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Long-term impact of the Deepwater Horizon oil spill on deep-sea corals detected after seven years of monitoring

Fanny Girard*, Charles R. Fisher

Department of Biology, The Pennsylvania State University, 208 Mueller Laboratory, University Park, PA 16802, USA

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ABSTRACT

Cold-water corals form high biodiversity habitats in the deep sea. They are generally long-lived, slow-growing, and thus particularly vulnerable to anthropogenic impact. We used high-definition imagery to quantify the impact and assess the recovery of deep-sea corals that were affected by the 2010 Deepwater Horizon oil spill in the Gulf of Mexico. Over three hundred *Paramuricea* spp. colonies were imaged yearly between 2011 and 2017 at five sites, and the images were digitized to quantify health, hydroid overgrowth, identify branch loss, and track recovery patterns. Although the median level of impact decreased after 2011 at all impacted sites, it has been stable since then and remained higher than at the reference sites. Recovery depended on the initial level of impact to the colonies, which negatively affected the ability of individual branches to recover or remain healthy. The effect of initial impact on recovery between consecutive years was still visible seven years after the spill, indicating a long-term, non-acute, impact on the colonies. Injured corals were also more likely to lose branches, and branch loss was still significantly higher at some of the impacted sites between 2016 and 2017, indicating an ongoing effect of the spill, which may eventually lead to delayed mortality. The methodology we employed allows us to successfully detect small changes in the health of corals. We suggest the establishment of image-based coral-monitoring sites to collect baseline data on coral biology, assess the efficacy of Marine Protected Areas, and detect future anthropogenic impact to these vulnerable deep-sea ecosystems.

1. Introduction

With an ever-increasing human population (Roberts, 2011) and progress in technology, virtually all ecosystems on earth are affected by human activities, resulting in a fast decline in global biodiversity (Dirzo et al., 2014; Pimm et al., 1995). To limit this loss in biodiversity, several national and international policies have been focusing on ecosystem protection (e.g. creation of protected areas and restoration) (Dobson et al., 1997; Lubchenco et al., 2003; Margules and Pressey, 2000). Yet, in order for policy makers to take appropriate conservation decisions, baseline information on the functioning of each ecosystem and their resilience to anthropogenic disturbances are necessary. In the case of most ecosystems, and especially in the inaccessible deep sea, this information is lacking.

Because deep-sea organisms are often slow-growing and long-lived, deep-sea ecosystems are generally expected to have a low resilience to anthropogenic perturbations. As a result the use of a precautionary approach to protect deep-sea ecosystems has often been recommended (Huvenne et al., 2016; Mengerink et al., 2014; Van Dover et al., 2012). Among the longest-lived deep-water organisms are deep-sea corals. Indeed, based on isotope studies, several octocoral species can live for hundreds of years and a colony of the black coral *Leiopathes* sp. was determined to be over 4000 years old (Andrews et al., 2002; Prouty et al., 2014; Roark et al., 2009).

Cold-water corals are widespread around the world and can be found over a wide range of latitudes and depths (Watling et al., 2011). A large number of mobile animals, including commercially valuable species, use corals as feeding grounds, refuges from predators, or nurseries (Baillon et al., 2012; Du Preez and Tunnicliffe, 2011; Etnoyer and Warrenchuk, 2007; Krieger and Wing, 2002). As a result, whether they form reefs or occur in dense assemblages, deep-sea coral communities contribute to the formation of high biodiversity habitats (Buhl-Mortensen and Mortensen, 2005; Buhl-Mortensen et al., 2010; Jensen and Frederiksen, 1992). Because of their high longevity, deep-sea corals can support high diversity ecosystems for hundreds of years.

Nevertheless, this high longevity, in association with the generally low metabolic and growth rates documented for deep-sea corals, makes them more vulnerable to impact and slow to recover (Andrews et al.,

* Corresponding author at: Institut Français de Recherche pour l'Exploitation de la mer (Ifremer), Centre de Bretagne, Unité Étude des Ecosystèmes Profonds, Laboratoire Environnement Profond, BP70, 29280 Plouzané, France.
E-mail addresses: fanny.girard13@gmail.com (F. Girard), cfisher@psu.edu (C.R. Fisher).

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2002; Cordes et al., 2001; Risk et al., 2002). Deep-sea corals are facing a number of threats from human activities. Fishing, and bottom trawling in particular, have been shown to inflict considerable damage to deep-sea coral communities (Clark and Koslow, 2008; Fosså et al., 2002; Hall-Spencer et al., 2002; Koslow et al., 2001). There is a growing concern that the potential for mining cobalt-rich crusts on seamounts, as well as offshore oil and gas extraction could also have a significant impact on deep-sea coral communities. Although less well documented, the direct physical disturbance and sediment plumes produced by these activities could be as detrimental as trawling (Clark et al., 2010; Cordes et al., 2016; Van Dover, 2007).

The oil and gas industry is particularly active in the Northern Gulf of Mexico, where reserves at depths over 3000 m are being extracted (Cordes et al., 2016). Deep-sea corals are abundant and diverse in the Northern Gulf of Mexico with 258 species documented, including 132 species of octocorals (Etnoyer and Cairns, 2016). Although the deep sea floor in the Gulf of Mexico consists mostly of fine-grained sediment, exposed carbonate hardgrounds that form as a byproduct of microbial activity at seeps can provide the hard substrate necessary for the attachment of deep-water corals (Fisher et al., 2007).

The 2010 Deepwater Horizon blowout in the Northern Gulf of Mexico led to the release of approximately 4.9 million barrels (780 million liters) of crude oil at a depth of 1500 m over an 87-day period (McNutt et al., 2011). In addition, a total of 7 million liters of dispersant were applied at the surface or at the wellhead on the sea floor. Due to both the use of dispersant and the physics of the release, much of the oil remained at depth, forming a deep-water plume that persisted for months (Camilli et al., 2010). The oil that did reach the surface contributed to a large marine snow formation event, which may have also been affected by the presence of dispersant (Passow, 2014; Passow et al., 2017; Passow et al., 2012). Both the deep-water plume and sinking of oil-contaminated marine snow had the potential to affect vulnerable deep-sea communities.

Three months after the well was capped, an impacted coral community was discovered 13 km away from the Macondo well in the US Bureau of Ocean Energy Management (BOEM) lease block Mississippi Canyon (MC) 294 at a depth of 1370 m. At this time, the majority of coral colonies at this site were covered, at least in part, by a brown flocculent material (floc) that contained traces of oil from the Macondo well, as a well as dioctyl sodium sulfosuccinate, a surfactant contained in the dispersant deployed during the spill (White et al., 2012; White et al., 2014). This suggests that the corals at this site were exposed to both oil and dispersant. Toxicity experiments conducted on deep-sea and mesophotic octocorals from the Northern Gulf of Mexico showed that these corals were particularly vulnerable to mixtures of oil and dispersant (DeLeo et al., 2015; Frometa et al., 2017).

Two additional impacted sites were documented in October 2011 in lease blocks MC 297 and MC 344, 6 and 22 km away from the spill site (Fisher et al., 2014b). By this time, the corals at these two sites were no longer covered in floc, but did display a characteristic patchy covering of hydroids on exposed skeleton that was also observed at MC 294 at this point in time. The level of visible impact at MC 297 (1560 m depth) was comparable to MC 294, while it was less severe at MC 344 (1850 m depth). All three coral communities were dominated by the octocoral species *Paramuricea biscaya* (Grasshoff, 1981), which is known to occur throughout the Northern Gulf of Mexico and North Atlantic (Fisher et al., 2014b).

A monitoring study was initiated in 2010 at MC 294 and in 2011 at MC 297 and MC 344 to assess the recovery of corals that were impacted by the spill. A temporal study following impacted corals at MC 294 between 2010 and 2012 showed that, even though the median level of impact decreased during that period, corals that were impacted over 20% or more of their colony still showed signs of injury in 2012 (Hsing et al., 2013). Recovery from impact was negatively correlated to the initial level of impact in 2010, and hydroid overgrowth, which started in 2011, was still expanding on some colonies. Another study found that coral recovery was also affected by the presence of the brittle star *Asteroschema clavigerum* commonly associated with *Paramuricea biscaya* (Girard et al., 2016). Corals associated with ophuroids were on average less impacted than corals without associates and branches in the vicinity of ophiuroids were more likely to recover from impact and hydroid colonization. Ophiuroids protected corals and enhanced their recovery, likely by removing particles depositing on coral branches and preventing the settlement of epibionts.

Some of the data collected from 2011 to 2017 at the three impacted sites were used in another study to parameterize a model and project the time to full recovery of the impacted communities (Girard et al., 2018). We here use the totality of the dataset to characterize the long-term effect of the Deepwater Horizon oil spill on deep-sea corals and evaluate their recovery potential.

2. Materials and methods

2.1. Study sites

Individual coral colonies were imaged every year from 2011 to 2017 at three impacted sites (MC 294, MC 297 and MC 344). Two reference sites (Atwater Valley (AT) 357 and Green Canyon (GC) 852 located 183 and 325 km away from the Macondo well, respectively), where there was no visual evidence of recent impact, were also monitored during this time period. One of the reference sites, AT 357 (1050 m depth), was shallower than the impacted sites and dominated by a different *Paramuricea* species, *Paramuricea* sp. B3 (Doughty et al., 2014). Although, differences in sclerite morphology indicate that *P. biscaya* and *P.* sp. B3 are different species, there is a low level of genetic divergence between the two species (Doughty et al., 2014). AT 357 was originally chosen as a reference site because *P.* sp. B3 is a close relative to *P. biscaya* with similar growth form and ecological niche, and the community at AT 357 was the only community with abundant *Paramuricea* in the region we were confident had not been affected by the spill. For logistical reasons, AT 357 was monitored from 2011 to 2016 but not in 2017. The other reference site, GC 852 (1400 m depth), was dominated by *Paramuricea biscaya*, the species that was the most impacted by the oil spill. Corals at this site were monitored for the first time in 2016, and again in 2017. Although data was available at MC 294 prior to 2011, we chose 2011 as the baseline for this study for two reasons. The first was that 2011 was the first complete, high-quality, image dataset collected at all impacted sites and the AT 357 reference site. The second was that much of the impact detected in 2010 at MC 294 consisted of branches covered with floc, many of which were not visibly impacted when next imaged in 2011. Plexaurid corals, such as *P. biscaya* and *P.* sp. B3, have a planar morphology and thus make excellent candidates for image analysis, as all branches are generally visible in the same image.

2.2. Monitoring and image analysis

A total of 326 coral colonies were monitored between 2011 and 2017 (49 at MC 294, 56 at MC 297, 61 at MC 344, 100 at AT 357 and 60 at GC 852). Coral colonies were imaged every year with a digital still camera using the same headings and camera settings (Table 1). Images taken in 2011 (or the year a colony was discovered if it was after 2011) were digitized using Inkscape 0.48.5 (The Inkscape Team 2011), and branches coded based on four categories: healthy, unhealthy (covered in floc, excess mucous or exposed skeleton), colonized by hydroids, and unclassified (branch obscured or image quality not sufficient to determine the condition of the branch) (Fig. 1A&H). Branches were coded conservatively; whenever it was not clear whether a branch was unhealthy it was coded as healthy, and when material on a coral branch was not unambiguously hydroids the branch was coded as unhealthy. To determine the condition of coral colonies after 2011, we used the 2011 image as a template, and re-coded branches every year based on

Table 1
Dates of the different expeditions during which the data used in this study were collected. The ships, ROVs and cameras used are indicated.

Expedition date	Research vessel	Submergence vehicle	Camera
October 2011	Holiday chouest	Schilling ultra-heavy-duty ROV	13-megapixel AquaPix AquaSLR digital still camera
November 2012	Falkor	ROV global explorer	Digital still camera with 18–55 mm lens
June 2013	Nautilus	ROV Hercules	13-megapixels AquaPix AquaSLR digital still camera
July 2014	Nautilus	ROV Hercules	18-megapixel Canon EOS Rebel T5i digital still
July 2015	Nautilus	ROV Hercules	18-megapixel Canon EOS Rebel T5i digital still
September 2016	Ocean inspector	ROV global explorer	24-megapixel Canon EOS Rebel T6i DSLR Camera
June 2017	Ocean intervention II	ROV global explorer	24-megapixel Canon EOS Rebel T6i DSLR Camera

their new state. Two colonies at MC 297 were partially colonized by a stoloniferan species. However, colonization by stoloniferans was not added as a category and these colonies were excluded from the analyses due to the small sample size. To track changes in coral condition over time, the 2011 images were used as templates, and branches were re-coded every year based on their new state (Fig. 1B to N). After 2011, a new coding category was added to follow branches that were lost between consecutive years. The proportion of branches in each category was measured every year, and changes in the state of individual branches were followed to estimate the proportion of branches that transitioned from one category to another as well as the number of branches that broke off between each consecutive year. Each coral colony was digitized independently by two observers. After ensuring that there was no significant difference between observers using the Student's *t*-test, the arithmetic mean of the digitized values was calculated and used for all analyses. In the case of branch loss, the images digitized by both observers were compared and the number of branches that broke was estimated once a consensus was reached.

The total number of internodes (segment that separates two branches) on each coral colony was quantified for 2011 using the Cell Counter tool in ImageJ 1.48. This number was adjusted each following year by subtracting the number of branches that fell off. As in other studies (Brazeau and Lasker, 1988; Mitchell et al., 1993; Coma et al., 1998), the number of internodes per colony was used as a proxy for the number of branches. Unlike branches, that have extremely variable lengths within colonies (e.g. main axis vs small terminal branch), internode lengths are relatively constant between and within colonies and are thus more appropriate for this type of analysis.

Coral colonies were excluded from the analyses when the image quality was not sufficient to distinguish between different branch states or when the colony was sampled as part of other research projects (on average, 5.4% of coral colonies were excluded in a given year).

2.3. Recovery and effect of the initial level of total visible impact on changes in the state of individual branches

The median level of total visible impact was calculated two ways for each year; the sum of the proportions of unhealthy and hydroid-colonized branches, including the proportion of lost branches and not including the proportion of lost branches. Each year, the median level of total visible impact measured at each impacted site was compared to the appropriate reference site.

The correlation between the initial level of total visible impact in 2011 and the total visible impact (sum of the proportions of unhealthy,

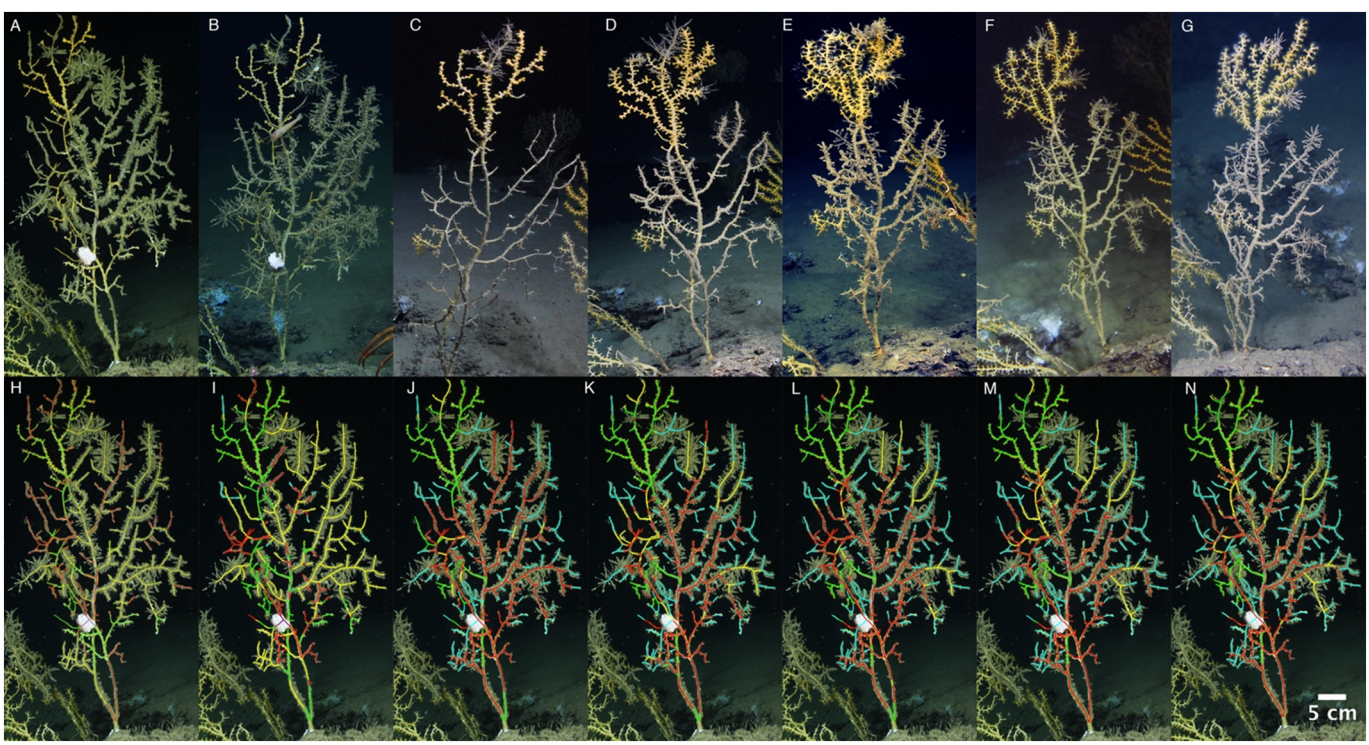

Fig. 1. Changes in an impacted coral colony at MC 294 between 2011 and 2017. The 2011 image (A) was digitized (H) and branches coded as healthy (green), unhealthy (red), colonized by hydroids (yellow) or unclassified (purple). To quantify changes over time, branches were re-coded based on their new condition in 2012 (B, I), 2013 (C, J), 2014 (D, K), 2015 (E, L), 2016 (F, M), and 2017 (G, N). A new category was added after 2011 to account for branches that broke between consecutive years (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hydroid-colonized and lost branches) in 2017 was tested using Spearman's rank correlation.

The proportion of healthy branches that remained healthy, as well as the proportions of unhealthy or hydroid-colonized branches that became healthy (recovered) were quantified between every consecutive year and plotted against the initial level of total visible impact.

2.4. Total branch loss

The number of breaking events (number of times a portion of the colony disappeared between years) was measured for each coral colony. This parameter measures the rate at which corals are losing branches and, unlike the number of lost branches, is independent of breakage location. To account for differences in coral size, the total number of breaking events on each colony was divided by its total number of branches. The ratio between the total number of breaking events in healthy portions of the colony and the total number of healthy branches was also calculated. In order to quantify changes in branch loss over time, the ratio between the total number of breakpoints per month (the number of months separating data collection varied from one year to another – Table 1) and total number of branches was calculated for each coral at each site between every consecutive year. To assess changes in branch loss over time, the differences in branch loss between different pairs of consecutive year were tested with the pairwise Wilcoxon Signed Rank test. A Bonferroni correction was applied to account for multiple comparisons.

2.5. State of lost branches

Breakpoints were sorted depending on whether breakage occurred in healthy, unhealthy or hydroid-colonized areas of the colonies. At each site, the null hypothesis that breakage was random was tested with Fisher's exact test, and expected values under that hypothesis were estimated based on the total number of branches in each category (healthy, unhealthy or hydroid-colonized) observed in 2011. The proportions of breaking events in unhealthy and hydroid-colonized areas of the colonies were compared with a two-proportion z-test. Additionally, the number of breaking events that occurred in unhealthy parts that were previously colonized by hydroids was recorded.

2.6. Rank of lost branches

For each colony, branches were classified using the branch ordering system developed by Brazeau and Lasker (1988). In this system, distal branches are considered first order branches. When two first order branches join, a second order branch arises. Similarly, when two second order branches join, a third order branch arises, and so on. Higher order branches only arise when branches of equal lower order join. As a result of this ordering system, branches with similar functional aspects will have the same rank. In order to determine whether the rank of lost branches changed over time, each branch was assigned a rank based on the 2011 images, and the proportion of branches that broke in each rank between every consecutive year was followed.

2.7. Statistical models

Because the data analyzed in this study were not normally distributed, Generalized Linear Models (GLMs) were used for the following analyses.

The effect of the initial level of total visible impact (fixed effect – continuous variable) was tested on the following response variables: proportion of healthy branches that remained healthy, proportion of unhealthy or hydroid-colonized branches that recovered between each consecutive year (ratio between the number of healthy, unhealthy or hydroid-colonized branches that remained/became healthy and the total number of branches in the focal state), and proportion of all branches (ratio between the number of breakpoints and total number of branches) and healthy branches (ratio between the number of breakpoints in healthy areas of the colonies and total number of healthy branches) that broke between 2011 and 2017. The relevant subset of the data was used for each model (for instance, only healthy branches were used when modeling the transition from healthy to healthy).

Differences in the proportion of visibly impacted branches and number of breaking events between the reference and impacted sites were tested with GLMs. The effect of site (fixed effect – categorical variable with four categories) on the ratio between the number of visibly impacted branches, or number of breaking events, and the total number of branches was tested each year or between consecutive years, respectively. The appropriate reference site (AT 357 or GC 852) was used as the reference for comparisons in all models.

Temporal changes in the proportion of branches of each rank that broke between every consecutive year were tested at each site using GLMs. The effect of year (fixed effect – categorical variable with seven categories) on the proportion of branches that broke in each rank was tested for each contrast separately (first vs second order, first vs third order and second vs third order). For this analysis, a series of binomial GLMs was used as an alternative to a more complex multinomial model. Only three levels were considered, as no branches with a rank higher that three broke during the study period.

A binomial error distribution (commonly used for this type of proportion data with many zeros) with a logit link function was used in every GLM. Additionally, both residuals and standardized residuals were plotted against predicted values to check the models fit and identify potential outliers. Influential points that had a negative influence on the goodness of fit of the model were occasionally identified. However, these points were not removed from the dataset as they generally corresponded to the most heavily impacted corals. When overdispersion was detected (the residual deviance is greater than the residual degree of freedom, indicating that the variability in the data is larger than the variability expected under the assumed binomial distribution), a quasibinomial, instead of a binomial family, was used in the model.

All statistical analyses were performed in R using the *stats* package (version 3.3.1) (R Core Team, 2014).

3. Results

3.1. Changes in total visible impact between 2011 and 2017

No obvious signs of impact were detected at any time at either reference site; between 2011 and 2016 at AT 357 or in 2016 or 2017 at GC 852. The median level of background “total visible impact” varied between 0 and 0.67% in different years at AT 357 and was equal to 0.15% in both 2016 and 2017 at GC 852. Every year, between 55 and 77% of the corals at AT 357 had a level of impact lower than 1% and between 4 and 19% of corals were impacted over 5% of the colony. At GC 852, 66% of coral colonies had an impact level lower than 1%, and only 7% of all corals were impacted over 5% of the colony. Thus, a low level of visible damage in the absence of external stressors is characteristic of both sister species. The few unhealthy branches visible on some coral colonies were generally at the bottom edge of the colony in close proximity to the sediment. Hydroid colonization was rare at the reference sites (the median proportion of branches colonized by hydroids was always 0 and the maximum observed average in a year was 0.4%).

Overall, the range of impact to individual corals at MC 294 and MC 344 was wider than that at MC 297 (Fig. 2A). The median level of total visible impact in 2011 was higher at MC 294 (14%) and MC 297 (13%) than at MC 344 (5%) (Fig. 2A). Although the median level of total visible impact decreased after 2011 and has been stable ever since (between 4 and 6% at MC 294, 6 and 7% at MC 297, and 3 and 4% at MC 344), the level of total visible impact remained higher than at the

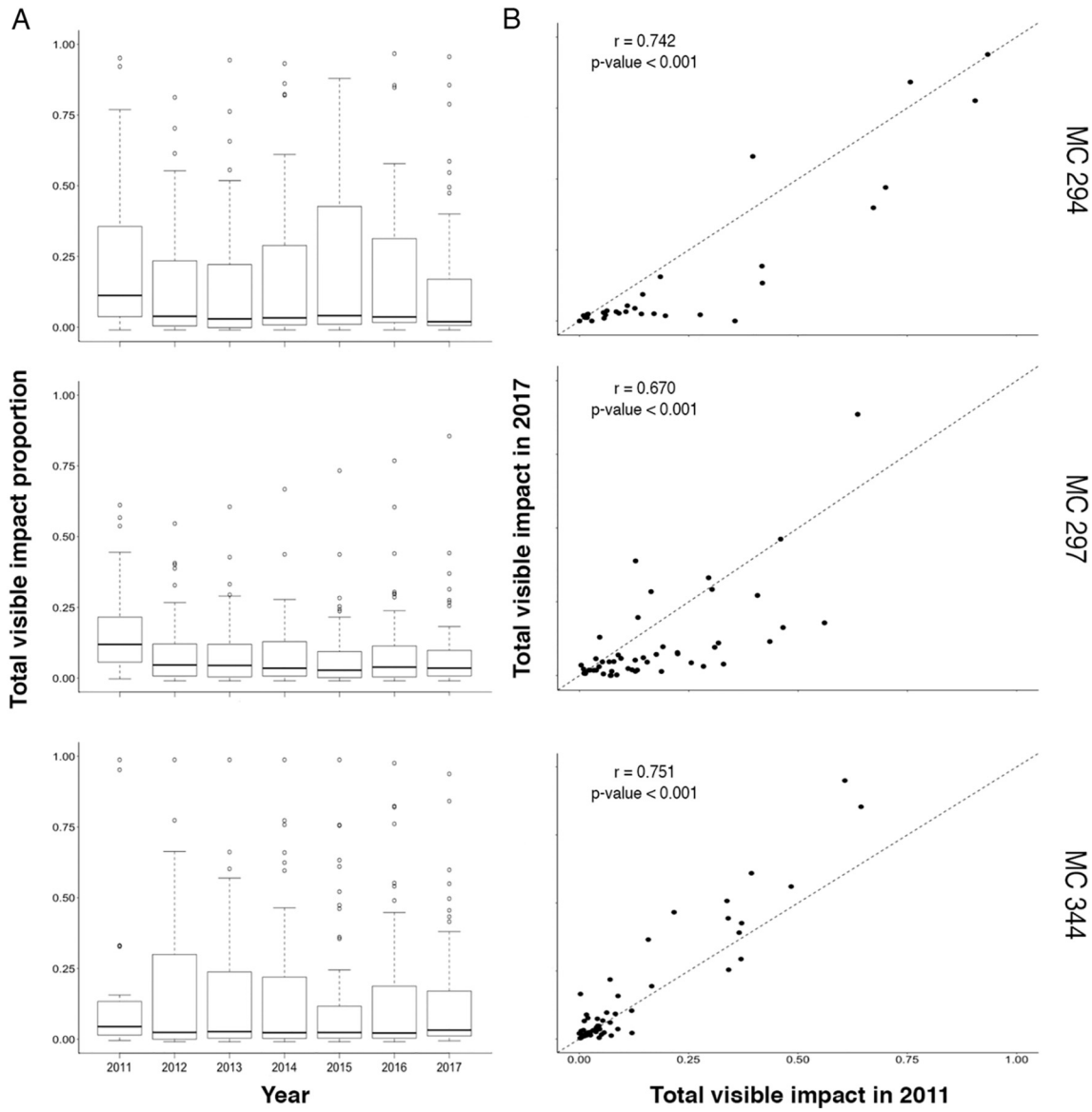

Fig. 2. Changes in total visible impact over time at the three impacted sites: MC 294, MC 297 and MC 344. (A) Boxplot representing changes in the median level of total visible impact (branch loss included) between 2011 and 2017 and (B) Total visible impact in 2017 as a function of total visible impact in 2011. The dotted line represents the 1:1 line and separates corals that recovered (bellow the line) from corals whose health deteriorated (above the line). The Spearman's correlation coefficients and their associated *p*-values are indicated.

reference sites every year (GLM: branch loss included: the total visible impact proportion was significantly higher than at the reference sites every year except for 2011 at MC 344, 2015 at MC 297 and 2016 at MC 297 and MC 344; Table A1). Even when branch loss was not included in the total visible impact calculation (GLM: branch loss excluded: the total visible impact proportion was significantly higher than at the reference sites every year except for 2011 at MC 344 and 2016 at MC 297; Table A2).

3.2. Long-term effect of the initial total visible impact on coral recovery and changes in the state of individual branches

The level of total visible impact on coral colonies in 2017 was significantly positively correlated with the level of total visible impact on these same colonies in 2011 (Fig. 2B). The health of the majority of coral colonies at MC 294 and MC 297 improved between 2011 and 2017, with an average increase in the proportion of healthy branches of 6% per colony. However, the condition of most corals deteriorated at MC 344 where, on average, the proportion of healthy branches decreased by 3% per colony.

The initial (2011) level of total visible impact had a significant negative effect on the proportion of branches that remained healthy between every consecutive year except for 2016–2017 at MC 294 and MC 297, and 2013–2014 at MC 344 (Fig. 3; Table A3). The initial level of total visible impact also had a significant negative effect on the proportion of unhealthy branches that recovered between each consecutive year except between 2013–2014, 2015–2016 and 2016–2017 at MC 297, and 2012–2013 and 2013–2014 at MC 344. The proportion of branches colonized by hydroids that recovered between consecutive years was also significantly negatively affected by the initial level of total visible impact, except between 2015 and 2016 at MC 294 and 2013–2014 at MC 297. This transition was not significantly affected by the initial level of total visible impact at MC 344.

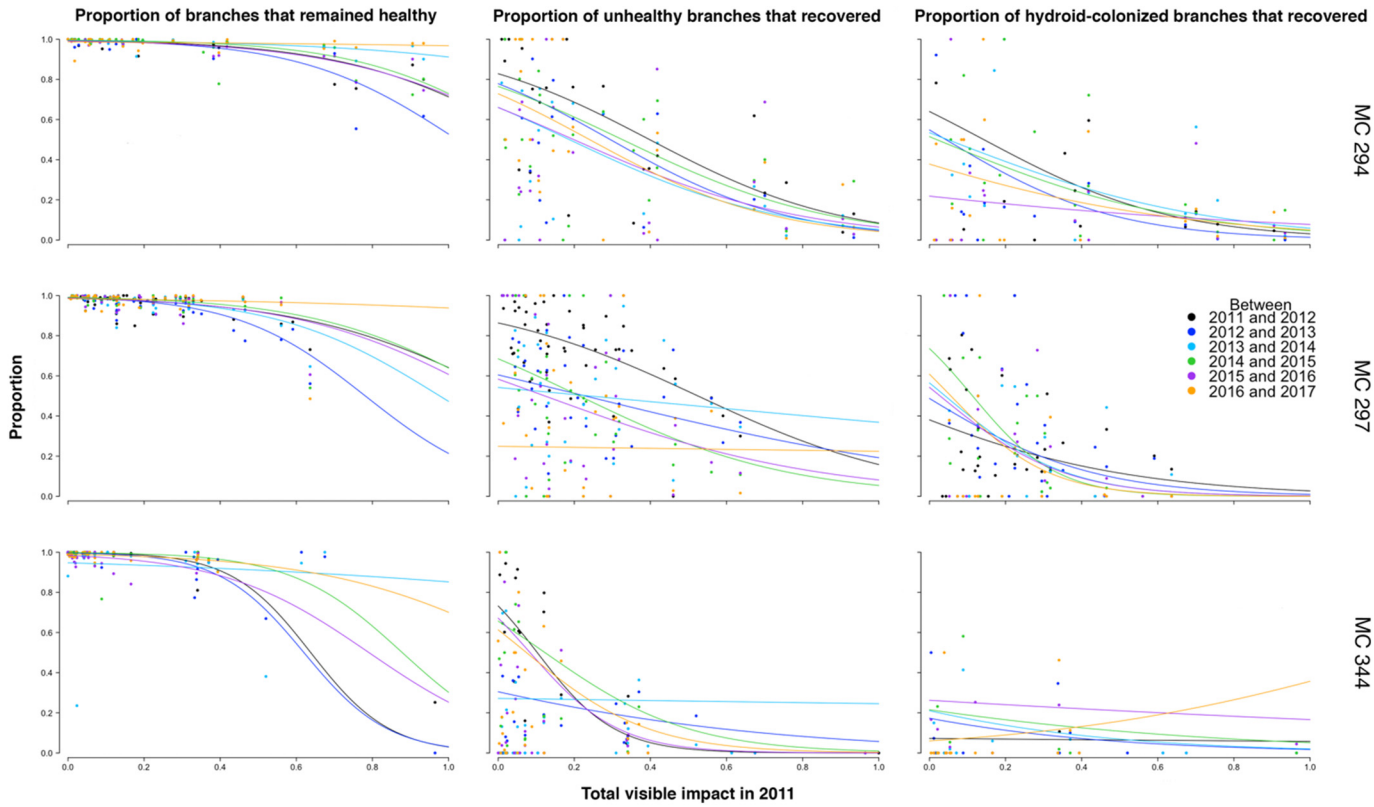

Fig. 3. Proportion of branches that remained healthy and that were unhealthy or colonized by hydroids and recovered between each consecutive year as a function of the initial level of total visible impact. Predictions from the Generalized Linear models were obtained and fitted to the dataset after back-transformation from the logit scale.

3.3. Branch loss comparisons between years and sites

Branch loss was observed at all sites, even the reference sites, throughout the study period. Between 2011 and 2016 branch loss at the impacted sites was compared to branch loss at AT 357. Branch loss between 2016 and 2017 at the impacted sites was compared to branch loss at GC 852. Branch loss was significantly higher at MC 294 than at the reference sites (AT 357 or GC 852) between every consecutive year (Fig. 4; Table A4). Branch loss at MC 294 was the highest between 2011–2012 and 2012–2013, it then decreased after 2013 and did not significantly change afterward (Fig. 4; Table A5). Branch loss at MC 297 was only significantly higher than at the reference sites between 2013 and 2014 and did not change significantly over time. Branch loss at MC 344 was significantly higher than at the reference sites between 2015–2016 and 2016–2017 but did not change significantly over time (Fig. 4; Table A4&A5).

3.4. Breakage location and effect of impact on branch loss

Although the majority of branches were healthy in 2011, breakage between 2011 and 2017 occurred significantly more often in areas of the colonies that were unhealthy or colonized by hydroids (Fisher's exact test: p-value < 0.001 at all sites; Fig. 5). The proportion of branches that broke in areas colonized by hydroids was significantly higher than the proportion of branches that broke in unhealthy parts of the colonies at MC 294 and MC 297 (two-proportion z-test: p-value < 0.001 at both MC 294 and MC 297), but not at MC 344 (two-proportion z-test: p-value = 0.433). Moreover, 42, 28 and 9% of the unhealthy branches that broke at MC 294, MC 297 and MC 344, respectively, were previously colonized by hydroids.

Branches breaking in visibly healthy parts of the colony were observed at all sites throughout the study period. The number of branches breaking in healthy areas was not significantly different between the impacted and reference sites, except at MC 294 and MC 297 between 2012 and 2013 (Fig. 4; Table A6). Moreover, no significant changes in healthy branch loss was observed over time at any of the impacted sites (Fig. 4; Table A7).

Overall, the initial total visible impact proportion had a significant effect on the total normalized number of breakpoints (total number of breakpoints divided by the total number of branches) between 2011 and 2017 at all three impacted sites (Table 2). The initial level of total visible impact also had a significant positive effect on the number of branches that broke in visibly healthy parts of the colonies between 2011 and 2017 at MC 294 and MC 297, but not MC 344 (Table 2).

The majority of breaking events occurred on first order branches (terminal branches) (Fig. 6). Second order branches broke every year at all three sites, while breakage of third order branches was observed every year at MC 294, and only between 2011 and 2012 at MC 297. The relative proportion of first, second and third order branches that broke did not significantly change between 2011 and 2017 at any of the impacted sites with the exception of MC 297 due to a few third order branches breaking in the first year (MC 294: first vs second: p-value = 0.0923, first vs third: p-value = 0.229, second vs third: p-value = 0.485; MC 297: first vs second: p-value = 0.448, first vs third: 0.0157, second vs third: 0.0306; MC 344: first vs second: 0.158; Results were considered significant for a p-value < 0.0167 after Bonferroni correction of $\alpha = 0.05$). No breakage of branches with an order higher than three was observed.

4. Discussion

Overall, recovery was slow and the level of visible impact (sum of the proportion of unhealthy and hydroid-colonized branches both including and not including the proportion of lost branches) at all three

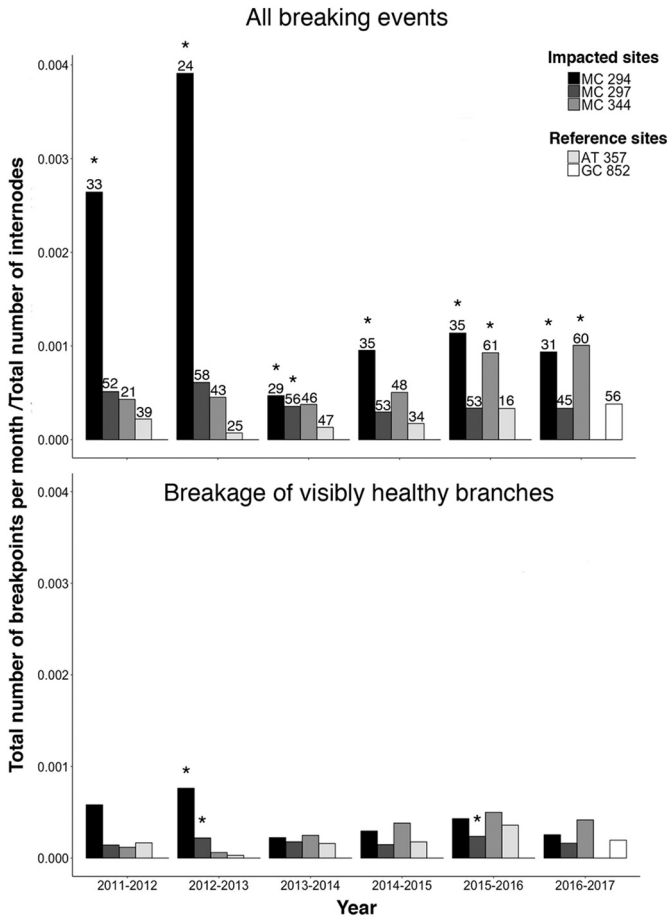

Fig. 4. Changes in the ratio between the total number of breakpoints per month and total number of branches between 2011 and 2017. The number of colonies used in the GLMs is indicated above each bar. The stars (*) indicate impacted sites for which branch loss is significantly different from the reference site (AT 357 between 2011 and 2016 and GC 852 between 2016 and 2017).

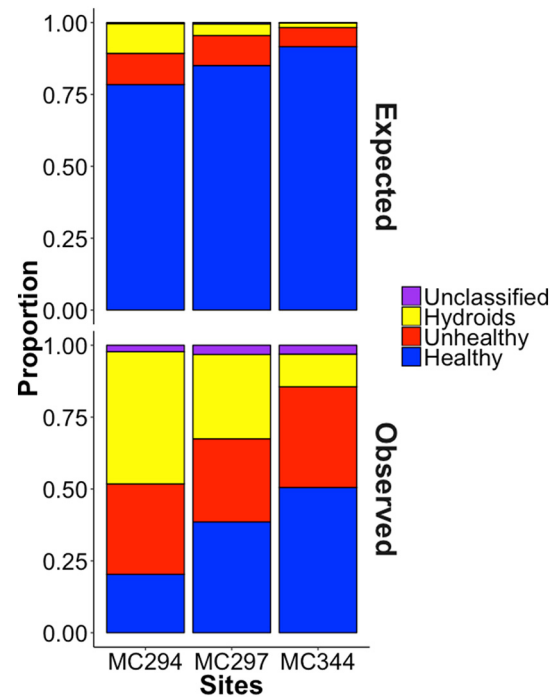

Fig. 5. Proportion of branches in each state in 2011 (Expected probabilities used for the proportion test) and observed proportion of branches that broke in each state between 2011 and 2017 at MC 294, MC 297 and MC 344 (impacted sites).

Table 2
Results from GLMs testing the effect of the initial proportion of total visible impact on the total proportion of branches that broke (number of breaking events divided by the total number of branches) and on the proportion of visibly healthy branches that broke (number of breaking events in healthy areas divided by the total number of visibly healthy branches) at all three impacted sites between 2011 and 2017. The stars (*) indicate a significant effect of initial impact on branch loss.

Site	All breakpoints		Healthy breakpoints	
	Estimate	Standard error	Estimate	Standard error
MC 294	5.11**	0.256	4.18**	0.437
MC 297	5.75**	0.897	3.30*	1.15
MC 344	4.38**	0.703	1.62	1.60

* p-Value < 0.05.
** p-Value < 0.001.

impacted sites remained significantly higher than at the reference sites through 2017. The positive correlation between the level of total visible impact in 2011 and 2017, as well as the negative effect of initial impact (2011) on the recovery of unhealthy and hydroid-colonized branches explain both the decrease in the median level of total visible impact after 2011 (lightly impacted corals recovered) and the following stabilization of this median (heavily impacted corals are not recovering). These observations align with early results showing that corals that were initially only lightly impacted with floc were more likely to show early signs of recovery (Hsing et al., 2013). However, even seven years after the spill, a negative effect of the initial total visible impact on the proportion of healthy branches that remain healthy between consecutive years and on the proportion of unhealthy or hydroid-colonized branches that recover between subsequent years remains. This long-term non-acute effect of initial impact on the condition of individual branches suggests that many more years will be necessary for coral recovery and that colonies with more extensive injury may never recover. Other studies have documented slow to no recovery for other octocoral species. The extent of injury on *Paramuricea clavata* colonies affected by the 1999 heat wave in the Mediterranean decreased significantly during the first two years and then stabilized to a level that was still higher than what was observed before the event (Linares et al., 2005). In contrast, the condition of mesophotic corals impacted by the Deepwater Horizon oil spill was still declining after four years, suggesting recovery for these corals is unlikely (Etnoyer et al., 2015; Silva et al., 2016).

Recovery is a complex process that can be influenced by a combination of intrinsic (size, age, morphology, genotype) and extrinsic (environment, predation, competition) factors (Henry and Hart, 2005). Corals are modular organisms, all replicated modules (polyps) are capable of all physiological functions but are interconnected, meaning that a change in a part of the colony is likely to affect the entire colony (Sánchez and Lasker, 2003). Colony integration likely explains the influence of the level of total visible impact on changes in individual branches also previously observed by Hsing et al. (2013). Moreover, several studies found that the presence of healthy tissue surrounding wounds facilitated recovery (Cerrano et al., 2005; Lirman, 2000; Meesters et al., 1997). Conversely, the presence of wounds on the colony may have disconnected and isolated visibly healthy branches from the rest of the colony, reducing their ability to remain healthy. Similarly, the initial level of total visible impact had a significant effect on the breakage of visibly healthy branches at both MC 294 and MC 297 between 2011 and 2017. These visibly healthy branches could have been less resistant to breakage due to being isolated from the rest of the

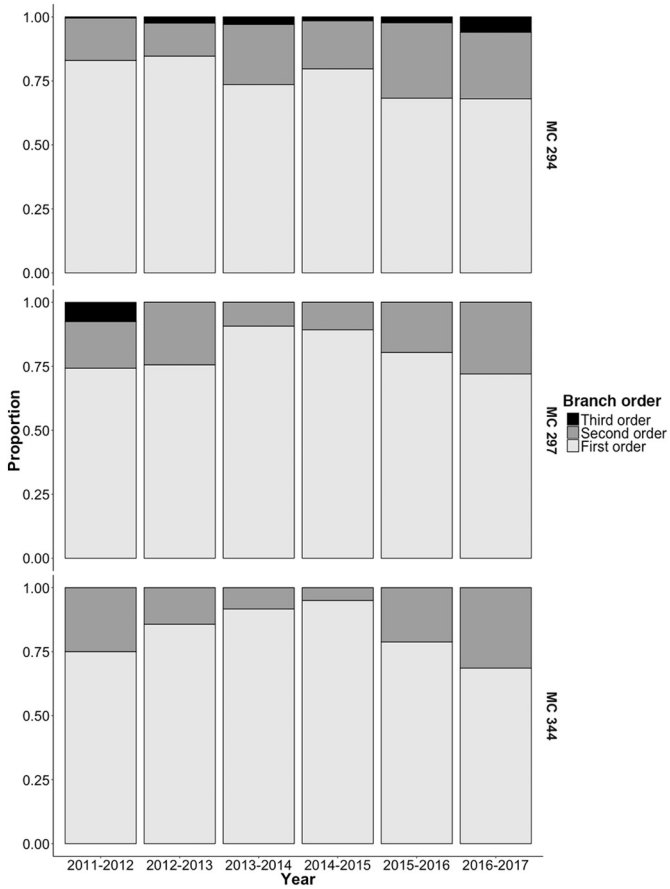

Fig. 6. Relative proportions of first, second and third order branches that broke each year between 2011 and 2017 at the three impacted sites.

colony, or could have been branches that were previously impacted and visibly (but not fully) recovered.

The initial level of total visible impact also had a significant effect on total branch loss, and impacted branches were more likely to break than healthy branches, particularly when they were colonized by hydroids. The presence of epibionts on coral's skeleton has been suggested to weaken the skeleton by increasing branch resistance to water movement due to the added epibiont mass (Bavestrello et al., 1997). The extensive hydroid colonization observed at MC 294 could explain the high level of branch loss observed at this site throughout the study period. Surprisingly, branch loss at MC 297 was not significantly higher than at the reference sites. This could be due to the lower levels of hydroid colonization observed at MC 297 compared to MC 294. MC 297 is deeper than MC 294 and hydroid's diversity and abundance have been shown to decrease with depth (Altuna, 2007; Gili and Hughes, 1995). Moreover, the number of corals impacted to over 50% of the colony in 2011 was smaller at MC 297 than MC 294 (5% of the corals at MC 297 compared to 13% at MC 294), and thus corals at MC 297 may have been more able to outcompete hydroids. Branch loss at MC 344 was similar to the reference sites until 2015, but was significantly higher after 2015. Several heavily impacted colonies discovered, and added to our study, in 2014 and 2015 contributed to the increase in the recorded number of breaking events.

Branch loss at MC 294 was the highest during the first three years that followed the spill. Even though it decreased and stabilized after that, the fact that branch loss at both MC 294 and MC 344 was still higher than at the reference sites between 2016 and 2017 also indicates an ongoing effect of the spill on these corals. Although the rank of the branches that broke did not significantly change between 2011 and 2017, with the majority of branches breaking so far being first order terminal branches, breakage of higher order branches is likely to increase in the future. For several heavily impacted coral colonies such as the one represented in Fig. 1, the fracture of the axial skeleton near the base, a major source of mortality in octocorals (Yoshioka and Yoshioka, 1991), is expected. Linares et al. (2005) documented a delayed mortality of *P. clavata* colonies that were heavily impacted during a mass mortality event in the Mediterranean. We suggest that a similar delayed mortality of impacted *P. biscaya* may occur in the next few years.

The high branch loss combined with the slow growth rates (estimated linear growth rates between 0.03 and 0.1 cm/year) previously estimated for *Paramuricea biscaya* in the Gulf of Mexico (Prouty et al., 2014) will lead to an overall decrease in colony size at the impacted sites, especially if corals keep losing branches at these rates in the next few years. A direct link between colony size and fecundity has been demonstrated for several octocoral species, sexual maturity occurring only once colonies reach a certain size and smaller colonies being less fecund (Coma et al., 1995; Page and Lasker, 2012). A decrease in coral sizes at the impacted sites could thus lead to a decrease in fecundity. Moreover, several studies found that the presence of wounds affected both growth and sexual reproduction in corals due to energy being reallocated for regeneration (Brazeau and Lasker, 1992; Guzmán et al., 1991; Linares et al., 2008; Meesters et al., 1997; Page and Lasker, 2012). A decrease in growth and fecundity at these sites could have long-term consequences for the regional coral metapopulation.

The analysis of seven years of data collected at different sites that were impacted by the Deepwater Horizon oil spill indicated that the resilience of *P. biscaya* was not the same at all impacted sites. Although the median level of impact at both MC 294 and MC 297 was still higher than at the reference sites in 2017, there was a general trend toward recovery at these sites. In contrast, the health of the majority of the coral colonies at MC 344, which was less visibly impacted in 2011 (Fisher et al., 2014b), deteriorated through 2017. MC 344 is deeper, corals are smaller and occur in lower density than at the other two impacted sites (Doughty et al., 2014). Furthermore, the ages determined from two *P. biscaya* specimens recovered from this site were both in excess of 600 years, suggesting much lower growth rates (on average between three and six times slower) than at the other two impacted sites (Prouty et al., 2014). Deep-sea fauna, such as corals, that live in non-chemosynthetic environments depend mostly on surface primary productivity, of which both quantity and quality decreases with depth (Suess, 1980). Further, not all locations at any depth will be equally favorable for corals due to differences in substrate availability, primary production in overlying surface waters, local current regimes etc. Therefore, we suggest that the lower resilience observed for corals at MC 344 may be due to food limitation, or some other site-specific factor making these corals less robust, and therefore less resilient to anthropogenic impact.

Although we only analyzed three coral communities that were impacted by the Deepwater Horizon oil spill here, we did discover another apparently impacted coral community in June 2014, at a depth of 1700 m in lease block MC 258 located 25 km west of the Macondo well. Thirteen coral colonies (eight *Stichopathes* sp., one *Bathypathes* sp., two *Paramuricea* spp., one *Keratoisis* sp. and one unidentified bamboo coral) were found at this site, two of which (one *Paramuricea* sp. and *Keratoisis* sp.) showed light, but notable, patchy impact, characteristic of corals that were impacted by the spill. Considering this discovery, as well as the large geographical area that was affected by the spill (Chanton et al., 2015; Valentine et al., 2014), it is likely that more impacted coral communities still remain to be discovered.

Long-term monitoring at sites that were not affected by the oil spill allowed the collection of baseline data on *P. biscaya* and *P.* sp. B3. Only very low levels of injury were detected at the reference sites. Damaged branches were observed on relatively few colonies at these sites, generally at the bottom edge of the colony at the sediment-water interface. These branches were likely damaged by repeated exposure to sediment due to localized hydrodynamic effects, and could have broken off for

the same reason, explaining some of the branch loss observed at these sites. However, about half of the branches that broke at the reference sites were visibly healthy suggesting that a certain level of branch loss occurs naturally in the apparent absence of anthropogenic impact. A greater diversity and abundance of associated species was also observed at the reference sites as compared to the impacted sites. At the impacted sites, the only coral associates documented were the ophiuroid *Asteroschema clavigerum* and, occasionally, hormatiid anemones. At GC 852, a species of hermit crab and aplacophorans were commonly observed on *P. biscaya* in addition to *Asteroschema clavigerum* and hormatiid anemones. Whether the lower diversity and abundance of associated species on *P. biscaya* at the impacted sites post spill was a result of the exposure of the communities to oil and dispersant, or some other factor inherent in the different sites, is not known.

A better understanding of the biology and ecology of deep-water corals is a prerequisite to informed conservation decisions and recognition of changes to the deep sea that may occur with increasing anthropogenic impact to the oceans. Monitoring has long been considered an essential tool in conservation biology. For instance, monitoring programs have been used to identify species in decline (Gerber et al., 1999), detect the effect of invasive species on native populations (Witte et al., 1992), characterize the interaction between different species (Karanth et al., 2004), and provide information on the efficacy of protected area (Bates et al., 2013; Edgar et al., 2014). However, little temporal data has been collected on deep-sea ecosystems due to their remoteness (Glover et al., 2010). Some notable exceptions include temporal studies of sedimented environments (Billett et al., 2010; Soltwedel et al., 2005) and chemosynthetic ecosystems, hydrothermal vents in particular (Cuvelier et al., 2011; Du Preez and Fisher, 2018; Podowski et al., 2010; Sarrazin et al., 1997; Sen et al., 2014; Shank et al., 1998). The few temporal studies on deep-sea coral ecosystems have mostly focused on the reef-forming coral *Lophelia pertusa* (Huvenne et al., 2016; Lundälv et al., 2008). The long-term monitoring project initiated after the Deepwater Horizon oil spill provided the first repetitive high-resolution study of deep-water octocorals we are aware of.

5. Conclusions

The analyses of high-definition images of individual coral colonies, collected during seven years of monitoring following the Deepwater Horizon oil spill, allowed us to detect relatively small changes in the state of individual branches between years and to precisely quantify branch loss over time. Overall recovery was slow. The ability of individual impacted branches to recover and branch loss, were still dependent on the initial impact to the colonies after seven years, indicating a long-term non-acute effect of the spill. Furthermore, there are trends in the data suggesting that subacute effects are increasing over time at the deepest site. These results indicate that many more years will be necessary for moderately to heavily impacted corals to recover, and that some coral colonies will likely never recover. Overall, our results highlight the necessity to prioritize the use of a precautionary approach for the conservation of long-lived organisms and demonstrate the effectiveness of monitoring to collect data on the resilience of vulnerable ecosystems. This study also highlights the importance of long-term monitoring after a disturbance, in order to fully document effects that may not be obvious until many years after the disturbance. The fact that the delayed effects manifested differently at different sites clearly demonstrates the importance of planning for a range of effects that may be site specific and dependent on environmental or historical variables that are not fully understood. In the case of the deep sea in general, and the Gulf of Mexico in particular, establishing image-based coral-monitoring sites at a variety of depths and locations would provide critical regional baseline data, significantly improve our understanding of the biology of these ecosystem engineers, and, if implemented as part of a Marine Protected Area, provide a tool to evaluate the efficacy of conservation measures. Moreover, deep-sea corals, and plexaurid corals in particular, are excellent biomonitors (sentinels) for anthropogenic impact (Fisher et al., 2014a). With ever increasing energy extraction and the deepening impacts from fishing, ocean acidification and increasing water temperature due to climate change, the need for baseline data and monitoring is becoming acute.

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Appendix A. Supplementary data

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