects at the individual level on some fishes (de Soysa et al. 2012) and on *F. grandis* from oiled sites impacted by the same spill (Whitehead et al. 2012; Garcia et al. 2012; Dubansky et al. 2013; Crowe et al. 2014). Embryos of *F. grandis* exposed to the water-soluble fraction of No. 2 fuel oil had pathological liver, kidney, and epithelial tissues at 25 % level while all of the embryos exposed to 50 % solution of this fraction died



**Fig. 6** Non-metric multidimensional scaling plot indicating oiling (black polygons = oiled sites, white polygons = unoiled sites) and subhabitat differences among samples. Outlier samples (zero catches) in the matrix were removed prior to this analysis but included in all other statistical comparisons

**Table 4** Assemblage structure analysis with species contributing most between subhabitat similarities in marsh edge, creek, pond, or depression habitats, as well as with or without oiling

HABITATS			
Creek	Edge	Pond	Depression
<i>F. grandis</i> (86.8)	<i>F. grandis</i> (100.0)	<i>F. grandis</i> (44.7)	<i>F. grandis</i> (62.3)
<i>F. xenicus</i> (12.7)		<i>F. xenicus</i> (37.0)	<i>F. xenicus</i> (31.6)
		<i>P. latipinna</i> (13.9)	
OILING			
Unooled	Oiled		
<i>F. grandis</i> (56.7)	<i>F. grandis</i> (69.7)		
<i>F. xenicus</i> (29.2)	<i>F. xenicus</i> (25.0)		
<i>P. latipinna</i> (10.3)			

Parenthesis values indicate percent contribution to Bray-Curtis similarity index for that treatment

before hatching (Ernst et al. 1977). Perhaps, while the oil is deleterious, it does not cause extensive mortality and does not interfere with reproduction at the levels encountered. Also, it may be that initial mortality occurred 2–3 years before sampling and there has been some recovery of the population or a recolonization of the affected marshes from nearby locations. Post-spill recruitment from adjacent marshes is possible but unlikely for several reasons. First, the large juveniles and adults (>37 mm TL) are very highly localized to small portions of the marsh based on our tag and recapture studies in Louisiana marshes (Jensen et al., unpublished data). These studies clearly indicate that over several months, tagged individuals did not move very far (maximum distance of 90 m). This interpretation was supported by the fact that we had very high recapture rates. This is also supported by similar studies in Mississippi for *F. grandis* (Nelson et al. 2014). Second, other studies of a closely related species (*Fundulus heteroclitus*) have shown high site fidelity for juveniles and adults suggesting, yet again, that these animals are highly localized and may not be recruited from very long distances (Able et al. 2012 and references cited therein). Third, the recently hatched larvae and small juveniles are not likely to move large distances either. The larvae of many killifishes are found only in marsh ponds and shallow depressions on the marsh surface (Hagan et al. 2007; Able et al. 2003). There is little evidence that the larvae are pelagic and thus would not be transported long distances. Together, these observations suggest that recruitment from adjacent unooled marshes after the spill is unlikely to explain the observed patterns. Alternatively, mobile fishes may be able to avoid localized spill effects. In a before and after study of a small oil spill in Barataria Bay, Roth and Baltz (2009) observed that the total number of individuals decreased, but there were no strong community responses, in agreement with our study. Perhaps,

we could not detect a change in total fish abundance because we had no pre-spill data to compare with our trap sampling. In another study of fish community response in a Louisiana marsh influenced by oil production facilities, the species composition was somewhat different from ours, with *F. grandis* clearly dominating the cyprinodontiform fauna in both oiled and unooled sites (May 1977). However, there were no differences in species composition between oiled and unooled sites. An alternative explanation for our inability to detect a difference between the oiled versus unooled marshes is that many intertidal fishes, including cyprinodontiform fishes, typically have high spatial and temporal variability in abundance and thus may be poor indicators of environmental quality (Ellis and Bell 2013). Another possibility is that all our sites have a history of oil exposure and completely “unooled” marshes do not exist in Louisiana (DeLaune et al. 1990; Marton and Roberts 2014); thus, these marsh fishes may have been pre-adapted to survive exposure to oil.

The inability to detect a fish assemblage response during our 2012–2013 sampling could be due to limitations related to our statistical power or study design. Further, our analysis should be placed in contrast to similar efforts relative to anthropogenic effects, in general (Rose 2000), and to the Exxon Valdez oil spill, in particular (Hilborn 1996). Hilborn (1996) suggested that detecting a response to an oil spill required several types of data including (1) counts of dead animals, (2) pre- and post-spill comparisons of abundance, (3) oil versus non-oiled comparison of abundance, (4) oiled versus non-oiled comparison of vital rates, and (5) direct experimental oiling. Our results only address one of these (no. 3) but include details of species composition where there was no response either. More generally, the negative responses to the Macondo oil spill by individual fish might not be reflected at the population level for a variety of reasons (Fodrie et al. 2014). Among these are the possibility of compensatory processes, as has occurred after the Arthur Kill (New Jersey) oil spill (Burger 1994), in which *F. heteroclitus* responded both negatively (reduction in larger, older individuals) and positively (increased abundance of young-of-the-year) 1 year after the spill (Brzozrad and Burger 1994).

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