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November 2020



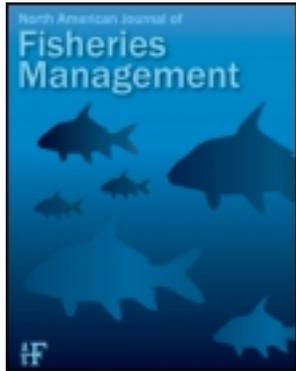
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North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujfm20>

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Published online: 01 Apr 2014.

To cite this article: Stephen T. Szedlmayer & Peter A. Mudrak (2014) Influence of Age-1 Conspecifics, Sediment Type, Dissolved Oxygen, and the Deepwater Horizon Oil Spill on Recruitment of Age-0 Red Snapper in the Northeast Gulf of Mexico during 2010 and 2011, North American Journal of Fisheries Management, 34:2, 443-452

To link to this article: <http://dx.doi.org/10.1080/02755947.2014.882457>

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ARTICLE

Influence of Age-1 Conspecifics, Sediment Type, Dissolved Oxygen, and the Deepwater Horizon Oil Spill on Recruitment of Age-0 Red Snapper in the Northeast Gulf of Mexico during 2010 and 2011

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Abstract

The Deepwater Horizon oil spill was one of the largest oil spills in U.S. history. The timing of this spill coincided with peaks in spawning and recruitment of Red Snapper *Lutjanus campechanus* and may have led to reduced recruitment or to year-class failure. Artificial recruitment reefs were deployed in 2010 ($n = 30$) and 2011 ($n = 30$) to measure Red Snapper recruitment off the coast of Alabama at four sites (three inshore sites, 13 km south: west, center, and east sites, each 30 km apart; and one offshore site, 25 km south). Substantial age-0 Red Snapper recruitment (density range = 0–34.5 fish/m³) occurred in 2010, with higher densities on inshore reefs than on offshore reefs. Age-0 Red Snapper recruitment was again observed in 2011 (density range = 0–108.5 fish/m³) along with age-1 Red Snapper (density range = 0–78.9 fish/m³) from the 2010 year-class. There was a negative correlation between the densities of age-0 and age-1 Red Snapper, indicating that older Red Snapper excluded younger fish from the reefs. Higher fractions of silt in the substrate at the west site compared with the center and east sites were associated with higher densities of age-0 Red Snapper, but the effects of sediment type were less important than exposure to hypoxic conditions at the west site in late August 2011 (dissolved oxygen fell to concentrations as low as 0.4 mg/L), which caused an almost complete loss of fish. The abundances of age-0 and age-1 Red Snapper in 2010 and 2011 provide evidence that the oil spill did not result in a year-class failure and that the most important variables affecting age-0 Red Snapper abundances were age-1 Red Snapper presence and dissolved oxygen concentration.

The 2010 Deepwater Horizon (DWH) oil spill introduced an estimated 4.1×10^6 barrels (7.0×10^5 m³) of unrefined crude oil into the Gulf of Mexico (GOM)—one of the nation's most productive and economically important water bodies—from April 20, 2010, until the well was capped on July 14, 2010 (Allan et al. 2012; Camilli et al. 2012). Extensive decontamination activities, fisheries closures, mobilization of environmental assessment resources, and restoration efforts also made this oil spill one of the most costly accidents in U.S. history. Complicating the environmental picture, dispersants with unknown environmental impacts were also introduced (Kujawinski et al. 2011). The oil plume from the DWH incident covered a wide area (180,000 km² of ocean), extending from the deepwater

habitats at the well head, onto the shelf, and into coastal estuarine ecosystems (Norse and Amos 2010).

Although some of the environmental impacts were obvious (contaminated shorelines and mortality of marine mammals and birds), the longer-term and sublethal impacts that may persist in marine fish species of the GOM are less apparent (Bue et al. 1998; Sumaila et al. 2012). Some long-term impacts can be relatively easy to detect (e.g., bioaccumulation of hydrocarbons), but others (e.g., community changes, trophic shifts, or year-class failures) are subtle and difficult to detect against normal background environmental and ecological variability. Thus, it remains unclear how marine fisheries in the GOM will ultimately be affected by these acute and chronic impacts.

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Received August 23, 2013; accepted December 19, 2013

For Red Snapper *Lutjanus campechanus* and many other important reef fishes, early life history—especially the larval stages and first recruits to reef structure—can be extremely important in the subsequent determination of year-class strength (Doherty and Fowler 1994; Szedlmayer 2011). These small, fragile larval-stage reef fish typically occupy the surface pelagic zones during their first month of life and are probably the most vulnerable life history stages. Detection of any effects from the surface oil plume originating from the DWH oil spill would be most apparent in these early larval stages and in the subsequent postsettlement stages. For example, the seasonal peaks of Red Snapper reproduction, pelagic eggs and larvae, and subsequent recruitment (Collins et al. 1996; Szedlmayer and Conti 1999) coincided with the peaks of oil plume coverage on the Red Snapper shelf habitats in the northeast GOM (Szedlmayer and Conti 1999; NOAA 2010). However, the available data are too limited to provide a valid assessment of the DWH oil spill's possible effects on these early stage marine fishes.

At the same time, there is little information on the value of various substrate habitat types for juvenile Red Snapper in the northern GOM (Szedlmayer and Conti 1999; Rooker et al. 2004; Wells et al. 2008b). For the most part, this lack of understanding is due to cryptic patterns of habitat use by reef fishes, which make quantitative sampling with typical gear (i.e., trawls) difficult at best. In the present study, we used a new approach of applying artificial reefs as the sampling methodology, thereby overcoming many of the past “sampling” problems encountered in evaluating habitat value for this important species.

We compared patterns of juvenile Red Snapper abundance by using artificial reefs as the sampling tool across various habitats as defined by substrate properties (grain size and potential polycyclic aromatic hydrocarbon [PAH] contamination) and water mass characteristics (temperature, dissolved oxygen [DO] concentration, and salinity). Artificial “recruitment” reefs were deployed at four sites in the northern GOM to allow for an assessment of habitat and possible DWH oil spill effects on the abundance patterns of juvenile (age-0 and age-1) Red Snapper. Importantly, due to the availability of previous studies that used the same recruitment reefs and survey methods, we were able to compare age-0 and age-1 abundances with those observed in previous years and to make valid assessments of Red Snapper year-class failure that might be associated with the DWH oil spill. For over 10 years, we have documented recruitment to reef structure by juveniles (age 0 and age 1) of Red Snapper and other reef fishes (Szedlmayer 2011). This artificial reef strategy may provide a better understanding of habitat value for Red Snapper and may offer insight into possible effects of the DWH oil spill.

METHODS

Small artificial reefs ($n = 60$) were deployed off the coast of Alabama in 2010 and 2011 to examine possible oil spill effects on Red Snapper recruitment and to compare density

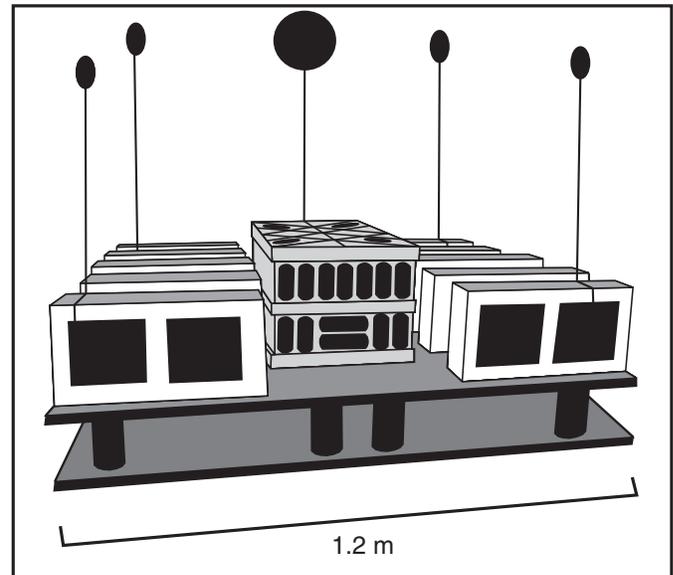


FIGURE 1. Illustration of the recruitment reef used to sample juvenile Red Snapper in the northeast Gulf of Mexico.

patterns over different substrate types. Each reef (Figure 1) consisted of a plastic pallet ($1.22 \times 1.02 \times 0.14$ m), 10 concrete half-blocks ($41 \times 20 \times 10$ cm), and two plastic crates ($38.7 \times 34.9 \times 26.7$ cm). Reefs were assembled by using 122-cm cable ties with a tensile strength of 79 kg. A small float (5.1×12.7 cm) was tied to each corner of the reef and floated 1 m above the top of the pallet. One larger float (15.2-cm diameter) was tied in the center of the reef, also at a height of 1 m. The floats added vertical structure to the reef and facilitated reef relocation with sonar. The reefs were anchored by attachment to a 1.2-m ground anchor with 1.3-cm-diameter nylon rope. The total volume of the reef was 1.42 m^3 .

Scuba divers identified and counted all fish that were present on the reef and visually estimated 25-mm size categories based on comparisons with the known sizes of background concrete blocks ($41 \times 20 \times 10$ cm). Red Snapper ages were estimated based on length. Red Snapper that were no larger than 76 mm in June and July, 102 mm in August, 127 mm in September, or 152 mm in October were considered to be age 0 (Szedlmayer and Conti 1999; Szedlmayer and Lee 2004). During reef surveys, the temperature, salinity, and DO at 1 m above the bottom were measured with a remote Yellow Springs Instruments (YSI) 6920 meter. If more than one YSI reading was taken at a site during a survey, then temperature, salinity, and DO were presented as means of those readings.

Standardized photographs were taken of each reef when visibility permitted. Horizontal-level photographs were taken 1.2 m from the reef at ground level. Photographs were used to verify and provide a permanent record of divers' identification of fish species.

The first set of reefs (set 1, an offshore site) was deployed 25 km south of Dauphin Island, Alabama, on July 14–15, 2010;

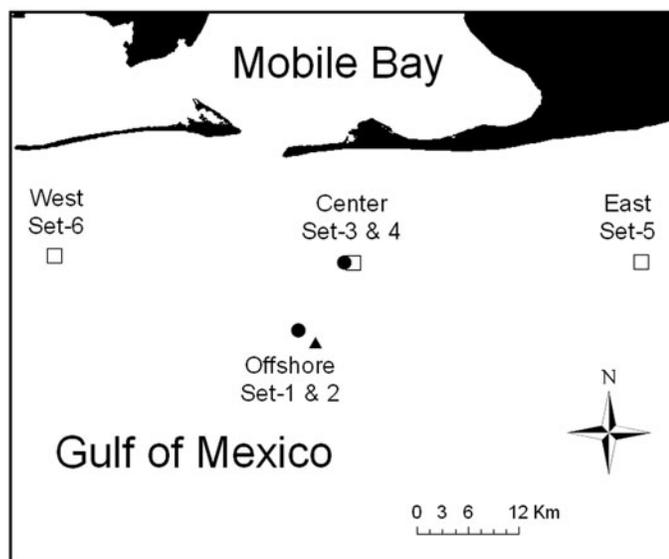


FIGURE 2. Map of the study area in the northeast Gulf of Mexico, where juvenile Red Snapper were sampled with artificial recruitment reefs. Each point represents 10 reefs (i.e., one set), with each reef situated at least 500 m apart from other reefs.

set 1 consisted of 10 reefs that were placed 1.7 km apart by using the same reef design, study area, and time period as described by Mudrak and Szedlmayer (2012). Each reef was placed in 18–22-m depths and at least 500 m from other known artificial reefs in the area (Figure 2; Mudrak and Szedlmayer 2012). Reefs in set 1 were surveyed three times: August 2–3, 2010 (all reefs); September 9–20, 2010 (all reefs); and July 13–21, 2011 (5 reefs).

On the first survey of reefs in set 1, it was apparent that substantial densities of age-1 Red Snapper already inhabited each reef. Thus, we were unable to assess 2010 year-class failure based on these reefs because the presence of age-1 and older Red Snapper prevents recruitment of age-0 Red Snapper (Mudrak and Szedlmayer 2012). In an attempt to further evaluate the question of 2010 year-class failure, we deployed two more sets of reefs on August 24–25, 2010, during the known peak recruitment of age-0 Red Snapper (Szedlmayer and Conti 1999). The reefs ($n = 10$) in set 2 were placed 25 km offshore in the same area as set 1. Reefs were again placed 1.7 km apart and at least 500 m from other known reefs. Reefs of set 3 (inshore site) were deployed in 15–18-m depths at a site that was closer inshore, approximately 18 km southeast of Dauphin Island. Reefs were placed in two rows of five reefs, with all reefs located 500 m apart (Figure 2). We surmised that (1) the reefs in sets 2 and 3 would provide new, uninhabited reefs without resident reef fishes; and (2) if in fact age-0 Red Snapper were present, they would recruit to these reefs and would be detected by visual surveys. Reefs belonging to sets 2 and 3 were initially surveyed on September 8–20, 2010, and a second survey was completed on October 18–21, 2010. Reefs

in set 3 were surveyed a third time (November 24, 2010), and reefs in sets 2 and 3 were also surveyed on June 9–30, 2011.

Three more reef sets were deployed on July 19–20, 2011, at three locations, with 10 reefs per location (2 rows of 5 reefs, each 500 m apart). Reefs belonging to set 4 (hereafter, center site) were deployed at depths of 14–17 m and were situated 18 km southeast of Dauphin Island and 500 m east of set 3. Reefs in set 5 (hereafter, east site) were built in depths of 16–20 m and at a location 30 km due east of the center site; reefs in set 6 (hereafter, west site) were built in 20–21 m of water and were 30 km due west of the center site (Figure 2). All reefs that were deployed in 2011 were surveyed on August 1–3, 2011; August 24–30, 2011; October 24–26, 2011; and June 7–19, 2012. One reef was lost from the center site after the passage of Tropical Storm Lee in September 2011; eight reefs from the west site were lost over the winter, most likely due to shrimp trawls.

In addition to diver counts, sediment samples for PAH analysis were taken from the 2011 reef sites. Sediment samples were collected within 1 m of all reefs at each site during late August 2011 and from five reefs at each site during October 2011. Divers collected sediment samples from the top 5 cm of substrate and placed them in pre-cleaned amber glass jars with Teflon-lined lids. Samples were placed on ice immediately upon collection in the field and were frozen after returning to shore. Sediment samples were analyzed for PAH concentration from the late-August 2011 collections: 11 samples were obtained from the center site, 10 were from the east site, and 6 were from the west site. Among the sediment samples collected during October 2011, PAHs were measured in five samples from the center site, five samples from the east site, and four samples from the west site. Hydrocarbon extraction and gas chromatography–mass spectrometry were completed using the methods described by Sloan et al. (2004).

During October 2011, sediment samples ($n = 3–4$) from each site were also taken for use in grain size analysis. Sediment samples for grain size analysis were oven-dried overnight at 100°C and were weighed to the nearest 0.01 g. Samples were then soaked overnight in a sodium hexametaphosphate solution (0.24 g/L of water) and were wet sieved through a 63- μ m screen (Buchanan and Kain 1971). Samples were again oven-dried at 100°C overnight and were weighed to determine the weight of silt in the sample. The remaining sediment was then dry sieved through 2,000-, 1,000-, 500-, 250-, and 106- μ m sieves. A chi-square test was used to examine for differences in sediment composition.

Scuba divers' visual counts of Red Snapper from each individual reef in each treatment and in each month were compared by using a repeated-measures (RM), two-way, mixed-model ANOVA with survey as the repeated measure. Assumptions of normality for ANOVA were verified by visually examining normal probability plots of the residuals. If significant differences were detected, specific differences within each survey were compared with Tukey's test. The correlation between age-0 Red Snapper abundance and age-1 abundance from the first

survey of each reef ($n = 60$) was estimated with Pearson's product-moment correlation coefficient. All differences were considered significant at $P \leq 0.05$.

RESULTS

Few age-0 Red Snapper were observed on reefs in set 1 (August 2010: mean density \pm SE = 1.0 ± 0.4 fish/m³, $n = 10$ reefs surveyed; September 2010: 4.5 ± 1.0 fish/m³, $n = 10$), but age-1 Red Snapper had recruited to these reefs. On the reefs of set 1, age-1 Red Snapper density was 6.8 ± 1.1 fish/m³ (mean \pm SE) in August 2010 and 8.9 ± 1.6 fish/m³ in September 2010. After two new reef sets were deployed in 2010 (sets 2 and 3), there were significantly lower densities of age-1 Red Snapper on the new reefs during the September 2010 survey (set 2: 1.4 ± 0.6 fish/m³, $n = 10$; set 3: 3.0 ± 1.9 fish/m³, $n = 10$) compared with the reefs from set 1 (RM-ANOVA: $F_{2,63} = 8.9$, $P < 0.001$; Figure 3). In contrast, age-0 Red Snapper (2010 year-class) were significantly more abundant on reefs of set 3 during September (mean density \pm SE = 17.0 ± 2.7 fish/m³, $n = 10$) and October (22.3 ± 2.4 fish/m³, $n = 10$) compared with reefs of set 2 (September: 5.6 ± 1.6 fish/m³, $n = 10$; October: 8.0 ± 1.1 fish/m³, $n = 10$). This difference persisted to June 2011, when Red Snapper of the 2010 year-class were age-1 fish (set 2: mean density \pm SE = 13.3 ± 2.2 fish/m³, $n = 10$; set 3: 21.8 ± 1.4 fish/m³, $n = 10$; RM-ANOVA: $F_{1,63} = 51.0$, $P < 0.001$; Figure 4). In addition, a significant effect was detected for time of survey (RM-ANOVA: $F_{3,63} = 5.1$, $P = 0.003$), whereas the survey \times reef type interaction effect was not significant (RM-ANOVA: $F_{2,63} = 1.1$, $P = 0.35$). No age-0 Red Snapper were observed in June and July 2011 on any of the reefs built in 2010, but (similar to sets 2 and

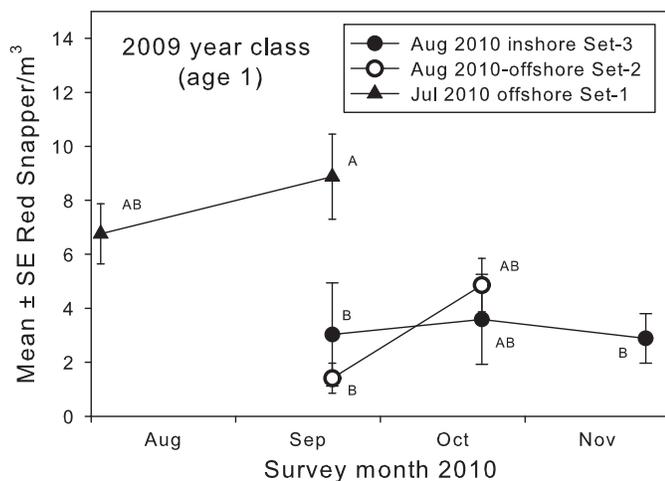


FIGURE 3. Mean (\pm SE) density of age-1 Red Snapper (2010 year-class) observed on the reefs deployed in 2010. Different letters indicate significant differences.

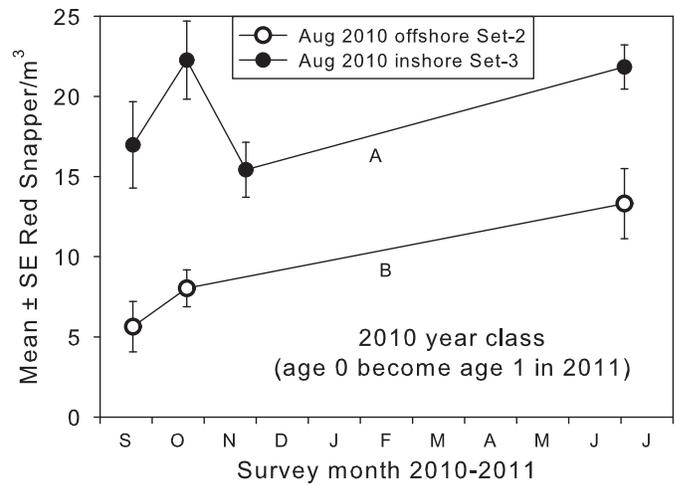


FIGURE 4. Mean (\pm SE) density of Red Snapper from the 2010 year-class observed on reefs (sets 2 and 3) that were deployed in August 2010 and surveyed in 2010 and 2011. Different letters indicate significant differences between inshore (set 3) and offshore (set 2) reefs; the survey \times reef type interaction effect was not significant.

3) the reefs of set 1 showed a substantial density of age-1 Red Snapper in July 2011 (23.8 ± 14.0 fish/m³, $n = 5$).

In 2010, at 1 m above the bottom, mean temperature ranged from 21.8 to 28.7°C, salinity ranged from 30.4 to 35.5‰, and DO ranged from 2.4 to 4.9 mg/L. In 2011, mean temperature ranged from 23.5 to 26.7°C, salinity ranged from 33.2 to 35.8‰, and DO ranged from 1.0 to 5.6 mg/L (Table 1). Hypoxic conditions were observed at the west site, where DO fell to levels as low as 0.4 mg/L (Table 1).

In early August 2011, age-0 Red Snapper were significantly more abundant on the reefs at the west site (mean density \pm SE = 66.6 ± 9.2 fish/m³, $n = 10$) than at the center site (37.3 ± 6.4 fish/m³, $n = 10$) or east site (23.9 ± 5.5 fish/m³, $n = 10$). However, in late August 2011, age-0 Red Snapper were significantly more abundant at the center site (58.7 ± 9.3 fish/m³, $n = 10$) than at the west site (2.4 ± 2.4 fish/m³, $n = 10$) or east site (11.1 ± 1.7 fish/m³, $n = 10$). In October 2011, age-0 Red Snapper were again significantly more abundant on reefs at the center site (mean density \pm SE = 37.2 ± 6.0 fish/m³, $n = 9$) than at the west site (8.9 ± 1.6 fish/m³, $n = 10$). No age-0 Red Snapper were observed in June 2012, but substantial densities of age-1 Red Snapper were observed at the east site (8.2 ± 1.8 fish/m³, $n = 10$) and center site (23.0 ± 4.8 fish/m³, $n = 9$; RM-ANOVA: $F_{5,97} = 14.6$, $P < 0.001$; Figure 5). Although the west site showed what appeared to be a higher abundance of age-1 Red Snapper (mean density \pm SE = 33.5 ± 1.8 fish/m³) in June 2012, it was removed from statistical analyses because only two reefs remained at the site.

During August–October 2011, the west, center, and east sites all had low age-1 Red Snapper densities ranging from 0 fish/m³ to 5.2 ± 1.6 fish/m³. The west site had the lowest densities of

TABLE 1. Mean (\pm SE) dissolved oxygen concentration (DO; mg/L), minimum (min) DO, mean temperature (temp; $^{\circ}$ C), and mean salinity (‰) observed at artificial recruitment reefs in the northeast Gulf of Mexico during 2010 and 2011.

Reef	Survey date(s)	Mean DO	Min DO	Temp	Salinity
Set 1, offshore	Aug 2–3, 2010	2.5 ± 0.32	2.1	24.4 ± 1.14	31.6 ± 0.87
	Sep 8–20, 2010	4.9 ± 0.44	4.0	27.1 ± 1.41	32.6 ± 0.90
Set 2, offshore	Sep 8–20, 2010	2.6 ± 0.69	1.4	26.4 ± 1.21	32.6 ± 1.26
	Oct 18–21, 2010			24.7 ± 0.22	33.5 ± 0.39
Set 3, inshore	Sep 8–20, 2010	2.4 ± 0.36	2.0	28.7 ± 0.35	30.4 ± 0.55
	Oct 18–21, 2010			24.1 ± 0.15	35.5 ± 0.64
	Nov 24, 2010			21.8 ± 0.04	34.7 ± 0.45
Set 4, center	Aug 30, 2011	3.0 ± 1.35	1.5	25.4 ± 0.65	35.3 ± 0.46
Set 5, east	Aug 3, 2011			26.2 ± 0.80	
	Aug 30, 2011	4.0 ± 0.87	2.9	26.7 ± 0.46	35.1 ± 0.59
	Oct 26, 2011	5.0 ± 0.13	4.8	23.5 ± 0.03	33.2 ± 0.02
Set 6, west	Aug 3, 2011			24.9 ± 0.08	
	Aug 30, 2011	1.0 ± 1.34	0.4	23.6 ± 0.09	35.8 ± 0.37
	Oct 26, 2011	5.6 ± 0.73	4.8	24.0 ± 0.06	33.9 ± 0.01

age-1 fish, while the east site had significantly higher densities in late August and October 2011 (RM-ANOVA: $F_{6,98} = 2.8$, $P = 0.02$; Figure 6). A significant negative correlation was found between the abundances of age-0 and age-1 Red Snapper ($r = -0.36$, $P = 0.004$) when compared over the first survey of all reefs in 2010 and 2011 ($n = 60$; Figure 7).

Sediment grain size was significantly different among the west, center, and east sites ($\chi^2 = 1,099.1$, $df = 12$, $P < 0.0001$; Figure 8). Fine sand and silt fractions decreased from west to east, whereas the coarse sand fraction increased from west to east. None of the 41 sediment samples showed detectable contamination from naphthalene, acenaphthylene, acenaphthene, or fluorene.

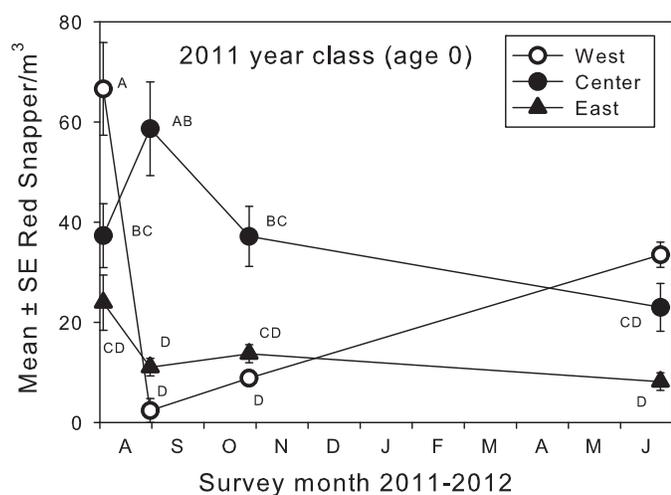


FIGURE 5. Mean (\pm SE) density of age-0 Red Snapper (2011 year-class) observed on the west, center, and east reefs deployed in July 2011. Different letters indicate significant differences.

DISCUSSION

Effects of the Deepwater Horizon Oil Spill

We failed to detect PAHs in the sediment samples at any reef site. These areas were well within the oil plume during much of the summer in 2010 (Crone and Tolstoy 2010; Norse and Amos 2010; Lindsley and Long 2012). It is reasonable to assume that these benthic habitats were simply not exposed to the oil because most of the oil floated at the surface rather than penetrating the average 20-m water column and accumulating in the benthic substrate. If any oil did reach the substrate, it had dissipated below detectable levels by 2011. It was clear that PAH contamination did occur at the surface in these

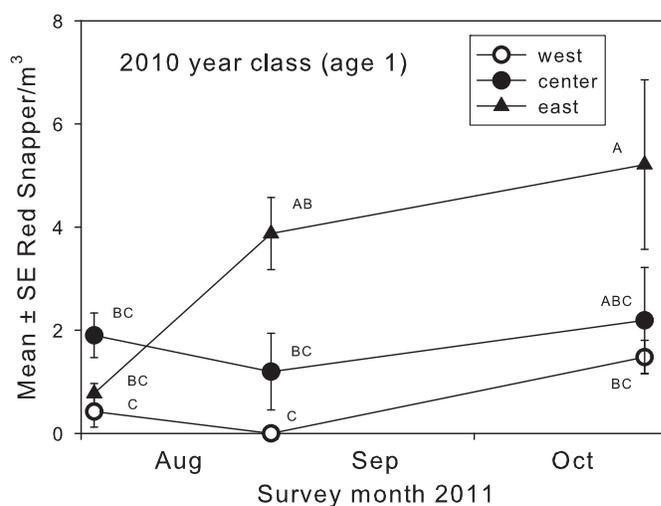


FIGURE 6. Mean (\pm SE) density of age-1 Red Snapper (2010 year-class) observed on the west, center, and east reefs deployed in July 2011. Different letters indicate significant differences.

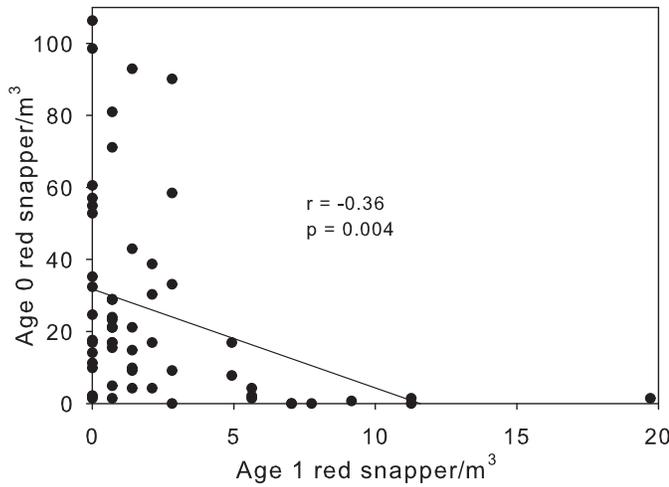


FIGURE 7. Pearson's product-moment correlation between Red Snapper age-0 abundance and age-1 abundance during the first survey of each reef.

areas of the northern GOM, and the contamination was predicted to significantly affect the early life stages (eggs and larvae) of Red Snapper, as the oil spill coincided seasonally with the June and July peaks of these pelagic life stages (Collins et al. 1996, 2001; Szedlmayer and Conti 1999; Jackson et al. 2006). The overlap between oil spill timing and early pelagic stages was predicted to result in reduced year-class strength or even total year-class failure, which would be reflected in a lack of postsettlement age-0 Red Snapper and reduced numbers of age-1 Red Snapper during the following year. However, we did not detect such patterns; postsettlement densities of age-0 Red Snapper in fall 2010 were similar to those observed in previous years by using the same assessment methods (Szedlmayer 2011), and

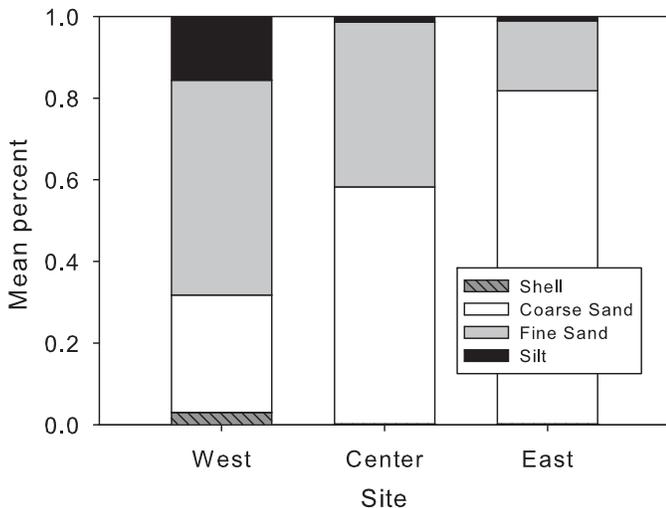


FIGURE 8. Mean percent composition of sediment samples taken from the reefs deployed in July 2011 (west, center, and east sites). To facilitate visual comparison, some substrate size categories have been combined (size categories are: shell, >1,000 μm ; coarse sand, >250 μm ; fine sand, >63 μm ; and silt, <63 μm).

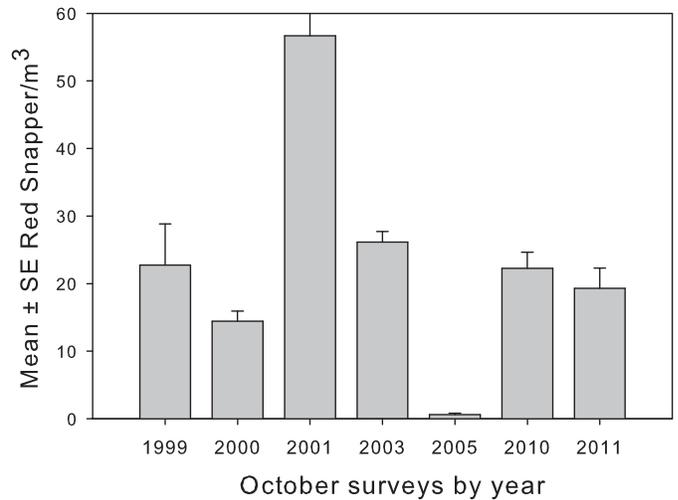


FIGURE 9. Comparison of age-0 Red Snapper abundance on small recruitment reefs as determined from October surveys in the present study (2010 and 2011) and a previous study (1999–2005; Szedlmayer 2011).

age-1 Red Snapper of the 2010 year-class were abundant on all reefs in 2011. For example, October density of age-0 Red Snapper at the reefs of set 3 (mean \pm SE = 22.3 \pm 2.4 fish/m³) reached levels similar to the October mean density from 1999 to 2005 (26.3 \pm 2.4 fish/m³; range = 0.6–56.7 fish/m³; Szedlmayer 2011) in the same area as examined in the present study (Figure 9). One might speculate that new recruits in 2010 could have originated from other areas (e.g., west of the oil plume); however, due to the short duration of the pelagic stage (25 d; Szedlmayer and Conti 1999; Rooker et al. 2004) and the large area affected by oil, this scenario is highly unlikely.

We did not directly measure PAH contamination in tissues from age-0 and age-1 Red Snapper. Instead, we examined sediments because they are the primary repository of PAHs in the environment, and if PAHs were available to the system they would be most readily detected in the sediments surrounding our recruitment reefs (Latimer and Zheng 2003). In addition, it is well known that PAHs are quickly metabolized by marine fishes and their detection in tissue samples is difficult due to a short half-life (Lemaire et al. 1990). The lack of PAHs in sediments surrounding our reef sites and the quick metabolism of PAHs by marine fishes thus made it highly unlikely that PAHs would have had any long-lasting effects in the age-0 and age-1 fish residing on these reefs. If PAHs did cause any mortality of eggs, larvae, or postsettlement recruits, the presence of normal densities of age-1 Red Snapper during the next spring demonstrated that enough recruits survived to saturate the high-quality habitat provided by the artificial reefs. Thus, any oil spill effects on early life stages of benthic Red Snapper were negligible.

Interactions between Age-0 and Age-1 Red Snapper

Consistent with past studies, resident competitors and predators had effects on the recruitment of age-0 Red Snapper. Mudrak and Szedlmayer (2012) found a negative correlation

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between age-0 and age-1 Red Snapper abundance, and both laboratory studies (Bailey et al. 2001) and field studies (Workman et al. 2002) have shown that older Red Snapper will exclude age-0 Red Snapper from structure. Age-0 Red Snapper abundance on the reefs of set 1 (1.0 ± 0.4 fish/m³) in August 2010 (present study) was lower than the densities observed on identical reefs at the same location in August 2008 (16.0 ± 3.9 fish/m³) and 2009 (23.6 ± 6.6 fish/m³; Mudrak and Szedlmayer 2012). In the present study, reef habitats were built in July 2010 with the intention that they would be located away from any larger fish aggregations and would provide open, unoccupied habitats. Unexpectedly, however, reefs belonging to set 1 were quickly colonized by age-1 Red Snapper before the first of the age-0 Red Snapper recruits arrived.

Age-1 Red Snapper densities (6.8 ± 1.1 fish/m³) in August 2010 (present study) were also higher than densities on the same reef design and location in August 2008 (1.0 ± 0.6 fish/m³) and 2009 (5.0 ± 2.9 fish/m³; Mudrak and Szedlmayer 2012). The difference between 2009 and 2010 age-1 densities appears to be small; however, in 2009, age-1 Red Snapper were aggregated on two reefs (21 and 22 fish/m³) and few age-1 fish were found on the other eight reefs (1 fish/m³), while in 2010 the age-1 fish were more evenly distributed (2 reefs with < 3.0 fish/m³ and 8 reefs with 6–11 fish/m³). Thus, because most (80%) of the reefs in set 1 were already occupied by age-1 Red Snapper in early August 2010, it was difficult to use those reefs to test for 2010 year-class failure. Due to the quick recruitment of age-1 Red Snapper to the reefs in set 1, we deployed two more sets of reefs (sets 2 and 3) in August 2010 to further test for 2010 year-class failure. In September 2010, these new reefs showed substantial age-0 Red Snapper recruitment, with higher densities on the inshore reefs belonging to set 3. This pattern suggested that the inshore sites provided higher-value nursery habitat for age-0 Red Snapper than the offshore (set 2) sites. However, more importantly, failure of the 2010 year-class did not occur, as indicated by the presence of age-0 fish on the inshore reefs (set 3) in 2010 and by the substantial densities (13.3–21.8 fish/m³) of age-1 Red Snapper on the reefs of sets 1, 2, and 3 during the next year (2011).

Dissolved Oxygen and Age-0 Recruitment

Of the reef sets that were deployed in July 2011, age-0 Red Snapper were observed at all three sites on the first survey in early August 2011. However, at the west site by late August, there was a complete absence of age-0 Red Snapper on nine individual reefs, with age-0 Red Snapper being observed on only one reef. At that time, critically hypoxic conditions were detected at the west site (≤ 2 mg/L; Craig and Bosman 2013). Also notable was a general disappearance of reef fishes and invertebrates from the reefs at the west site. No PAHs were detected in the sediments surrounding the reefs within the hypoxic conditions, indicating that this hypoxic event was not caused by the local decomposition of oil in the sediment. Dissolved oxygen returned to “normal” levels (≥ 4.6 mg/L; Vaquer-Sunyer

and Duarte 2008) by the October 2011 survey, but age-0 Red Snapper densities never recovered to the pre-hypoxic conditions where more age-0 Red Snapper were observed during surveys at the west site than at the center and east sites. We suggest that this lack of return to pre-hypoxic conditions resulted from fish mortalities rather than emigration. It would be easy to envision that for Red Snapper and other cryptic, benthic-oriented fish, individuals that are forced up into the open pelagic habitat would be exposed to substantially increased predation pressure (Kramer 1987). After the hypoxic event, age-0 Red Snapper densities at the center and east sites consistently were significantly higher than those at the west site. Based on age-0 recruitment patterns at the center site, we also suspect that the center site was exposed to hypoxic conditions, but we were unable to document this with DO measures because the event probably occurred between our surveys. For example, when the center site was first surveyed in early August 2011, all 10 reefs were occupied by age-0 Red Snapper and many other reef fishes. The center reefs were surveyed again in late August 2011, and rather than seeing the month-old Red Snapper that had already been observed in early August and an increase in other reef fishes, we only observed newly settled age-0 Red Snapper (based on the fish's small size and semitransparent appearance). This finding suggests that the center reefs were exposed to hypoxic conditions in mid-August, which caused age-0 fish mortality or movement. After DO increased in late August, we only observed recruits that had immigrated after the hypoxic event. The patterns of decreased age-0 Red Snapper densities along with hypoxia at the west site and the lack of recovery of age-0 densities to pre-hypoxic levels indicate that DO is a major factor in age-0 Red Snapper recruitment (Goodman and Campbell 2007; Vaquer-Sunyer and Duarte 2008; Craig and Bosman 2013). Hypoxic conditions in the study area are rare but have been reported. Szedlmayer and Shipp (1994) reported a DO of 0 mg/L that was associated with the total disappearance of all fish in trawl surveys conducted in similar areas. Hypoxic conditions were again observed in the same area during 1998, along with the total disappearance of all fish from small recruitment reefs (Nowlin et al. 2000; S. T. Szedlmayer, unpublished data). Thus, although the long-term effects of hypoxia on Red Snapper are difficult to assess, short-term (within a year) effects on age-0 Red Snapper can be significant.

Habitat Comparisons

It is well documented that age-0 Red Snapper prefer complex structured habitat over flat substrate (Szedlmayer and Howe 1997; Workman et al. 2002; Lingo and Szedlmayer 2006; Piko and Szedlmayer 2007; Szedlmayer 2011), but differential habitat value based on natural sediment type was unclear. This study differed from other studies by placing structured artificial habitats over different substrates and then using the reef habitats as the sampling gear to compare possible differential habitat values. The use of this type of sampling for juvenile Red Snapper has clear advantages over past studies that attempted

to conduct evaluations based on trawl surveys (Szedlmayer and Conti 1999; Wells et al. 2008b), as Red Snapper show an affinity for structured habitat very early in their first summer and trawling of these habitats is usually not possible (Szedlmayer 2011). Thus, conclusions based on trawl samples may have been biased because the trawls only sampled surplus production and missed the major concentrations of young Red Snapper on structured habitats. Present comparisons of age-0 Red Snapper densities support this contention: past trawl-based estimates have ranged from 0.001 to 0.16 fish/m² (Szedlmayer and Conti 1999; Rooker et al. 2004; Wells et al. 2008b), whereas the reef-based estimates in the present study were as high as 66 fish/m³.

Prior to the occurrence of hypoxic conditions, age-0 Red Snapper densities were significantly higher at the west site, which had silt substrate; intermediate at the center site, which had sand substrate; and lowest at the east site, which had the coarsest sand substrate. This pattern was strengthened further during the next spring, when age-1 Red Snapper were observed at lower abundances on the east site than on the center site. Despite the fact that the west site was affected by hypoxia during the peak of Red Snapper recruitment in the previous year, the two west-site reefs still remaining in June 2012 showed substantial densities of age-1 Red Snapper (mean \pm SE = 33.5 \pm 1.8 fish/m³).

The linkage between substrate type and juvenile Red Snapper is not well established, but it has been well documented that other juvenile fish found on the continental shelf are closely linked with benthic epifauna and substrate type (Diaz et al. 2003). Benthic habitats with their associated epifauna in turn provide an important source of prey for age-0 Red Snapper (Szedlmayer and Lee 2004; Wells et al. 2008a; Redman and Szedlmayer 2009). The differences in Red Snapper density from west to east may also have resulted from a general west-to-east population decline related to the species' distribution on the shelf. However, age-0 Red Snapper collections obtained east of our study sites (Sluis et al. 2012) indicate that density patterns were related to habitat differences that were well within the range of Red Snapper distributions rather than reflecting declines in density as the species approached the edge of its geographic range (Camber 1955; Rivas 1966). Although densities of age-1 Red Snapper were low on all three reef sites in 2011 and did not prevent age-0 Red Snapper from recruiting to the reefs, age-1 Red Snapper were completely absent from 8 of the 10 reefs at the west site during the early August survey, whereas all reefs at the center site and 8 of the 10 reefs at the east site had at least one age-1 Red Snapper present. Therefore, while substrate type appears to affect the carrying capacity of age-0 Red Snapper, the effect of older conspecifics was still present. These patterns indicate that the finer-grain sediments to the west were of higher habitat value for age-0 Red Snapper but that older conspecifics and environmental factors (e.g., DO level) were more important and were able to override the potential advantages (e.g., different prey resources) provided by finer substrate.

We did not detect a DWH oil spill effect on age-0 and age-1 Red Snapper. We suggest that any possible PAH contamination simply remained at the surface and did not penetrate the deeper benthic habitats on the continental shelf. Analyses of sediment samples failed to detect any PAHs. We did not assess whether other areas of the GOM showed more PAH contamination or possible effects on the 2010 year-class of Red Snapper. To our knowledge, such data were not yet published at the time of the present study. However, we surmise that if any effect was detectable, it would have been apparent from our study area because in the past, this area has shown the highest abundance of juvenile Red Snapper compared with any other area in the GOM (Szedlmayer and Conti 1999); and the coverage and duration of the oil plume were greater off the coast of Alabama than in many other habitat areas potentially used by juvenile Red Snapper (NOAA 2010).

In this study, significant differences in age-0 Red Snapper densities were related to substrate type, with fine silt showing the highest densities; however, such substrate effects were overridden by the presence of age-1 Red Snapper and the effects of hypoxia. Age-1 Red Snapper almost completely prevented age-0 Red Snapper from recruiting to occupied reefs. Hypoxia caused Red Snapper densities to decline from very high values to almost zero in a short time period (<3 weeks). In the habitats affected by hypoxia, densities of age-0 Red Snapper did not recover to the higher levels observed in the early survey. We suggest that reduced densities of age-0 Red Snapper were the result of increased mortality rather than emigration because DO reached lethally low levels (Goodman and Campbell 2007; Diaz and Rosenberg 2008; Vaquer-Sunyer and Duarte 2008; Craig and Bosman 2013). Furthermore, if fish managed to escape the lethal hypoxic conditions by moving up into the water column, there was substantial potential for increased predation as these cryptic, benthic fish were forced out of their protected habitat and into open pelagic habitats (Kramer 1987).

Management Implications

To set biologically appropriate quotas, managers need a valid measure of recruitment into a fishery before those year-classes are exposed to fishing. Red Snapper stock assessments in the GOM use Southeast Area Monitoring and Assessment Program (SEAMAP) trawl surveys to gauge Red Snapper recruitment (SEDAR-31 2013). Data from the SEAMAP trawl surveys suggested that 2010 and 2011 were the worst recruitment years since 1994 for Red Snapper in the eastern GOM (SEDAR-31 2013). As a result, the Gulf of Mexico Fishery Management Council approved more conservative quotas in anticipation of two weak year-classes moving through the fishery (Gulf of Mexico Fishery Management Council, unpublished). In the present study, the abundances of age-1 Red Snapper observed on our small recruitment reefs during the spring of 2011 and 2012 suggest that survival and recruitment of age-0 Red Snapper in 2010 and 2011 were high enough to saturate available habitat. Based on the present observations, we expect the 2010 and 2011

year-classes to appear normal in future age frequency distributions. If in fact normal age frequencies are observed as the 2010 year-class progresses through time, the present reduction in catch quotas based on a predicted weak 2010 year-class would be unnecessary. However, in 2013, these year-classes were just beginning to recruit into the exploited fishery as age-3 (2010) and age-2 (2011) individuals. Thus, the correct prediction (i.e., either normal year-classes [present study] or weak year-classes [Gulf of Mexico Fishery Management Council, unpublished]) remains to be verified in future studies. Both fishery-dependent and fishery-independent sampling efforts over the next 5–6 years will be needed to make such assessments as these year-classes move through the exploited fishery. We also conclude that sampling methods incorporating the use of small recruitment reefs will provide more accurate estimates of juvenile Red Snapper recruitment patterns compared with traditional trawl surveys, and the use of recruitment reefs in sampling should be continued and expanded to other areas in the northern GOM.

ACKNOWLEDGMENTS

We thank G. Grove, J. Herbig, D. Horn, M. Piraino, C. Roberts, T. Syc, and N. Wilson for help with laboratory and field collections. This project was funded by the Marine Resources Division of the Alabama Department of Conservation and Natural Resources; the Sportfish Restoration Fund; the Marine Environmental Sciences Consortium; and British Petroleum. This is a contribution of the Alabama Agricultural Experiment Station and the School of Fisheries, Aquaculture, and Aquatic Sciences at Auburn University.

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