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## REPORT

# Decline in condition of gorgonian octocorals on mesophotic reefs in the northern Gulf of Mexico: before and after the Deepwater Horizon oil spill

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**Abstract** Hard-bottom 'mesophotic' reefs along the '40-fathom' (73 m) shelf edge in the northern Gulf of Mexico were investigated for potential effects of the Deepwater Horizon (DWH) oil spill from the Macondo well in April 2010. Alabama Alps Reef, Roughtongue Reef, and Yellowtail Reef were near the well, situated 60–88 m below floating oil discharged during the DWH spill for several weeks and subject to dispersant applications. In contrast, Coral Trees Reef and Madison Swanson South Reef were far from the DWH spill site and below the slick for less than a week or not at all, respectively. The reefs were surveyed by ROV in 2010, 2011, and 2014 and compared to similar surveys conducted one and two decades earlier. Large gorgonian octocorals were present at all sites in moderate abundance including *Swiftia exserta*, *Hypnogorgia pendula*, *Thesea* spp., and *Placogorgia* spp. The gorgonians were assessed for health and condition in a before-after-control-impact (BACI) research design using still images captured from ROV video transects. Injury was modeled as a categorical response to proximity and time using logistic regression. Condition of gorgonians at sites near Macondo well declined significantly post-spill. Before the spill, injury was observed for 4–9 % of large gorgonians. After the spill, injury was observed in 38–50 % of large gorgonians. Odds of injury for sites near Macondo were 10.8 times higher post-spill, but unchanged at far sites. The majority of marked injured colonies in 2011 declined further in condition by 2014. Marked healthy colonies generally remained healthy. Background stresses to corals, including fishing activity, fishing debris, and coral predation, were noted during surveys, but do not appear to account for the decline in condition at study sites near Macondo well.

**Keywords** Octocoral · Gorgonian · Gulf of Mexico · Mesophotic zone · Oil spill · Health assessment

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## Introduction

The Deepwater Horizon oil spill released 4.3 million barrels of crude oil near 1500 m depth in the Gulf of Mexico over a period of 87 d in the spring of 2010 from the Macondo well MC 252 (McNutt et al. 2011). The oil formed a large subsurface plume and produced a large surface slick that was visible by airplane and satellite for nearly 90 d (NOAA 2014). The biological footprint of the DWH spill on infaunal sediments has been calculated as 148 km$^2$ (Montagna et al. 2013), but recent studies indicate that the chemical footprint of impacted areas may be substantially larger than previously anticipated (Valentine et al. 2014). There is a potential that the biological footprint of the spill, including injury to corals, could increase with increasing search effort (Fisher et al. 2014).

The surface oil slick from the DWH blowout persisted in the northern Gulf of Mexico for several weeks over a series of deep-water rocky reefs called the Pinnacle Trend (Fig. 1). Fishermen refer to these as the 'broken grounds' (Gittings et al. 1992). The rocky plateaus occur along the 60- to 90-m depth contours between the Mississippi Delta and Pensacola, FL. Recreational and commercial fishermen recognize these '40-fathom' reefs as good fishing habitat for snapper and grouper, conferring social and economic value on these natural resources (Prytherch 1983; Scott-Denton et al. 2011).

There are nine named reefs in the Pinnacle Trend (Gardner et al. 2000). Among the largest of these are Alabama Alps Reef (AAR), Roughtongue Reef (RTR), and Yellowtail Reef (YTR), which were situated below the spill for 19–39 d (NOAA 2014). AAR (39 d), RTR (19 d), and YTR (19 d) are 57–109 km from the well. The reefs have been surveyed by remotely operated vehicle (ROV) since 1989. Two other reefs about 200 km to the east of the Macondo wellhead, Madison Swanson South Reef and Coral Trees Reefs, were below the slick for 0–3 d, and surveyed by ROV since 1997.

Gorgonian octocorals (sea fans), black corals, and scleractinian corals occur on all of these reefs, providing structure and refuge for small demersal fishes that are prey to larger fishes (Weaver et al. 2002). The corals contribute substantially to biodiversity in high relief areas on the reefs (Gittings et al. 1992). Suspension feeding corals are vulnerable to oil and dispersants (NOAA 2010) so these animals were considered as part of the Natural Resource Damage Assessment (NRDA) for DWH. Injury to gorgonian octocorals has been demonstrated adjacent to the wellhead, and this injury has been linked to DWH (White et al. 2012) for sites up to 22 km from the Macondo well (Fisher et al. 2014). Additional findings have linked

numerous injured coral colonies observed in the Pinnacle Trend to exposure to DWH oil (Silva et al. 2015).

Deep-water gorgonian octocorals (Alcyonacea) and black corals (Antipatharia) are common and conspicuous in the 60–90 m 'mesophotic' depth range in the northern Gulf of Mexico, from Texas to Florida (Bayer 1961; Rezak et al. 1985; Cairns and Bayer 2009). The gorgonians are important components of deep-reef habitat because they provide structural complexity, substrate, and refuge for fish and invertebrates (Krieger and Wing 2002; Buhl-Mortensen and Mortensen 2005). The soft coral colonies grow on rocky, current-swept habitat, and prefer high relief features.

Gorgonian octocorals on the Pinnacle Trend reefs are predominantly heterotrophic suspension feeders. Their branches grow in a flabellate, reticulated (sea fan) shape with an orientation perpendicular to prevailing currents in order to maximize particle flux and rates of capture for the polyps along the branches (Peccini and MacDonald 2008). These are not technically 'mesophotic coral ecosystems' (sensu Kahng et al. 2010) because the corals are azooxanthellate, but we refer to them as 'mesophotic reefs' because they occur in the deeper portion of the photic zone.

Gorgonian octocorals and antipatharians are susceptible to exposure to water-borne toxicants because they are large, emergent epifauna with polyps adapted to straining small particles of food from the water column. The diet and prey of these heterotrophic corals consist of holoplankton—small particles of phytoplankton and zooplankton. Stable isotope studies indicate that the colonies feed on surface-originated and re-suspended photosynthetic material (Sherwood et al. 2005; Sulak et al. 2008). Transport of surface particulates to deep-water corals can be rapid (Davies et al. 2009).

The most likely mechanism for oil/dispersant exposure to the reefs would be passive or active sinking of



Fig. 1 A map showing the surface oil slick generated by the Deepwater Horizon blowout at Macondo wellhead (*gray triangle*), overlaid with the location of four mesophotic reefs assessed in this study (*yellow circles*)—Alabama Alps Reef (AAR), Roughtongue Reef (RTR), Coral Trees Reef (CTR), and Madison Swanson South Reef (MSSR). Yellowtail Reef is adjacent to RTR
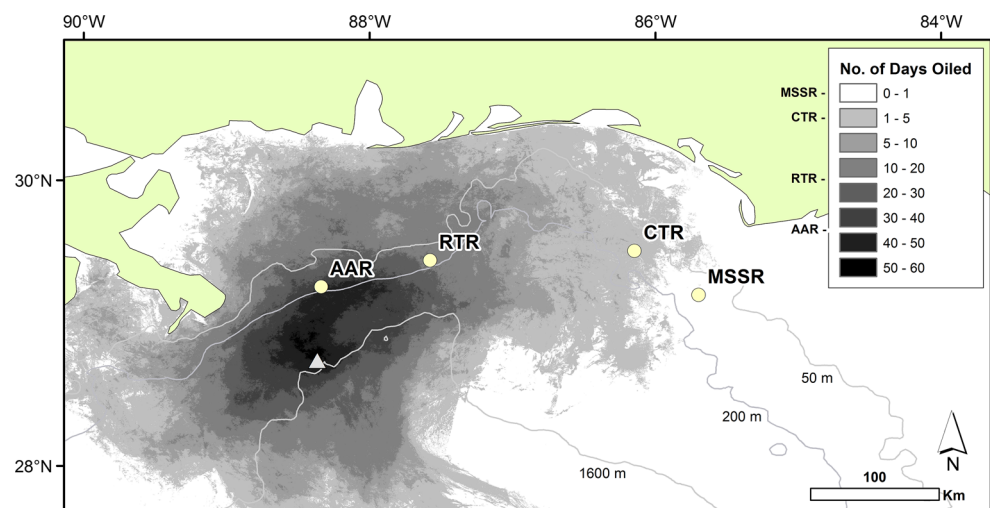
contaminated surface material toward the benthos (Passow et al. 2012) and/or re-suspension and advection of contaminated surface material in sediments from the reef perimeter onto the reef. These processes may have been intensified by storm events during the time when floating oil was present over the reef sites (Silva et al. 2015). Multiple studies have shown deleterious effects of oil and dispersant exposure on coral colonies and coral larvae (e.g., Loya and Rinkevich 1980; Goodbody-Gringley et al. 2013; DeLeo et al. 2015). Scleractinian coral tissue exposed to oil will break down (Johannes 1975), resulting in a thinning of coenosarc cell layers (Peters et al. 1981). The few studies that examined octocorals noted deleterious effects including polyp mortality and discoloration (DeLeo et al. 2015; Silva et al. 2015), inhibition of metamorphosis (Kushmora et al. 1997), and behavioral changes (Cohen et al. 1977).

Octocorals may be exposed to contaminants through the ingestion of contaminated plankton or suspended organic material. Octocorals ingest a wide variety of food resources, including zooplankton (Coma et al. 1994), detrital particulate organic matter (POM), nanoeukaryotes, ciliates (Ribes et al. 1999), and phytoplankton (Fabricius et al. 1995). Zooplankton can bio-accumulate toxic polycyclic aromatic hydrocarbons (Almeda et al. 2014) and exhibit isotopic field signatures that indicate oil-derived hydrocarbons have entered the food web (Graham et al. 2010). Effects of ingesting contaminated material by coral have not yet been studied.

Gorgonian octocoral colonies are good subjects of study to test for effects from the DWH spill because there is a precedent for injury to gorgonians from this oil spill (White et al. 2012; Silva et al. 2015). Furthermore, there is a potential for exposure to suspended and falling particles, and the reliance of these colonies on surface POM suggests a strong connection to surface plankton. This study asks: is there evidence of injury to gorgonian octocorals on mesophotic reefs near DWH? What types of injury were observed and to what degree? How does condition of gorgonians compare between sites near and far? Was there a change in condition to gorgonians before and after the DWH oil spill? We provide this information to assess potential injury to biota in the mesophotic zone relative to the DWH oil spill in the Gulf of Mexico.

## Methods

### Field methods

A before-after-control-impact (BACI) research design was used to study demersal fish and coral populations 50–100 m deep between Louisiana and West Florida at sites near and far from the Macondo well MC252 as part of the NRDA for DWH. BACI is a powerful research design that allows for detection of change over time. Two 'impact sites,' Alabama Alps Reef (AAR) and Roughtongue Reef/Yellowtail Reef (RTR/YTR), were near the Macondo well within 109 km of the wellhead, 60–88 m below floating oil discharged during the DWH spill for >19 d, and were subject to dispersant applications (Fig. 1). In contrast, two other 'control' or 'reference sites' called Coral Trees Reef (CTR) and Madison Swanson South Reef (MSSR) were far from the Macondo well (~200 km), below the surface slick for <3 d or not at all, respectively, and were not subject to dispersant application. RTR and YTR were treated as one impact site because they are directly adjacent (~1.5 km apart) with similar crest depths (Table 1).

The reefs were surveyed before the spill in 1989 (MAMES: Brooks 1991) and 1997–2003 (USGS: Weaver et al. 2002) and then after the spill, in 2010, 2011 and 2014 as part of the NRDA effort (Table 2). Remotely operated vehicles (ROVs) equipped with still and video cameras were used to conduct slow moving, low altitude, 2–5 min video transects on the reeftop biotope. The survey methods supported a BACI research design to compare condition and abundance of corals at mesophotic sites near and far from DWH, before and after the oil spill.

**Table 1** Study site characteristics

| Reef | Lat | Long | Distance (km) | Days under slick | Area (km²)[a] | Reef base depth (m) | Reef crest depth (m) | Mean density (corals 100 m⁻²) | Density SE | Max. density (corals 100 m⁻²) |
|---|---|---|---|---|---|---|---|---|---|---|
| Alabama Alps | 29.255 | −88.339 | 57 | 39 | 0.126 | 88 | 72 | 21.1 | 2.1 | 47.7 |
| Roughtongue | 29.442 | −87.579 | 109 | 19 | 0.082 | 78 | 64 | 4.0 | 0.8 | 11.6 |
| Yellowtail | 29.440 | −87.575 | 109 | 19 | 0.038 | 68 | 60 | 17.0 | 2.8 | 35.9 |
| Coral Trees | 29.505 | −85.146 | 231 | 3 | 0.324 | 94 | 84 | 11.0 | 2.6 | 37.7 |
| Madison Swanson | 29.187 | −87.679 | 266 | 0 | 5.026 | 94 | 73 | 11.4 | 1.6 | 25.4 |

Days under slick are from NOAA (2014) and distance (km) refers to the distance in km from the Macondo well. Reef areas ([a]) are from Nash and Randall (2015). Reef depths are from Weaver et al. (2002). Coral densities and standard errors (SE) are reported for target taxa in 2014, of the large sea fan group including *Swiftia exserta*, *Hypnogorgia pendula*, *Thesea nivea*, and *Placogorgia* spp

**Table 2** Cruise expeditions that contributed video for health assessment of corals

| Cruise | Year | Month | Reef survey sites | | | | | Transect time (min) | Video frames | | Analyses |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | AAR | RTR | YTR | CTR | MSSR | | Total | Verified | |
| Pre-spill | | | | | | | | | | | |
| MAMES | 1989 | June | X | | | | | 70.0 | 307 | 170 | I |
| USGS | 1997 | August | | X | | | | 43.9 | 109 | 48 | I |
| USGS | 1999 | August | X | | | | | 21.7 | 126 | 51 | I |
| USGS | 2000 | March | | | X | | | 7.6 | 25 | 12 | I |
| USGS | 2001 | May | | | X | | | 12.8 | 52 | 25 | I |
| USGS | 2001 | August | | | | X | X | 44.6 | 367 | 166 | I |
| USGS | 2002 | August | | | | X | X | 53.6 | 482 | 265 | I |
| USGS | 2003 | June | | X | X | | | 41.4 | 182 | 109 | I |
| Total | | | | | | | | **295.6** | **1650** | **846** | |
| Post-spill | | | | | | | | | | | |
| NRDA | 2010 | August | X | X | | X | | 62.5 | 263 | 90 | C |
| NRDA | 2011 | September | X | X | X | X | X | **340.3** | **1055** | **439** | I, M, S |
| NRDA | 2014 | June–July | X | X | X | X | X | 1448.0 | 2848[a] | NA | M, D |

Bold values represent total time and total number of video frames used in analyses

Cruises: *MAMES* Mississippi/Alabama Marine Ecosystem Survey, *USGS* United States Geological Survey, *NRDA* National Resource Damage Assessment. Reefs: *AAR* Alabama Alps, *RTR* Roughtongue, *YTR* Yellowtail, *CTR* Coral Trees, *MSSR* Madison Swanson South. Analyses: *I* injury, *C* chemistry, *M* markers, *S* species diversity, *D* density

[a] Incomplete; full video review completed at impact sites only

Pre-spill video transect methods were comparable to post-spill methods, but standard definition cameras used pre-spill were generally lower resolution than high-definition cameras used after the spill. Full details on the ROVs and cameras are provided as Electronic Supplementary Materials (ESM—ROV Methods). Together the USGS, MAMES, and NRDA datasets comprised 295 min of pre-spill video to compare with 340 min of post-spill video in 2011. By combining these various datasets, a minimum of 30 min of high-quality transect video was available for each reef before and after DWH oil spill (ESM Fig. S1). While transect time differed among sites and time periods, total observations were comparable with large enough samples to facilitate robust statistical analyses based on proportions (see 'Statistical methods' section). Variable transect times were included as a continuous covariate in the statistical model with near and far sites run separately, thereby adjusting for any potential effect of effort.

All octocorals appearing along transects in 2011 were enumerated for analyses of species abundance and diversity. A group of select taxa were identified for assessment of health and condition based on discernible species and condition. Species that attain large colony sizes (>20 cm in mean height or width) were readily identifiable in standard and high-definition video, and their condition could be assessed (Fig. 2). The species used in health analyses included *Swiftia exserta*, *Hypnogorgia pendula*, *Thesea nivea*, *T. rubra*, *Placogorgia* spp., *Paramuricea* spp., and

*Muriceides* cf. *M. hirta*. *Paramuricea* and *Muriceides* could not be distinguished from *Placogorgia* spp. in video and still images based on gross morphology, and were thus binned together for health analyses. *Placogorgia* were most common among the yellow plexaurid specimens collected, particularly *P. rudis*. A species identification guide to large gorgonian taxa is provided in ESM—Species guide. Small gorgonians (*Nicella* and *Bebryce* spp.) were difficult to discern in video due to image quality, colony size, and reproducibility of results, so these taxa were not assessed.

Due to differences in species composition among sites, the large, discernible gorgonian species were binned together into a single group (large gorgonians) for the BACI analysis. These were treated as one generic taxon in order to achieve comparable sample sizes among reef sites. This treatment rests on the assumption that the largest gorgonians at different sites have similar exposure to currents and similar feeding modes.

To monitor change in injury to gorgonians over time, weighted nylon rope markers flagged with syntactic foam and reflective tape were deployed at 12 locations in 2011. Deployments included six markers at AAR and six at RTR. Of these 12 markers, 11 were re-photographed in 2014. Gorgonian corals at each flagged location were photographed in 2011 with an AquaSLR digital still camera and then again in 2014 using a DPC-8800. The time-series images sought to reproduce ROV heading, camera angle, zoom, and lighting.
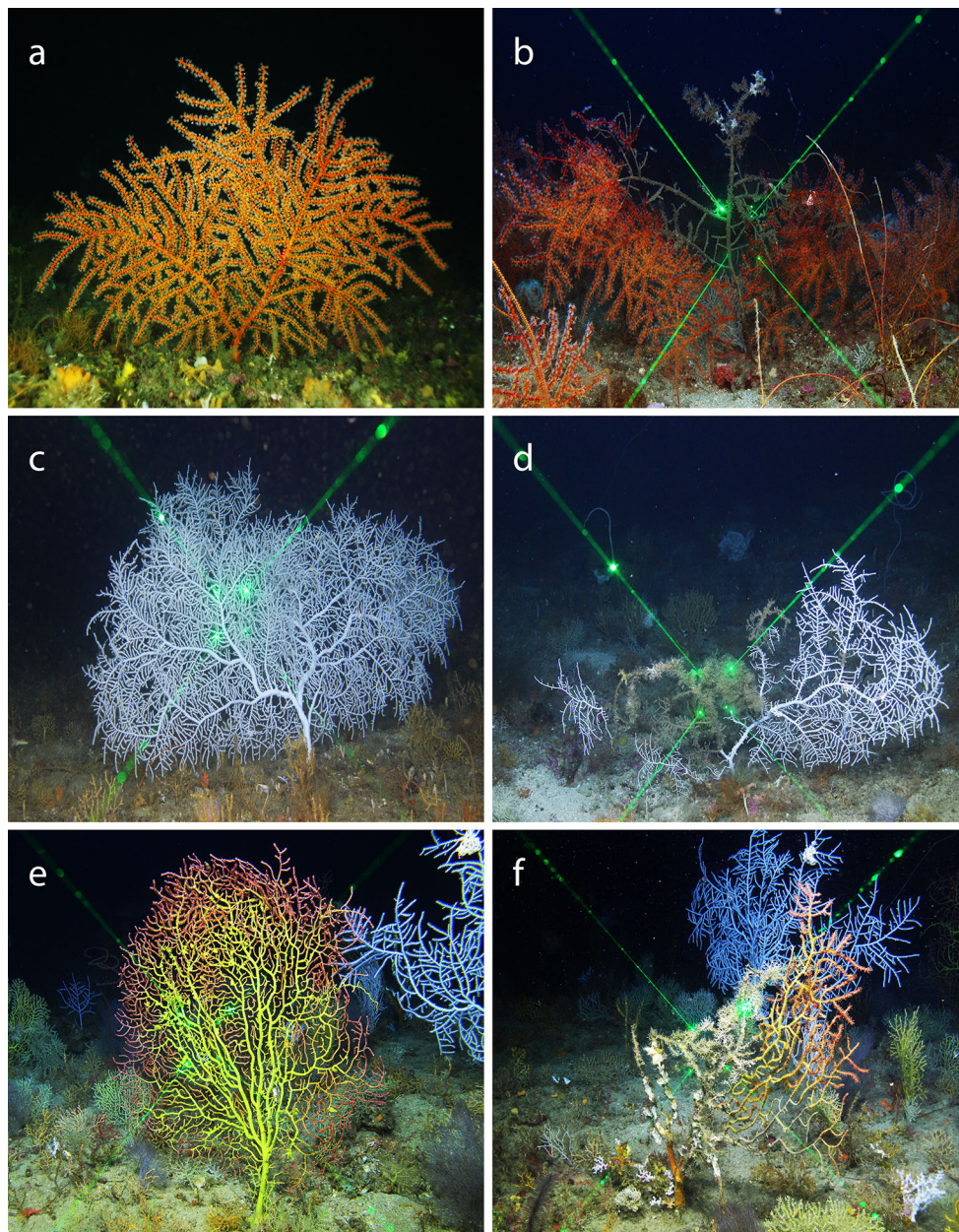
**Fig. 2** Healthy and injured colonies of the gorgonian octocorals *Swiftia exserta* (**a**, **b**), *Hypnogorgia pendula* (**c**, **d**), and *Placogorgia* sp. (**e**, **f**) similar in appearance to *Paramuricea*

## Laboratory methods

A total of 153 biological samples of octocorals were collected by ROV in 2010 ($n = 31$), 2011 ($n = 58$), and 2014 ($n = 64$) for the purposes of species identification and/or chemical analyses. Specimens were documented and preserved according to established protocols (Etnoyer et al. 2006). Morphological diagnosis was achieved by scanning electron microscopy (JEOL JSM5600LV) and light microscopy (Olympus SZX16). Genus-level determination was based upon the criteria set forth by Bayer (1981). Species-level identifications were made using the best

available keys, and species identities were confirmed through consultation with experts at Smithsonian National Museum of Natural History (See ESM Figs. S4–S22).

For image-based analyses of in situ coral health and condition, target taxa were identified from video and a framegrab was generated for detailed assessment of health and condition. Health assessment was a three-stage process. Framegrabs were selected from each sequence so as to optimize resolution and visibility of the coral colonies being assessed. In the second review, gorgonians were 'verified,' i.e., assessed for discernible condition. Gorgonians were 'discernible' when the whole colony was clearly visible

(e.g., cloudy water, fish, or colony orientation did not obscure large parts). In the third stage, injured and healthy regions on gorgonians were outlined using the software photoQuad (Trygonis and Sini 2012). Injury impact rankings (degree of injury) were assigned based on the categorical scale (0–4) described by White et al. (2012) where '0' denoted healthy and '4' indicated >90 % damage.

Injured colonies were categorized both in terms of their degree and type of injury. Types of injury included bare or denuded branches, broken branches, overgrowth, abnormal polyps, and/or severe discoloration. In the case of broken branches, the flabellum shape and condition were referenced to observed patterns of branching for the given taxa, and then breakage was coded at the holdfast, primary or secondary branch. Degree of injury was upweighted (increased by one level) when there was clear evidence of major branch loss.

## Statistical methods

### Community composition

The nonparametric analysis of similarity (ANOSIM) global R statistic (Clarke and Green 1988) was employed to test the null hypothesis of no difference in species composition among reef sites using non-metric multidimensional scaling techniques (nMDS) with an underlying Bray–Curtis similarity matrix based on counts of morphospecies along transects in 2011. Similarity percentages (SIMPER) were calculated using Bray–Curtis distance to identify the species groups contributing significantly to the differences among groups near and far from DWH. Multivariate analyses were conducted using the software PRIMER 6.1 (Clarke and Gorley 2006). Univariate analyses employed the nonparametric Kruskal–Wallis statistic with Tukey's honest significant difference (HSD) post hoc test to test the null hypothesis of no difference in frequency of occurrence for small and large gorgonians, fishing gear, and gear interactions.

### Health assessment

The health assessment considered an ordered, categorical range of injuries by degree of intensity (0–4; White et al. 2012) in a BACI design. The categorical scale for injury was 0 = healthy colony, <1 % injury; 1 = 1–10 % injury; 2 = 10–50 %; 3 = 50–90 %; and 4 = >90 % (White et al. 2012). These ranks were used for consistency with other DWH-NRDA studies (White et al. 2012; Hsing et al. 2013; Fisher et al. 2014). The values were pooled together in two ways. Injury was considered in the binary sense, as absent (0) or present (1–4), and as low ranks (0, 1) or high ranks (2, 3, 4). Dead gorgonian stolons and toppled colonies were treated in a separate class or injury rank (=4) as

appropriate. The marker study also used an ordered categorical response, in the form of 0 = healthy, 1 = injured, 2 = more injured.

Severity of injury to large gorgonians was modeled as a function of proximity to Macondo well (near and far) and time (post-spill vs. pre-spill). Injury was treated as a binary response (logit, dependent variable) using logistic regression to obtain odds ratio estimates and Wald confidence intervals. The predictor variables were proximity and time frame, and the response variable was presence or absence of injury. Transect duration was included as a continuous covariate to adjust for variable transect lengths.

A sign test was used to measure the direction of change (from 2011 to 2014) in injured status for marked colonies revisited in 2014. The test statistic was calculated from the difference in injury (injury 2014–injury 2011) to evaluate the direction of change in status (more injured, less injured, or no change).

## Results

### Community composition

At least 31 octocoral species were collected (Table 3). Biological species richness ranged from nine species at CTR to 17 species at RTR. Morphospecies richness in video samples ranged from six at RTR to 11 at AAR. Species composition in video was significantly different among sites (ANOSIM test, Global R = 0.66, $p < 0.01$) and among groups near and far from DWH (ANOSIM test, Global R = 0.40, $p < 0.01$). Small gorgonian octocorals *Bebryce* spp., *Nicella* sp., and *Villogorgia* sp. contributed a cumulative 51.6 % to the dissimilarity among distance groups, while large gorgonians *S. exserta* and *Placogorgia* spp. contributed an additional 18 % to the dissimilarity among distance groups.

No single species occurred in equivalent abundance at all study sites. Small colonies <20 cm (e.g., *Bebryce* and *Nicella* spp.) were highly abundant at some sites and relatively rare at others. The frequency of small fans was significantly different among sites (Kruskal–Wallis, $p < 0.001$). The frequencies of large gorgonians were more consistent among sites ($p = 0.05$; ESM Fig. S2). Maximum densities of large gorgonians ranged from 12 to 48 colonies 100 m$^{-2}$ (Table 1).

### Health assessment

#### Was there a change in condition to gorgonian octocorals before and after the DWH oil spill?

There was a significant change in condition to gorgonian octocorals before and after the oil spill at sites below the

**Table 3** Octocoral species identified in sample collections 2010–2014

| | Northwest | | | Northeast | |
|---|---|---|---|---|---|
| Species ID | AAR | RTR | YTR | CTR | MSSR |
| *Bebryce cinerea* | | X | | X | X |
| *Bebryce grandis* | X | X | | | X |
| *Bebryce parastellata* | X | X | | | X |
| *Carijoa riisei* | | X | | | |
| Ellisellidae sp.1 | | X | | | X |
| Ellisellidae sp.2 | | X | | | |
| Ellisellidae sp.3 | | X | | | |
| *Hypnogorgia pendula* | X | X | | X | X |
| *Leptogorgia* sp. | X | X | X | | |
| *Muriceides* cf. *M. hirta* | X | | | | |
| *Nicella* cf. *N. americana* | X | X | | | |
| *Nicella* spp. | | X | | | X |
| *Paramuricea* spp. | X | | | | X |
| *Placogorgia* cf. *P. mirabilis* | | X | | | X |
| *Placogorgia tenuis* | | | | X | |
| *Placogorgia rudis* | X | | | | X |
| *Placogorgia* sp.1 | X | X | | X | |
| *Placogorgia* sp.2 | X | | | X | X |
| *Scleracis* cf. *S. guadalupensis* | | X | | | X |
| *Scleracis* sp. | | X | | | X |
| *Swiftia exserta* | X | X | X | | |
| *Thesea* sp. | X | | | | |
| *Thesea* cf. *T. citrina* | X | | | | |
| *Thesea* cf. *T. granulosa* | X | | | | X |
| *Thesea* cf. *T. guadalupensis* | | | | X | |
| *Thesea* cf. *T. hebes* | | | | X | |
| *Thesea nivea* | X | X | | | X |
| *Thesea* cf. *T. parviflora* | | | | | X |
| *Thesea rubra* | | | | X | X |
| *Villogorgia* sp.1 | | X | X | X | X |
| *Villogorgia* sp.2 | | X | | | |

Reefs are: Alabama Alps Reef (AAR), Roughtongue Reef (RTR), Yellowtail Reef (YTR), Coral Trees Reef (CTR), and Madison Swanson South Reef (MSSR). Species in the shaded rows were 'large taxa' included in health/injury analyses

surface oil slick ($p < 0.0001$, OR = 7.0–16.7; Table 4). Odds of injury after the spill were 10.8 times higher than injury before the spill for all injury types (all ranks 1–4; Fig. 3a) and 6.9 times higher for injuries >10 % (ranks ≥2; Fig. 3b). The historical injury rate for large gorgonians at impact sites was 4.3 % (9/210) at RTR/YTR and 8.9 % (24/271) at AAR, with all taxa pooled together (Fig. 4). Injury rates after the spill increased to 38 % (35/93) and 50 % (105/210) for RTR/YTR and AAR, respectively. Injury was documented across all taxa, ranging from 21 % (5/24) of *Placogorgia* spp. to 62 % (35/56) of *Thesea* spp. post-spill (Fig. 5).

Before the spill, the condition of gorgonians at sites AAR and RTR/YTR near DWH was healthy compared to far sites (Fig. 4). The odds of injured gorgonians far from the wellhead were historically 7.7 ($p < 0.0001$, OR = 4.6–13.0) times higher than the odds of injured gorgonians near DWH. Pooling taxa at reference sites yield historical injury rates of 28.4 % (92/324) and 10.8 % (24/222), for Madison Swanson South Reef (MSSR) and Coral Trees (CTR), respectively. Pooling reference sites (CTR/MSSR) showed a moderate increase in gorgonian injury from 21 % pre-spill to 26 %

post-spill. The change in condition at reference sites was not significantly different ($p = 0.651$, OR = 0.7–1.7) before and after the spill (Table 4, Fig. 3a, b).

Taken together, these results indicate a significant effect of time only at sites near the wellhead; gorgonian condition did not change significantly at sites far from the wellhead (Fig. 6). Before the spill, reference sites were degraded relative to impact sites, but after the spill the pattern reversed, with the odds of injured gorgonians near DWH 2.5 (=1/0.4) times higher than far sites.

Several different statistical models were tested: an ordinal logistic regression model (OLRM) using all five ordered response (impact ranking) categories; a binary logistic regression model (LRM0) defining healthy versus injured as impact ranking 0 versus (1, 2, 3, 4) combined, and a binary logistic regression model (LRM1) defining healthy versus injured as impact rankings (0, 1) versus (2, 3, 4) combined. Each of the various models gave the same interpretation and similar odds ratio (OR). The binary logistic regression model was presented, due to concerns about low cell frequencies for some of the impact ranking categories. Goodness-of-fit tests suggested some degree of lack of model fit, although receiver operating characteristic (ROC) curves indicate reasonably good predictive power for sites near the wellhead (area under the ROC curve ranged from 0.74 to 0.78).

### What types of injury were observed and to what degree?

Types of injury to large gorgonians were similar among sites near and far, both pre-spill and post-spill. While most injured gorgonian colonies exhibited more than one form of injury, the most common *primary* forms of injury across all sites post-spill were overgrowth (47 %), broken branches (12 %), or bare branches (10 %). Frequency of primary injury types across all sites was similar pre-spill, with examples of overgrowth (49 %), broken branches (26 %), and bare branches (14 %). Overgrowth consisted primarily of hydroids or sedimented material. Bare branches had clear loss of the coenosarc and polyps, with only the axis remaining. Post-spill, overgrowth was also the predominant form of injury at sites both near (48 %) and far (45 %). Less common forms of injury included severe discoloration, eroded polyps, and toppled colonies. Severe discoloration was unusually dark tissue of brown or gray (*S. exserta*, *H. pendula* and *Placogorgia* spp.) or unusually light tissue with erosion of polyps (*T. nivea*).

### Was there a change in condition to marked colonies after the DWH oil spill?

Colonies at the marked locations included six *Hypnogorgia* and 12 *Swiftia*. Of the 18 total marked colonies, eight were

**Table 4** Summary statistics showing results of logistic regression models

| Effect | Sites | df | p | Odds ratio[a] (and 95 % CL) | Model | Area under ROC curve |
|---|---|---|---|---|---|---|
| Time frame (post vs. pre) | Near | 1 | <0.0001 | 10.8 (7.0–16.7) | LRM0 | 0.78 |
| | | 1 | <0.0001 | 6.9 (4.4–10.7) | LRM1 | 0.74 |
| | | 1 | <0.0001 | 10.0 (6.5–15.4) | OLRM | N/A |
| | Far | 1 | 0.651 | 1.1 (0.7–1.7) | LRM0 | 0.58 |
| | | 1 | 0.360 | 1.2 (0.8–2.0) | LRM1 | 0.60 |
| | | 1 | 0.491 | 1.2 (0.8–1.8) | OLRM | N/A |
| Proximity (far vs. near) | Pre | 1 | <0.0001 | 7.7 (4.6–13.0) | LRM0 | 0.70 |
| | | 1 | <0.0001 | 5.8 (3.3–9.9) | LRM1 | 0.68 |
| | | 1 | <0.0001 | 7.2 (4.3–12.0) | OLRM | N/A |
| | Post | 1 | <0.0001 | 0.4 (0.3–0.6) | LRM0 | 0.60 |
| | | 1 | 0.0057 | 0.5 (0.3–0.8) | LRM1 | 0.57 |
| | | 1 | <0.0001 | 0.4 (0.3–0.6) | OLRM | N/A |

LRM0 is a logistic regression model (binary response) with healthy defined as impact ranking = 0, and injured defined as impact ranking = (1, 2, 3, or 4). LRM1 is a logistic regression model (binary response) with healthy defined as impact ranking = 0 or 1, injured defined as impact ranking = (2, 3, or 4). OLRM is an ordinal logistic regression model using five ordered response categories (impact rankings 0, 1, 2, 3, 4)

[a] Odds of injured coral
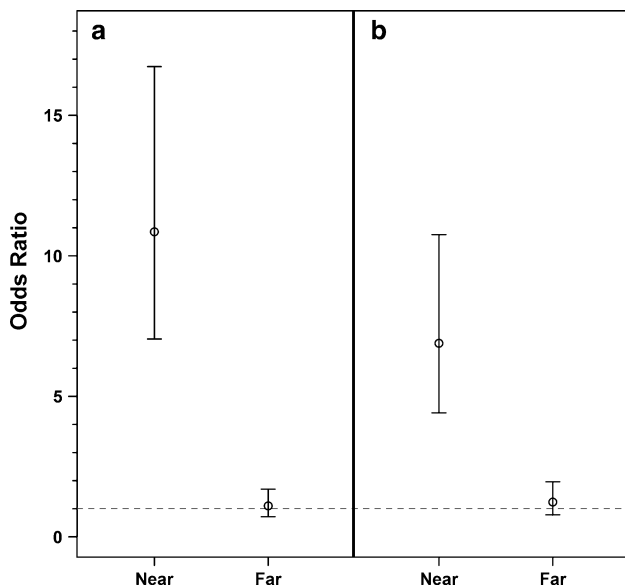


**Fig. 3** Odds ratio estimates (*circles*) with 95 % confidence intervals (*error bars*) for odds of injury post-spill versus odds of injury pre-spill at sites near and far from Macondo wellhead. **a** Odds ratios with rank 0 = healthy, and ranks 1–4 = injury. **b** Odds ratios with ranks 0, 1 = healthy; and ranks 2–4 = injury. The *dashed line* at y = 1 indicates no significant difference from pre-spill

considered healthy and ten injured in 2011. Marked corals imaged in both 2011 and 2014 (n = 18) indicated that most healthy corals remained healthy (7/8 = 88 %) and most colonies that were injured in 2011 progressed in injury (8/10 = 80 %). The null hypothesis of no change was rejected (p < 0.01, two-sided sign test), and the test statistic was positive, indicating a direction of change from less injured to more injured. Injuries included loss of tissue, expanded overgrowth, pruning of branches, and toppling of the colony. One injured colony of *Swiftia* remained at the same level of injury. In the only case where a colony progressed from injured to healthy, injury in 2011 was to 4 % of the *Swiftia* colony in overgrowth on secondary branches. The location of initial injury appeared to have some influence on the rate of injury progression. For example, injury of <3 % at the base of a *Hypnogorgia* colony resulted in rapid progression of overgrowth, loss of branches, and collapse of the colony. Thus, low percentages of injury (3–4 %) could be followed subsequently by either colony recovery or colony collapse (Fig. 7).

## Discussion

This study found clear evidence of injury to at least four species of gorgonian octocorals on mesophotic reefs situated below the surface oil slick from the Deepwater Horizon blowout at Macondo wellhead. Results indicate a highly significant decline in condition at sites nearest the wellhead after the spill. Decline in condition was severe, from <10 % of colonies injured before 2003 to more than 50 % of colonies injured in 2011. Nearly all injured colonies marked in 2011 declined in condition, suggesting that recovery of corals is unlikely. The majority of healthy colonies marked in 2011 remained healthy, suggesting that the cause of injury was ephemeral. Injury occurred in all taxa of large gorgonians, including *S. exserta*, *H. pendula*, *Thesea* spp., and *Placogorgia* spp., in the form of eroded polyps, discoloration, bare branches, overgrowth, missing branches, and broken branches.

Fig. 4 Overall frequency of injury to large gorgonians, with all ranks (1–4) combined, before and after Deepwater Horizon oil spill at the Macondo well
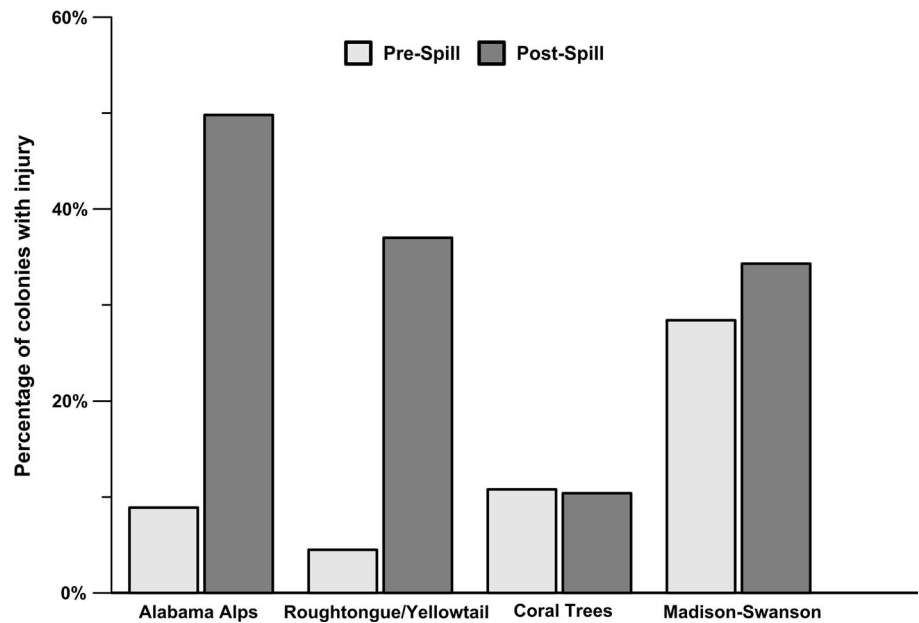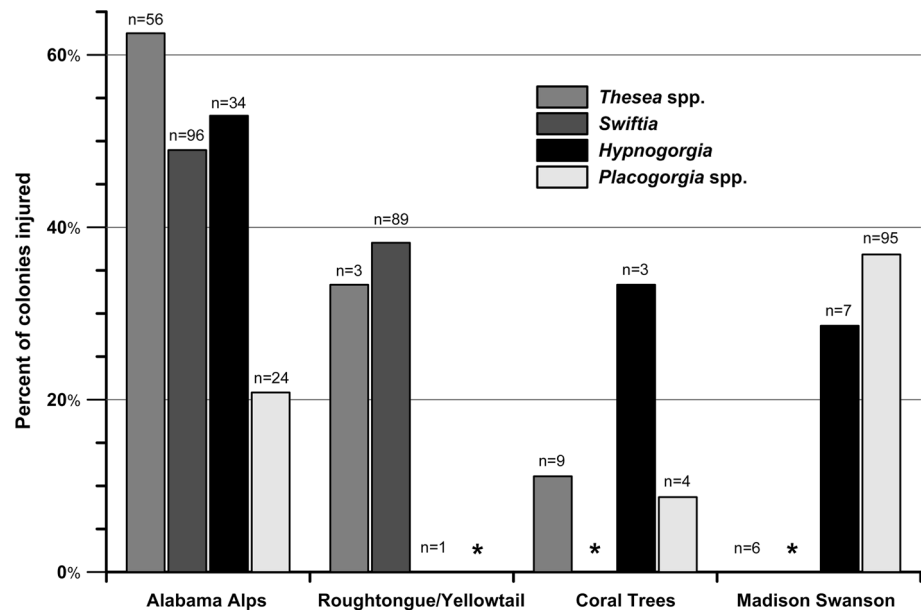


Fig. 5 Frequency of injury post-spill for four large sea fan taxa (*Thesea* spp., *Swiftia exserta*, *Hypnogorgia pendula*, and *Placogorgia* spp.) occurring on northwest Gulf of Mexico mesophotic reefs. *Asterisks* indicate taxa were absent on the transects



The findings are consistent with the results of other studies showing benthic impacts to deep-sea corals from the Deepwater Horizon oil spill (White et al. 2012; Hsing et al. 2013; Fisher et al. 2014; Silva et al. 2015). Injuries to *Paramuricea* gorgonians were linked to oil from the Macondo well by White et al. (2012). Those results were later extended to other sites up to 22 km from the wellhead (Fisher et al. 2014). These studies reported a patchy distribution of injury (i.e., not mass mortality) with healthy and injured colonies co-occurring, much like the observations presented here. A decline in condition of marked injured gorgonians ($n = 19$) was also reported near 1500 m depth (Hsing et al. 2013). This temporal decline is

consistent with marker observations ($n = 18$) in the mesophotic zone. These studies near Macondo wellhead were able to produce evidence linking the DWH spill by 'fingerprinting' oiled sediments recovered from the branches and polyps of gorgonians (White et al. 2012).

One key difference between this and other studies of deep-sea corals (White et al. 2012; Fisher et al. 2014) is that this is the first to employ a BACI design. The context gained through this approach was demonstrable evidence of pre-spill injury to gorgonians at reference sites far from the wellhead, nearly 200 km away. It is unlikely injuries at reference sites can be attributed to DWH because injuries to large gorgonians were apparent in the earliest ROV

Fig. 6 Frequency of observation for each degree of injury (0 = <1 %, 1 = 1–10 %, 2 = 10–50 %, 3 = 50–90 %, 4 = >90 %) for large gorgonians on study sites near and far from Macondo well, before and after the Deepwater Horizon spill
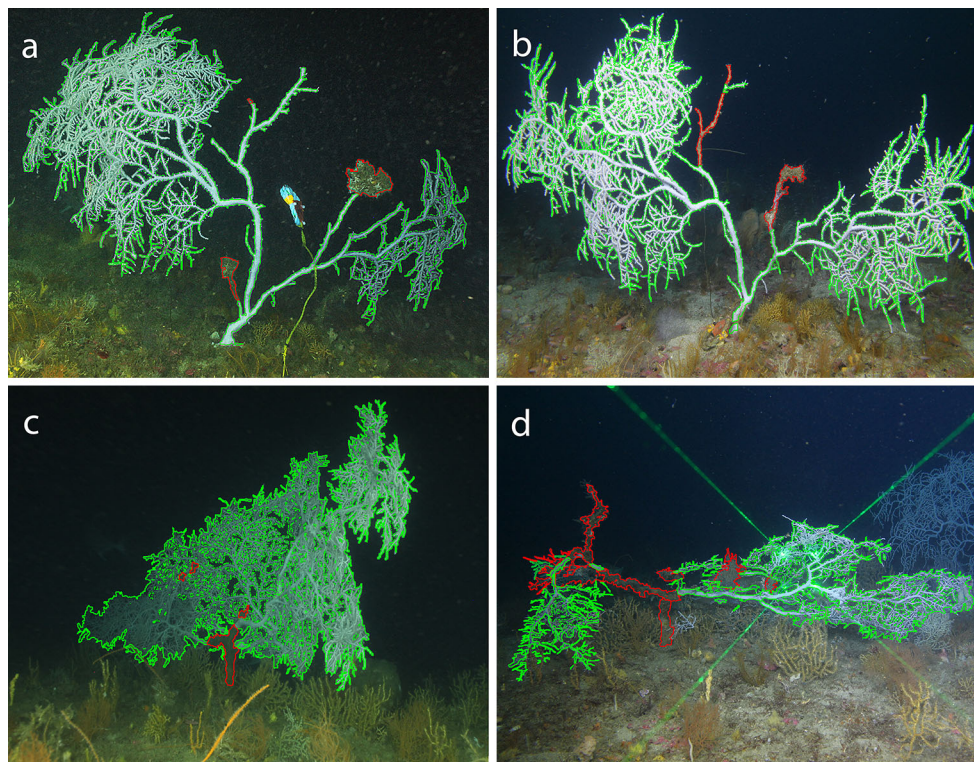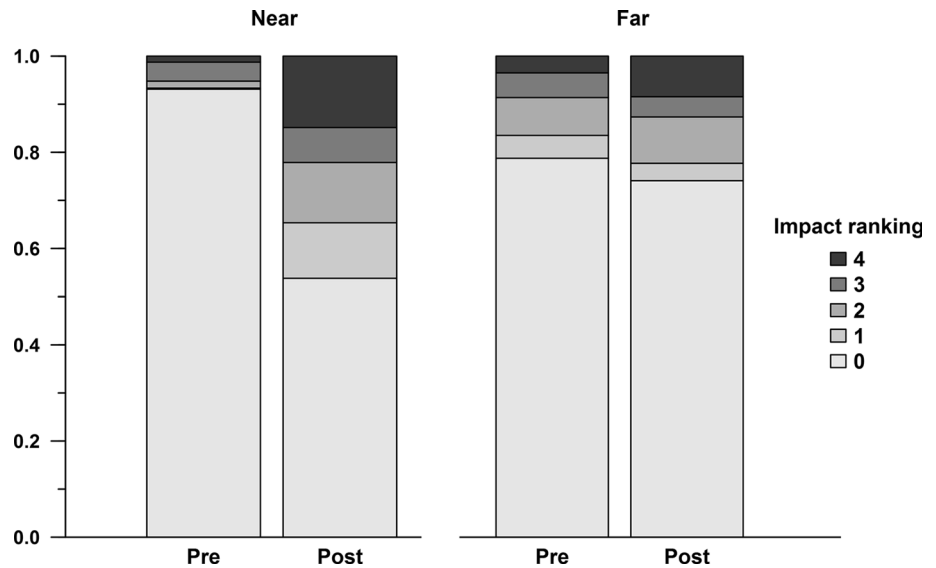


Fig. 7 Two colonies of *Hypnogorgia pendula* marked in 2011 (**a**, **c**) and revisited in 2014 (**b**, **d**). *Green outlines* indicate healthy sections, and *red outlines* indicate injured sections

surveys of the reefs available to the study in 1997. Additionally, condition of colonies was unchanged pre- and post-spill, in contrast to the dramatic changes observed at reefs near Macondo well. Reference sites were under surface slicks for <3 d or not at all.

The most probable cause of injury to corals on reference sites was bottom-contact fishing. Bottom-contact fishing is a known stressor to deep-sea coral habitats and the likely source of pre-spill injury at reference sites. Bottom long-lines in particular are recognized as a threat to gorgonian octocorals (Sampaio et al. 2012). Monofilament line occurred in and around gorgonian colonies, with significantly more line and more interactions observed at reference sites (Kruskal–Wallis, $p < 0.01$; ESM Fig. S3).

Coral Trees Reef and Madison Swanson South Reef are both situated in a region known as the 'northern grounds' for the Gulf of Mexico bottom longline fishery. The northern grounds are "the area of the Gulf where fishing actually began in the 1800's" (Prytherch 1983). Intense fishing pressure at MSSR led to closure in 2000, when the Fishery Management Council put all bottom-contact gear off limits. Low levels of bottom longline fishing effort were reported from the Pinnacles region in 2001, but the vast majority of effort was concentrated in the eastern Gulf, near Tampa, Florida (Scott-Denton et al. 2011). Observations of fishing line on transects at Pinnacle Trend sites were few. Impact sites are not likely to have incurred higher levels of injury from fishing than reference sites in a relatively brief time frame.

Octocorals are subject to a wide variety of natural and anthropogenic stressors beyond fisheries. Known stressors to octocorals include disease, ocean warming, predation by corallivores, toppling by hurricanes, and sedimentation. These alternatives are recognized here as counterpoint explanations for potential causes of injury unrelated to the Deepwater Horizon incident.

While fungal infections have been shown to eradicate gorgonian populations in tropical waters (Kim and Harvell 2004), few diseases have been reported for deep-water octocorals. Disease has not been reported from Gulf mesophotic taxa to our knowledge. Furthermore, disease outbreaks are typically reported to occur in one or a few host taxa (e.g., *Gorgonia ventalina*, *Eunicella verrucosa*; Hall-Spencer et al. 2007) and are not ubiquitous to a reef. The indiscriminate nature of the observed injuries suggests that disease is not the cause of injury at impact sites.

Octocorals are susceptible to surface warming in shallow waters (Sánchez et al. 2014), but there is presently no evidence of warming-related injury to octocorals in deep water. A dramatic warming event occurred in 2005 that caused bleaching to 40–60 % of shallow water corals at Flower Garden Banks in the western Gulf of Mexico, but no observations were deeper than 30 m and no mortality was evident (Eakin et al. 2010). Maps of temperature anomalies indicate impact sites were minimally affected. The reduced severity of the anomalies and depth of the mesophotic reefs suggest that surface warming is not the cause.

Corallivore predators can occur in deep water (Mah et al. 2010), but they do not explain the injuries observed in the Gulf of Mexico. Predators of gorgonian octocorals include asteroid sea stars, flamingo tongue snails, gastropods, and cidaroid urchins, among others. However, there were no obvious infestations of any of these predators in pre- or post-spill video. The frequency of occurrence for predators was very low among sites, with no obvious examples of predator-inflicted injury.

Hurricanes and storms can impact shallow coral reefs in the Caribbean, and topple gorgonian octocoral colonies attached to poorly consolidated substrate. Multiple hurricanes have passed over the Pinnacles sites in the past few decades, but the reef depths should provide an insulating effect from surface winds. Hurricanes Ivan and Katrina both passed near to the Pinnacles sites as strong Category 4 storms, in 2004 and 2005, respectively, yet other storms of similar strength (Andrew in 1992 and Opal in 1995) occurred prior to the pre-spill surveys, and the effects of those storms were not apparent in pre-spill surveys. It is not likely that hurricanes were the cause of injury observed in 2011, as prior hurricanes were not associated with subsequent damage to the mesophotic reefs.

Other studies have invoked DWH as the causative agent for declines in the mesophotic zone, including lesions observed in deep-water crabs (Felder et al. 2014) and fishes (Murawski et al. 2014) and up to 50 % injury to a broad range of corals on Pinnacle Trend reefs (Silva et al. 2015). The latter analysis included black corals and sea whips and used a different dataset of high-resolution still images from another set of pre-spill surveys, reaching the same conclusions presented here.

Unlike other studies documenting DWH impacts to deep-sea corals (White et al. 2012; Fisher et al. 2014), the current study of mesophotic corals at sites 50–100 km from DWH did not include fingerprinting of 'Macondo 252' oil on injured octocorals nor in sediments, but some chemical analyses were conducted. Total polycyclic aromatic hydrocarbons (PAHs) in tissues of corals on Pinnacle Trend reefs were observed in 2010 at low levels (Silva et al. 2015). Cooksey et al. (2014) also reported total PAHs in shelf sediments after the spill (August 2010) at very low levels, below sediment quality bio-effect guidelines developed with data for estuarine species. However, the low levels of PAHs observed near Pinnacle Trend were slightly higher compared to eastern sites with sandy sediments. There are no well-established bio-effect levels for offshore sediments (Cooksey et al. 2014), nor deep-water octocorals, so it may be possible that bio-effect thresholds for estuarine invertebrates are higher than thresholds for deep-water species. Furthermore, dispersants may have also played a role in the development of injury (DeLeo et al. 2015).

The lack of accumulation of DWH-related hydrocarbons in nearby shelf sediments does not preclude the possibility of DWH-related impacts to mesophotic corals located in these same areas. It is likely that oil and dispersant particles would have been patchily distributed in the water column this far from the wellhead (Valentine et al. 2014). Therefore, oil contaminants would be unlikely to accumulate in large quantities on the sediment surface, but suspended material could still cause harm to suspension feeders as it came into contact with upright corals.

In the absence of compelling evidence attributable to other known potential sources of injury, the oil slick from Deepwater Horizon remains the likely causative agent for injury observed on mesophotic reefs in the Pinnacle Trend. The persistence and proximity of the surface slick and dispersant applications, as well as evidence of oil-contaminated marine snow (Passow et al. 2012) and seafloor deposition of surface-derived carbon (Chanton et al. 2014) all suggest a pathway for contaminants to reach the mesophotic reefs. Contact of surface slick-derived oil or dispersants with mesophotic octocorals may have occurred directly with sinking of oil or oil-contaminated material, or indirectly, through ingestion of contaminated plankton or suspended organic material.

In conclusion, there is clear evidence of injury and decline to gorgonian octocorals at sites that were situated below the surface slick in the spring of 2010. The degree of injury is substantial, with up to 50 % of sea fans affected; the time frame suggests that the Macondo blowout was a likely causative agent of the decline. Other potential sources of injury, including fisheries, hurricanes, water temperature, and predators, were included in analyses, but do not appear to account for changes to octocoral health at sites in the Pinnacle Trend.

Alabama Alps Reef, Roughtongue Reef, and Yellowtail Reef were selected as representative sites in this study, but are only a few of many reefs known to harbor octocorals and abundant fishes in the Pinnacle Trend. Recent GIS-derived areas of potential reef habitat indicate that the study sites evaluated may encompass <3 % of total mesophotic reef area in the mapped area below the slick (Nash and Randall 2015). The results presented here may vastly underestimate the extent of impacts to mesophotic reefs in the northern Gulf of Mexico.

This study identifies multiple potential sources of injury to gorgonian octocorals of the Gulf of Mexico mesophotic reefs, both within and outside the scope of the Deepwater Horizon oil spill. Monitoring to date suggests recovery to injured colonies is unlikely. Nevertheless, a number of healthy colonies still remain on these reefs, and data suggest that healthy colonies will remain so in the absence of new stressors. Habitat protection and habitat restoration efforts are recommended to ameliorate collateral damage from fishing and to accelerate the recovery rates to gorgonian aggregations in the northern Gulf of Mexico; deepwater monitoring programs should be established to document the progress and effect of the new conservation measures.

**Compliance with ethical standards**

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