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Sponge Communities in Mesophotic Reefs of the Gulf of Mexico Before and After the Deepwater Horizon Oil Discharge

Samantha Christina-Marie Politano

THE FLORIDA STATE UNIVERSITY COLLEGE OF ARTS & SCIENCES

SPONGE COMMUNITIES IN MESOPHOTIC REEFS OF THE GULF OF MEXICO BEFORE AND AFTER THE DEEPWATER HORIZON OIL DISCHARGE

By

SAMANTHA POLITANO

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Dr. Ian MacDonald
Thesis Director

Dr. Jeff Chanton
Outside Committee Member

Dr. Molly Hand
Committee Member

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I. Abstract

Mesophotic reefs across the outer continental shelf of the northeastern Gulf of Mexico were examined for possible impacts of the Macondo well's Deepwater Horizon 2010 oil spill. For weeks following the spill, Alabama Alps Reef and Roughtongue Reef were situated 60-88 m under floating oil, with Alabama Alps closer to the spill and under oil for 20 more days. ROVs surveyed the reefs in 2011, 2014, and from 1997 to 1999. Sponges were present, but they are difficult to identify with taxonomic precision from photographic evidence. The sponges were visually quantified using still images captured from ROV video transects and the average number of sponges per photo for each site was calculated along with morphological forms. Following the spill, the number of sponges at Alabama Alps Reef notably declined while those at Roughtongue Reef increased. Both sites experienced growth by 2014, though Roughtongue Reef's sponge population increased much more dramatically. Encrusting morphologies overwhelmingly dominated populations until 2014. These changes in morphology reinforce the numerical reduction in the number of sponge individuals and represent probable sublethal impacts of the oil discharge. Predation and disease, among other mortality factors, possibly influenced the changes within the populations.

II. Introduction

A. Introduction

Sponges (Porifera) serve as a host to a wide array of species and possess a multitude of other significant functions in their associated ecosystems, making their presence in the Gulf of Mexico integral to reef survival (Wulff, 2006). As sessile filter filters, they can pump up to 35 ml min^{-1} (cm $sponge)^{-3}$ of water (Weisz et al., 2008) while retaining suspended solids (Morganti et al., 2019). The vast majority of sponges are of the soft-bodied class Demospongiae with spicule skeletons (Morrow, 2015) and are distributed worldwide (Van Soest et al., 2018). They lack any organ systems, yet they possess a collection of canals to pump water through after filtering particles (typically less than 50 micrometers) between a series of progressively smaller mesh size sieves (Bergquist, 1978). Sponge pumping activity patterns are incredibly varied, with different strategies exercised by species within the same community, but are generally more efficient than other filter feeders (Bergquist, 1978).The structure of sponges facilitates this ecological interaction—for some invertebrates, sponges operate as both a source of food and a stratum of camouflage, but for others like polychaetes; echinoderms; and crustaceans, they can function as “sponge hotels” to live amongst (Wulff, 2006). Sponge aggregations draw a broad range of organisms and develop local biodiversity by increasing the structural complexity of their habitats (Maldonado et al., 2018). Despite their simplicity, sponges react to external and internal stimuli and help regulate their environments, and there is some evidence that sponges aid in nutrient cycling (Hoffmann et al, 2009; Yahel et al., 2007; Pawlik and McMurray, 2019).

In 2010, the Deepwater Horizon drilling rig caught on fire after a failure of well control, causing an explosion. After it sunk, an oil leak was discovered which ultimately resulted in millions of barrels of oil, over 500,000 T of hydrocarbon gas, and over a million gallons of dispersant to be released into the surrounding Gulf of Mexico waters (McNutt, 2012; Joye, 2011), causing broad negative impacts on marine flora and fauna, including those on octocorals (Silva et al, 2015, Etnoyer et al, 2016), bivalves and echinoderms (Steffanson, 2015), and many others. However, in reviews of the biological impacts of the spill (Chen, 2011; Beyer, 2016), sponges are scarcely mentioned. Since these organisms are integral to their environments, it is vital to consider the DWH event's possible effects on their populations.

The northeast Gulf of Mexico, off the coasts of Mississippi and Alabama, contains a variety of hard-bottom mesophotic reefs including the Pinnacles Trend, containing dense and diverse assemblages of epibenthic communities, including stony corals, gorgonians, antipatharians, and sponges (Gittings et al., 1992). Mesophotic coral ecosystems (MCEs), generally between 30-105 meters in depth, consist of many species common to shallow-water coral reefs and are defined by the presence of zooxanthellate corals (Andradi-Brown et al., 2016). Coral reefs at intermediate depths are understudied in comparison to their shallow and deep water counterparts due to SCUBA's depth limits and the expense of submersibles, but advances in technical diving methodologies and image sampling have allowed for further inquiry into these systems (Hinderstein et al., 2010; Kahng, et al., 2010). Hard-bottom areas across the Gulf of Mexico, such in the waters of the Louisiana-Texas Shelf and portions of the West Florida Shelf, provide habitat for diverse community assemblages within a wide range of depths (Amendment 9 NOAA, 2018). Within the northern Gulf, sponge presence was noted in moderate relief bottom features (ranging from 2-6 m) and was especially prolific in high relief features (ranging from 6-18 m) with extensive reef flats on their summits, though the sponges were noted to have been particularly difficult to identify (Gittings et al., 1992). Known mesophotic sponges of the Gulf of Mexico currently number over 100 taxa, including lithistid reef-building sponges and a spectrum of morphologies (Andradi-Brown et al., 2016). Oftentimes, sponge identification requires cutting and drying tissue samples to conduct spicule complement analysis, skeleton preparation, or molecular analysis. Sponge identification is effectively nonexistent in the mesophotic Pinnacles Trend despite making up the dominant taxa in many MCEs (Andradi-Brown et al., 2016), as the only distribution or taxonomic work within the last five decades researched shallow species (Kaiser, 2018), and there are few species-specific photographic guides dedicated to Gulf of Mexico mesophotic sponges, with the exception of the Flower Gardens National Marine Sanctuary (Hickerson et al., 2012). Their exclusion from monitoring assays is for a number of reasons. As noted previously, sponges can rarely be identified without sampling, but their high species diversity, the variation within and among species as well as over space and time, and the time required to document individual sponge volume also contribute to the difficulties in quantifying populations (Edmunds et al., 2020). Unfortunately, photographs alone cannot measure sponge biomass and volume (Wulff, 2016) which is essential to understanding the ecological significance of sponge density. Nonetheless, image surveys provide one of the few means to reconstruct historical communities of these reefs (Lenz et al., 2015).

The Pinnacles Reefs encompass nine named reefs (Figure 1), two of the largest being Alabama Alps Reef and Roughtongue Reef (Etnoyer et al., 2015). The region has been the subject of multiple previous studies, which provide baseline information on their bathymetry, distribution, and biodiversity, including photographic evidence for the sponge population (Gittings et al., 1992; Continental Shelf Associates, 2001). Thus, it is essential to understand these environments to ensure the survival of these diverse communities and evaluate threats and their effects.

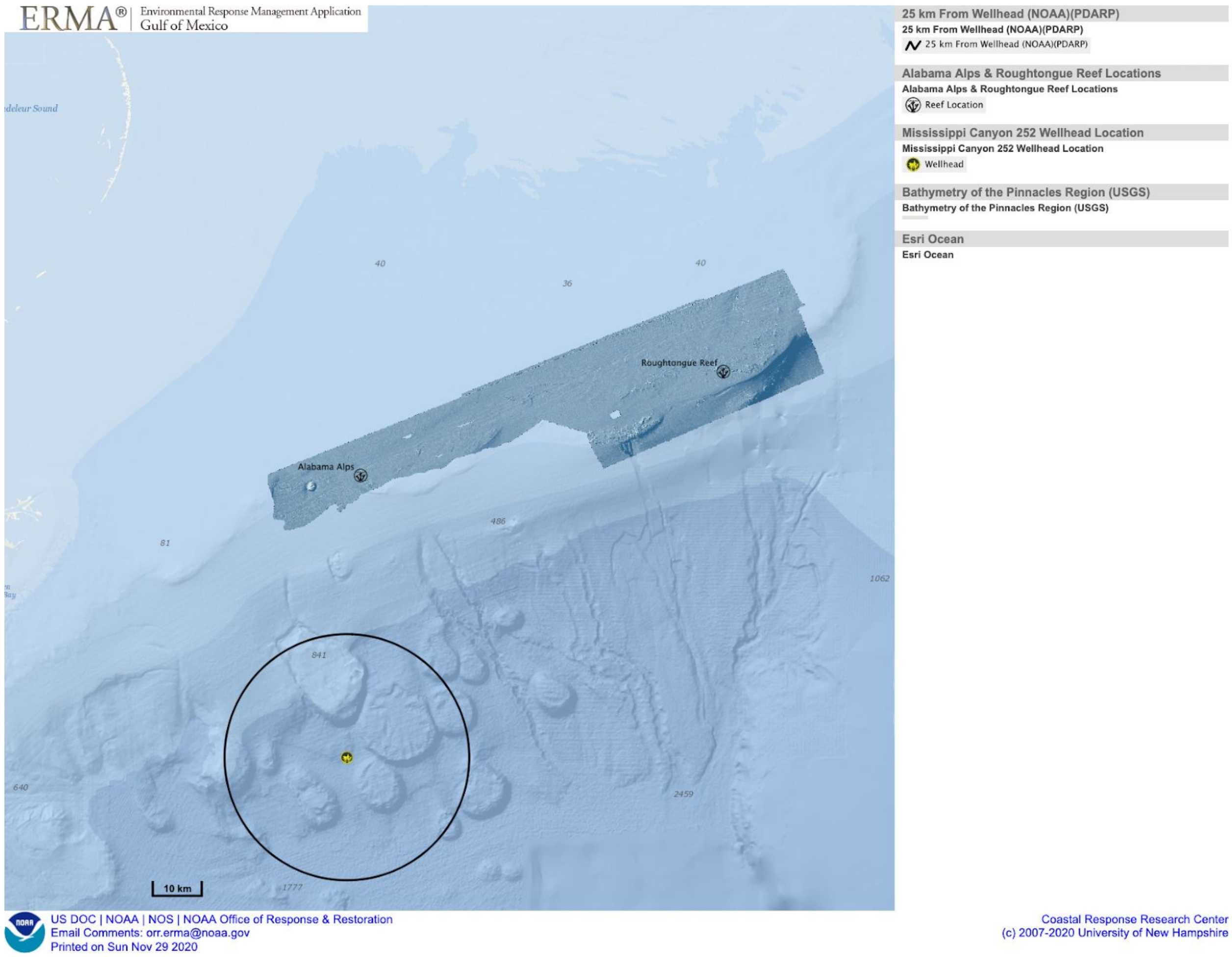

Figure 1. A map of the Pinnacles reef trend, including Alabama Alps and Roughtongue. Data sourced from NOAA's Environmental Response Management Application.

Dr. MacDonald's lab conducted several surveys using high-resolution photographic imaging to inspect the sites affected by the DWH spill and compared this to historic (1997-1999) photographic database in order to quantify pathologies of mesophotic octocorals and anthipatharians which were under the influence of floating oil in the weeks following the DWH incident (Silva et al, 2016). This project seeks to reevaluate the sets of images for evidence of marine sponge mortality.

Table 1. Summary of visited sites during the MAPTEM (1997-9) and NRDA (2011 and 2014) research expeditions. Distance indicates proximity to DWH discharge site (Silva et al., 2015). Reef data sourced from Etnoyer et al., 2016.

Reef	Latitude	Longitude	Distance (km)	Days under slick	Area (km^2)[a]	Reef base depth (m)	Reef crest depth (m)
Alabama Alps	29.255	-88.339	57	39	0.126	88	72
Roughtongue	29.442	-87.579	109	19	0.082	78	64

By determining the extent of sponges before and after the DWH incident, this project may allow for further understanding of the effects of the BP oil spill on the biota of the Gulf of Mexico. This project will compare sponge populations of Alabama Alps and Roughtongue Reefs using images collected between 1997 and 1999 during the Mississippi–Alabama Pinnacle Trend Ecosystem Monitoring program and during 2011 and 2014 post-discharge assessments. Using visual analysis, the number of visible sponges in each sample was quantified and binned by color. This will provide an opportunity to compare sponge pathologies across a decade of change and after a major catastrophe.

Table 2. Cruise expeditions that contributed still photos for population studies of sponges

Cruise	Year	Month	Reef survey site	Still photos	Mean sponges per photo
USGS	1997	August	RTR	539	3.33
USGS	1999	August	AAR	500	4.45
NRDA	2011	September	RTR	773	5.40
NRDA	2011	September	AAR	639	1.26
NRDA	2014	June-July	RTR	201	13.14
NRDA	2014	June-July	AAR	158	2.18

Cruises: *USGS* United States Geological Survey, *NRDA* National Resource Damage Assessment. Reefs: *AAR* Alabama Alps, *RTR* Roughtongue.

Unlike corals (Silva et al., 2016; Fisher et al., 2014; Girard et al., 2019), sponge health is difficult to document visually as they typically heal after injury or vanish post-mortem (Wulff, 2016). A variety of afflictions can affect sponges, so it is also vital to consider other possible causes of damage, such as hurricanes and predation. Sponge reactions to events and ailments differ, ranging from rubble stabilization post-hurricane (Wulff, 2016; Stevely, 2011) to species-specific responses after cyanobacteria blooms (Stevely, 2011). Recovery of sponges is difficult to identify for a multitude of reasons. Rapid disintegration of portions or entire sponges can cause mortality to become largely invisible (Wulff, 2013). Even in areas commonly afflicted by mortality events such as algal blooms and tropical weather, recovery can take over a decade (Stevely and Sweat, 1995). In addition, it may be impossible to define a population typical of a deepwater region (Wulff, 2008), effectively preventing any understanding of recovery. Although regeneration provides numerous advantages to sponges, characteristics of both the damage sustained and the sponge species itself can influence recovery (Wulff, 2010). These extrinsic and intrinsic factors limit regeneration, with proximity to resources and sponge size and age playing significant roles in the quality of regeneration (Henry and Hart, 2005). Amongst regenerating sponges, sexual reproduction and somatic growth are reduced, resulting in populations more susceptible to predation and competition (Henry and Hart, 2005).

Crude oil and dispersant impacts on sponges is not well documented. In shallow-water species, such as *Rhopaloeides odorabile,* larval settlement, metamorphosis, and gene expression were negatively affected by environmentally relevant concentrations of petroleum hydrocarbons (Luter at al, 2019). High concentrations of PAHs have been shown to disturb larval settlement and development (Negri et al., 2016; Cebrian and Uriz, 2007). Deep-sea sponges also lack scientific data regarding the effects of oil spill events. It is suggested that the release of hydrocarbons may cause individual mortality, benthic diversity decrease, larval settlement disruption, and oxidative stress on deep-sea sponges (Vad et al., 2018). Six months after the Deepwater Horizon spill, deep-sea sediments still held dispersants (White et al., 2014), which suggests long-term impacts on deep-sea benthic organisms when hydrocarbons and dispersants enter the sediments.

III. Materials and Methods

A. Image Collection

Etnoyer et al. used a before-and-after-control (BACI) design to evaluate changes in abundance of corals and demersal fishes over time in two impact sites, Alabama Alps Reef (AAR) and Roughtongue Reef (RTR). These sites were surveyed prior to DWH from 1997-1999 (MAPTEM) and in 2011 and 2014 (Etnoyer et al, 2016). Both sites were under floating oil for weeks, within 109 km of DWH, and were subjected to dispersants (Fisher et al., 2014). In 2011, a remote operated vehicle (ROV) containing a digital still camera (AquaSLR) at a 45° angle and two high-output LED lamps reviewed the sites 0.5-1 m above the bottom in transects, recording positions at 1 minute intervals and noting the presence of corals. In areas where corals were found, the ROV returned during multiple dives to randomly photograph points within the sectors of the two sites. Each surveyed eight equal sectors each containing 16 randomly chosen points within a 200 m-diameter circular region. Pre-spill procedures were similar to post-spill methods, but utilized a SeaRover ROV with a standard definition film camera angled at 45° and a 150 Ws strobe light. The MAPTEM expedition still film photos were then scanned. The pre-spill datasets comprised 1039 relevant photos compared to the post-spill's 1636 photos, providing substantial samples allowing for statistical analysis.

B. Visual Analysis

For each photoset opened in Adobe Photoshop CC 2019 software, sponges were binned by color (yellow, orange, and other) due to image quality and the difficulty of accurate sponge identification. Individuals can vary widely in size, and as such each photo was examined methodically to ensure each individual was counted. A sponge individual was defined by its area of distinct biomass, separated from sponges of differing color bins. This may overestimate

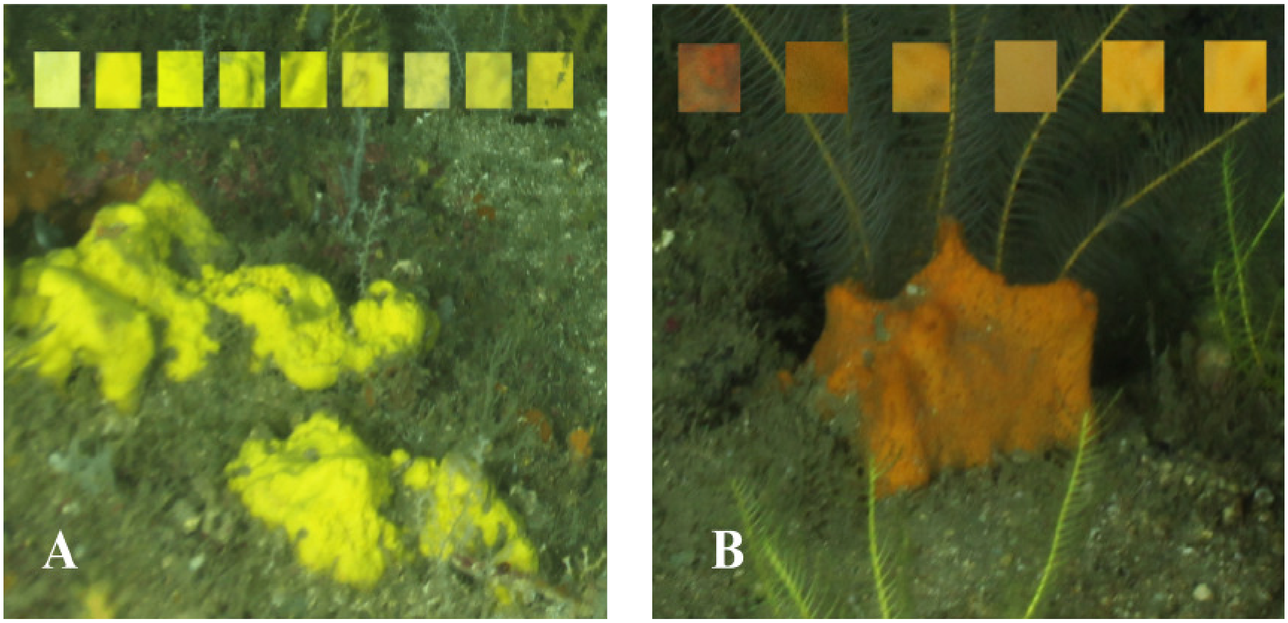

Figure 2. Series of samples from each color bin in Roughtongue Reef and Alabama Alps reef in 2011 and 2014 are presented to express chromatic variation. **A**, Two encrusting, yellow sponges in Roughtongue Reef photographed in 2011. **B**, An erect, orange sponge in Roughtongue Reef photographed in 2014.

sponge individuals as sediment, algae, water quality, other individuals, other organisms, and complex topographical structures can visually separate portions of continuous sponge tissue. These constraints have been well documented since this method's inception (Loya, 1972), but the rugosity of the surfaces affects the degree to which these issues impact analysis (Edmunds et al., 2020). The flat-topped carbonate mound structures of Alabama Alps and Roughtongue Reefs produce benthic surfaces of relatively mild relief which scarcely impeded visual analysis (Silva & MacDonald, 2017).

Because of their starkness, yellow sponges were counted first (Figure 2A). Each photo was visually separated into thirds, and analysis began at the top left corner continuing to the top right. This method continued with both subsequent sections. After the yellow sponges, orange sponges were counted (Figure 2B) followed by the other colored sponges (see Figure 3A, 3B, and 3D for examples). Then, each photo was recounted in the same order (yellow, orange, other) starting from the bottom right corner and working in reverse to confirm the accuracy of the initial count. When discrepancies occurred, the entirety of the visual analysis process was repeated. Photos were magnified when necessary to clarify sponge individuals from one another. Fish and other fauna were noted when present. The total number of sponges in each photograph was tabulated and the mean number of sponges per photo was calculated to standardize across expeditions with varying quantities of photos.

Since planar photographs are unable to establish sponge biomass and volumetric approximations require gross estimations and specific taxonomic categorization (Edmunds et al., 2020), sponge morphology was used to demonstrate community dynamics of the sponge populations. This could provide further insight on the susceptibility of sponge morphology to environmental stressors. Schönberg and Fromont (2014) suggest the use of growth forms to quickly classify sponges from monitoring surveys. When a sponge exhibited erect morphology (a vertical growth strategy away from the substrate) as opposed to the encrusting morphology (a thin coating of the substrate in sheets) commonplace throughout the photosets, the number of erect individuals was documented (Boury-Esnault et al., 1997). Erect morphologies (Figure 3)

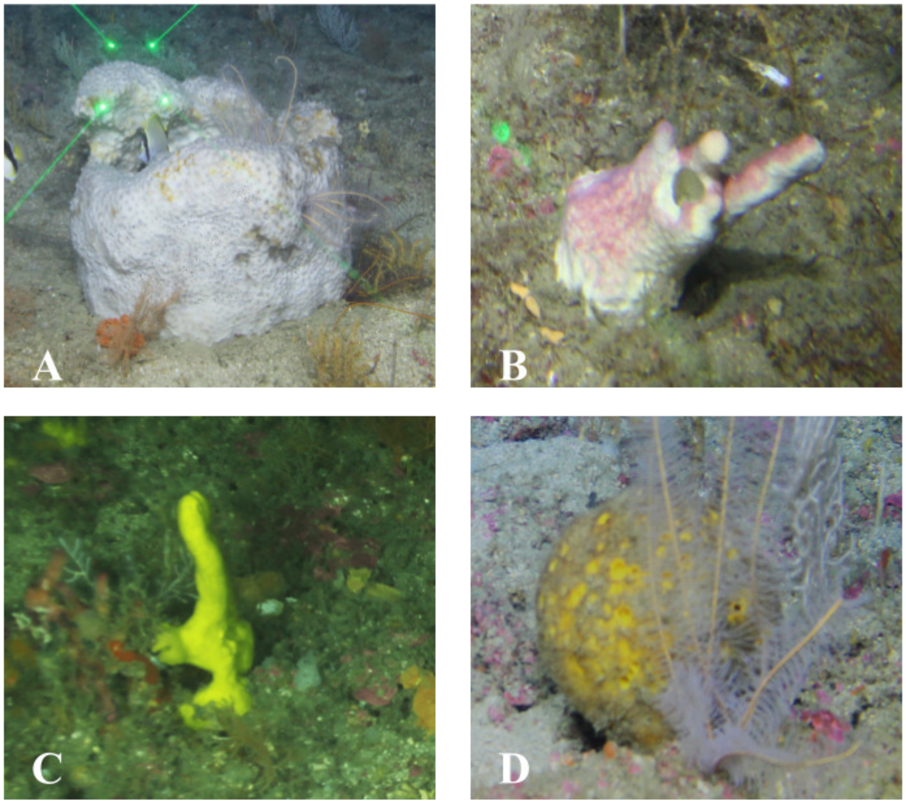

Figure 3. Examples of erect morphology. **A**, a massive white sponge in AAR from 2014; **B**, a tubular pink-white sponge in RTR in 2014; **C**, a fistulose yellow sponge in RTR from 2011; **D**, a globular yellow sponge in RTR in 2014.

can include massive (large and without a discernable shape), globular (spherical), conulose (an underlying skeleton projecting cone-shape tissue), arborescent (branching), turbinate (resembling an inverted cone), and dozens more (Boury-Esnault et al., 1997).

Using images collected between 1997 and 1999 during the Mississippi–Alabama Pinnacle Trend Ecosystem Monitoring program and during a 2011 post-discharge assessment, this project compared two sites photographed by both expeditions which will provide an opportunity to compare sponge presence across a decade of change and after a major catastrophic event.

C. Statistical Methods

A one-way analysis of variance (ANOVA) was employed to test the null hypothesis that mesophotic reef-dwelling sponges in the Alabama Alps Reef and Roughtongue Reef sites of the Mississippi-Alabama Pinnacles Reefs in the Gulf of Mexico will not present a statistically different mean amount of sponges between the three samples from 1997-9, 2011, and 2014. A chi-square test of independence was performed to examine the relation between morphology and changes in populations over time.

IV. Results

A. Changes in Populations

One-way between subjects ANOVAs were conducted to compare the effect of time on the mean number of sponges in pre-spill (1997-9) and post-spill (2011 and 2014) conditions for both Alabama Alps Reef (AAR) and Roughtongue Reef (RTR).

In AAR, there was a significant effect of time on the mean number of sponges at the $p<.05$ level for the three conditions [$F(2, 1294) = 126.72$, $p = <.0001$]. Post hoc comparisons using the Tukey HSD test ($HSD[.05] = 0.65$) indicated that the AAR mean score pre-spill ($M = 4.45$, $SD = 3.76$) was significantly different than the 2011 condition ($M = 1.26$, $SD = 2.12$). The 2014 condition ($M = 2.18$, $SD = 5.59$) was significantly different from the 2011 and pre-spill conditions.

In RTR, there was a significant effect of time on the mean number of sponges at the $p<.05$ level for the three conditions [$F(2, 1510) = 139.82$, $p = <.0001$]. Post hoc comparisons using the Tukey HSD test ($HSD[.05] = 1.23$) indicated that the RTR mean score pre-spill ($M = 3.33$, $SD = 3.09$) was significantly different than the 2011 condition ($M = 5.40$, $SD = 5.91$). Additionally, the 2014 condition ($M = 13.1$, $SD = 14.95$) was significantly different than the 2011 and pre-spill conditions.

Taken together, these results suggest there was a significant change in populations of mesophotic sponges before and after the oil spill event at sites 57 km (AAR) and 109 km (RTR) from Deepwater Horizon. In AAR, closer to DWH, experienced a significant drop in the mean number of sponges per photo from its historic population between its pre-spill populations and 2011, but increased slightly by 2014. RTR, which was further from DWH, experienced an increase in the mean number of sponges per photo from its historic populations and a significant increase from 2011 to 2014.

Pre-Discharge Conditions

From 1997 to 1999, mesophotic sponges at AAR and RTR were present. Large individuals were present accompanied by a significant amount of encrusting sponges. The community amongst the sponges was robust; morays, jellies, and sea stars appeared throughout each site. Proportions of sponges in each bin were relatively similar across sites. Yellow sponges comprised the lowest number of sponge individuals at both sites, making up 21.46% of all sponges in AAR and 19.72% in RTR. Orange sponges made up approximately a third of sponges at each site, and "other" sponges were about half of all sponges with 46.25% in AAR and 50.08% in RTR.

Post-Discharge Conditions

In both 2011 and 2014, mesophotic sponges at AAR and RTR were present. In 2011, the average number of sponges in AAR (1.26) was much lower than in RTR (5.4). Three years later, this trend persisted, with AAR at 3.47 sponges per photo and RTR at 13.1 (Figure 4). The proportion of yellow, orange, and other sponges also changed. In 2011, each bin comprised approximately a third of all sponges in AAR, while in RTR "other" sponges were the majority of all sponges at 53.8%. This changed again in 2014, with "other" sponges dominating both AAR and RTR at 76.5% and 42.4%, respectively.

Across the years, AAR experienced significant changes in the means of its sponge population. AAR showed a 51.0% decrease in the average number of sponges in 2014 compared to its historical values. In the years following the spill, AAR experienced a 73.0% increase in its average number of sponges.

RTR also experienced significant changes in the means of its sponge population from 1997 to 2014. RTR, however, experienced a 294.6% increase from its historical numbers to 2014. From 2011 to 2014, RTR exhibited a 143.3% increase in average sponges.

While RTR was experiencing a 62.2% increase in its mean numbers of sponges per photo from 1997-9 to following the spill in 2011, AAR experienced a 71.7% loss.

The communities in both 2011 and 2014 saw little faunal diversity. The occasional school of large fish or lobster were rarities within both image sets; the starfishes and jellies from the historic photos were no longer present.

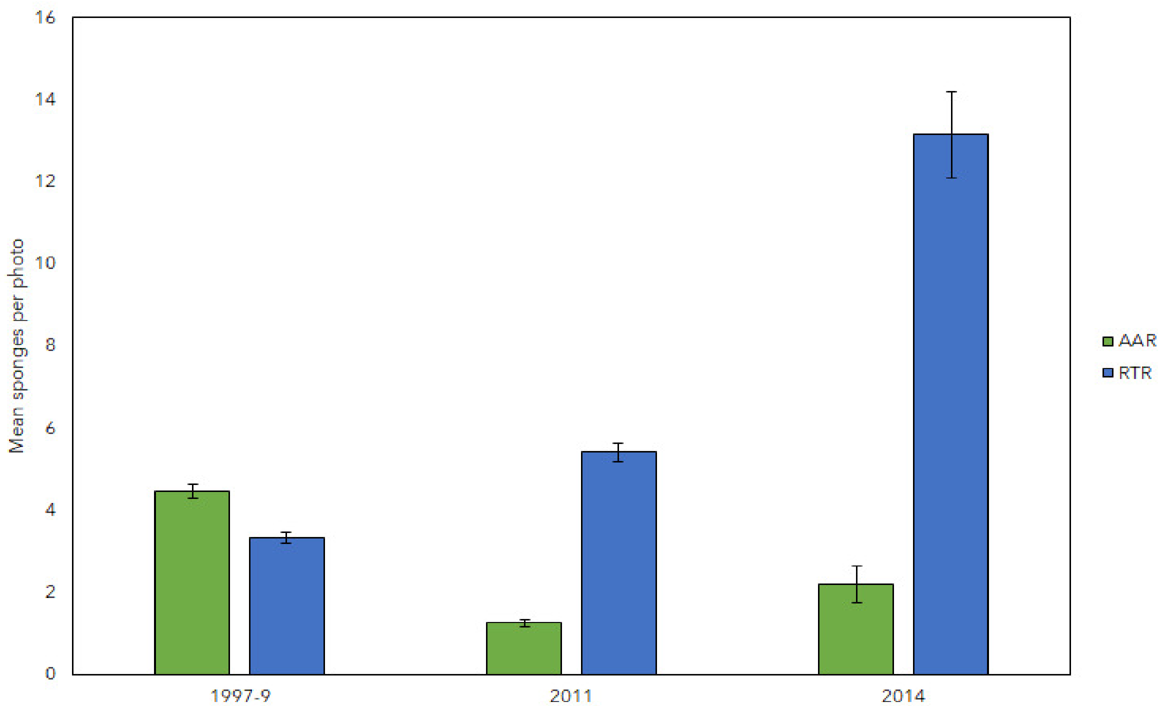

Figure 4. Effects of reef and year on mesophotic sponge populations (mean sponges per photo ± SE) in the Pinnacles reef trend of the Gulf of Mexico from MAPTEM (1997-9) and NRDA (2011 and 2014) ROV surveys for study sites Alabama Alps Reef (AAR) and Roughtongue Reef (RTR).

B. Morphological Changes

A chi-square test of goodness of fit was performed to determine if morphology was equally distributed over the years sampled. Morphology was not equally distributed over time, X^2 8622.93 (6, N = 29767) = 10159.84, $p < .05$.

Pre-discharge conditions

In AAR, of the 2227 sponges quantified, 14 were noted to be erect with 12 massive and 2 globular morphologies present. Of the 1795 sponges found in RTR, 37 were erect. All other sponges displayed an encrusting morphology.

Post-discharge conditions

In 2011, 2 sponges in AAR and 33 sponges in RTR were noted to possess erect morphology; all other sponges were encrusting.

In 2014, however, a broad spectrum of morphologies were present. In AAR, 89 arborescent, 7 massive, 4 tubular, and 2 globular morphologies were noted of the 344 sponges present. Encrusting sponges comprised the remaining 70.4% of sponges. In RTR, 214 arborescent, 327 massive, 26 globular, and 13 tubular sponges were amongst the 2641 sponges in the reef.

V. Discussion

Photo analysis can be used quantitatively to show changes in population over time. Using three photographic sample sets documenting conditions at two reefs over four years, this study expands on the present understanding of changes in abundance of octocorals due to the Deepwater Horizon oil spill (Silva et al., 2016). Though historic photographs cannot capture the full breadth of knowledge required to definitively address sponge community dynamics of the Pinnacles, this study found evidence that the sessile sponge community in the Alabama Alps and Roughtongue Reefs were potentially affected by the 2010 Deepwater Horizon oil spill.

These results suggest a dampening effect occurred on the potential population growth of sponges in AAR when compared to RTR, which had a population initially lower than AAR. The sharp decrease in population from the historic community size in 1997-9 to 2011 in AAR compared to an increase in populations in RTR during the same time suggests that proximity to the site of the spill affected sponge populations, and continued to do so after the spill. Recovery was marked in RTR from 2011 to 2014, while AAR experienced population growth to a much lesser extent.

Sponges are active suspension feeders, in contrast to passive suspension feeders such as corals, and pump water within choanocytes to capture particles. This mechanism operates as a filter, removing particulates from the suspension. Thus, sponges can function as bioindicators for microparticulate pollutants (Montagna & Girard, 2020; Girard et al., 2020) and oil-derived polycyclic aromatic hydrocarbons (PAHs) (Batista et al., 2013). PAHs have also been shown to induce negative impacts on larval and juvenile sponge survival (Cebrian & Uriz, 2007). This is particularly noteworthy in the context of DWH, as oil contaminants were distributed unevenly throughout the water column, rather than quickly settling on the sediment surface (Valentine et al., 2014). Though little research has been conducted regarding the relationship between sponge morphology and filter feeding rates (Blair, 2012), vertical distance in a water column compromised by contaminants may influence exposure to PAHs.

Morphologies of sponges in situ are indicative of their functional operation. The composition of sponge functional morphology varied over time, with the average number of erect sponges per photo decreasing slightly in both AAR and RTR following the spill in 2011 and increasing by 2014. This shows a potential sublethal stress response to contaminants, since the change in the established community demonstrates the lack of adaptation to pollutants such as petroleum hydrocarbons and oil dispersants. Although it is not possible to detect a correlation between morphology and color to sponge density, there is reason to conclude a functionally significant change in sponge community composition. The overwhelming domination across all sites and over time by encrusting forms is consistent with previous studies (Vacelet & Vasseur, 1977; Bell & Smith, 2004; Bell, 2007). Morphological change as an evolution of acclimatory control is linked to environmental predictability, and in high stress environments sponges will swiftly form stiffer and tougher tissues (Palumbi, 1984; Bell & Barnes, 2000). In non-temperate regions, functional roles of specific sponge morphologies were not shown to be restricted to particular environmental regimes, however, reef flats have been shown to restrict nearly all sponge morphologies except encrusting forms (Bell, 2007). Flat, cryptic, and other low-profile specimens filter smaller volumes of water and have a lesser influence on the flow regime than larger sponge forms, but generally occupy larger areas of the bottom substrate per unit volume (Abdul Wahab et al., 2018). In high-sedimentation environments, for example, erect growth forms are likely to be selected over encrusting forms (Alcolado, 2007; Bell & Barnes, 2000; Schönberg & Fromont, 2014; Pineda & Webster, 2016). The effects of contaminants on sponges and vice versa is not extensively studied, but species richness has been shown to decrease in filter feeders toward polluted sites (Carballo et al., 1996; Turner et al., 1997) as heavy metal biomarkers increase (Berthet et al., 2005). An alternative explanation for the change in morphology and increase in number of individuals is that encrusting forms readily fragment, allowing for an effective increase in population without necessarily increasing biomass (Edmunds et al., 2020).

The dominance of encrusting morphologies may reflect an adaptation to maximize surface area and thus light exposure for photosynthetic symbionts (Cheshire & Wilkinson, 1991). When using sponge morphology as a replacement for taxonomic classification, the role of light in sponge populations may be obscured because morphological forms can include both phototrophic and heterotrophic species (Abdul Wahab et al., 2018). However, the lower mesophotic zone is likely dominated by heterotrophic species. In other environments also ill-adapted to sudden change, patterns of biomass loss differed across species and within morphological forms, with patterns of loss being attributed to differences in skeletal fibers and speed of fragment reattachment (Wulff, 1995). These changes in morphology reinforce the numerical reduction in the number of sponge individuals and represent probable sublethal impacts of the oil discharge.

In the absence of light, in this study potentially caused by the days of oil slick cover at both sites, typical sponge stress response is to acquire a greater number of suspended particles and massive and erect morphologies are predicted to maximize surface area to accomplish this (George et al., 2018). Although there are some correlations between morphology and biophysical factors, to definitively conclude this connection time series analyses of environmental and water quality factors and particulate matter influx are needed. Further research is necessary to understand the possible role of suspended oil in mesophotic sponge morphological change.

It is not possible to determine from the present data whether the increases in sponge abundance and morphological variation in the years following DWH would have been greater if DWH had not occurred. Regardless, the changes in sponge individuals over time, coupled with changes in morphology and proportion of color, is notable and warrants further inquiry. Sponges are susceptible to myriad stressors, both anthropogenic and natural in origin, that may include hurricanes, changes in seawater temperatures, and predation.

Hurricanes have caused major mortality events in shallow sponge communities (Wulff, 2013), but the depth of the Pinnacles reefs may have prevented damage from surface winds. Although two Category Four hurricanes (Ivan in 2004 and Katrina in 2005) passed near the study sites, historical populations of other species were unaffected by Hurricane Andrew of 1992 and Hurricane Opal of 1995 (Etnoyer et al., 2016). Presently, deepwater communities have been unaffected by bleaching events impacting shallow water reefs caused by surface warming (Etnoyer et al., 2016), and sponges have been shown to experience less negative impacts as a result of ocean warming (Bell et al., 2018). Known spongivores (hawksbill sea turtles, shallow water reef fishes, and nudibranchs) were not visible in transect video or still photos.

Though understudied in sponge populations in particular, these factors could be raised as contrasting explanations of the changes in sponge communities attributed here to DWH. These results could be bolstered with inquiry into community dynamics of reference sites further from DWH. Gorgonian coral injury was unchanged at reference sites in comparison to the marked AAR and RTR pre- and post-spill changes in condition (Etnoyer et al., 2016), which may indicate a similar pattern for sponge communities. In addition, these results may underestimate the impacts to sponge populations of mesophotic reefs, as the study areas comprise less than 3% of mesophotic reef area under the oil slick caused by DWH (Etnoyer et al., 2016).

DWH has caused declines in populations or health of fishes (Murawski et al., 2014), crabs (Felder et al., 2014; Zengel et al., 2016), sediment infauna (Demopoulos et al., 2016), plankton (Buskey et al., 2016), and corals (White et al., 2012, 2014; Hsing et al., 2013; Fisher et al., 2014; Silva et al., 2015; Cordes et al., 2016; DeLeo et al., 2018). These demonstrated impacts on Gulf of Mexico fauna set a precedent of association with DWH for the observed changes in sponges populations, but no studies have investigated the potential impacts of DWH on the mesophotic sponges of the Pinnacles reefs. These data, coupled with the extensive effects on associated communities, suggest that DWH may have caused lethal impacts on mesophotic sponge populations and sublethal impacts on the morphological structure of such populations.

VI. Acknowledgements

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