Deep Benthic Ecosystem Impacts of the Deepwater Horizon Event: Assembling the Record of Species and Community Change

Patrick T. Schwing1\*, Paul A. Montagna2, Samantha Joye3, Claire B. Paris4, Erik E. Cordes5, Craig R. McClain6, Joshua P. Kilborn7,Steve A. Murawski7

# Supplementary Statistical Methods and Data

Multivariate statistical analyses were performed in MATLAB version 2019a, and implemented using the Fathom (Jones, 2017) and Darkside (Kilborn, 2020) Toolboxes. To test the hypothesis of ‘no difference’ in beta-diversity among treatment factors (e.g. before the 2010 Deepwater Horizon oil spill [DWH] vs. after), we employed permutation-based multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle and Anderson 2001). Multivariate dispersions were calculated using the permutation-based dispersion method (PERMDISP; Anderson et al., 2006), and the assumption of homogeneous dispersion was tested via a multivariate equivalent of Levene’s test (Anderson, 2006; Anderson et al., 2006; Anderson and Walsh, 2013). Species indicator values (IndVal; Dufrene and Legendre, 1997) were calculated to determine the most representative suites of taxa for each treatment level, and all PERMANOVA results were visualized using canonical analysis of principal coordinates (CAP; Anderson and Willis, 2003). Lastly, 10,000 iterations were used for all permutation-based methods, and *p*-values’ significance was determined using *α* = 0.05.

## Benthic Foraminifera

Benthic foraminifera were extracted from sediment cores and identified to the lowest taxonomic level possible. A total of 463 taxa were enumerated, and after reduction to only those taxa present in at least 5% of all samples, 128 unique taxa remained for multivariate community analyses. Abundance data were square-root transformed to downweight highly abundant taxa, and ecological dissimilarity was assessed via the Morisita-Horn resemblance (Chao et al., 2005, 2006; Legendre and Legendre, 2012) measure. A before vs. after DWH analysis was conducted to examine potential changes in beta-diversity of foraminifera assemblages based on this treatment factor using the sediment cores described in Table S2. Lastly, time series plots of species richness and diversity (Shannon index) were created to visualize each cores’ biodiversity dynamics over time (Figure S1).

The results of the PERMANOVA based on samples designated as before 2010 and those after (excluding all 2010 samples) showed significant results (*F* = 3.8081; *p* = 0.0074; *dfRx* = 1, *dfTotal* = 39) indicating a non-random change in beta-diversity between the two time periods. A similar check of the dispersion (i.e., variability in foraminifera beta-diversity) using PERMDISP corroborated these results, and showed that the period after DWH (disp. = 0.2356) was 34% more variable than the period before (disp. = 0.1887) with respect to the underlying composition and abundance of taxa in the cores’ samples (*F* = 11.0; *p* = 0.0080; *dfRx* = 1, *dfTotal* = 39). Twenty taxa were selected as indicators across both factor levels (Table S3) and all were subsequently used in a CAP visualization of the separation among the two levels.

## Megafauna

Benthic megafauna data were used for multivariate analyses of community composition based on remotely operated vehicle surveys conducted by Valentine and Benfield (2013) in 2010 (*n* = 19) and McClain et al. (2019) in 2017 (*n* = 17). In both years, the data were collected at 500 m (*n2010* = 9; *n2017* = 9) and 2000 m (*n2010* = 10; *n2017* = 8) distant from a reference point near the DWH wellhead. For the purposes of this investigation, grouping treatments were assigned by year of sampling and differences in beta-diversity were assessed via PERMANOVA, PERMDISP, and IndVal, while visualization was achieved via CAP. Forty taxa were included in the original dataset and were reduced to the 15 that were present in at least 10% of samples. Abundance data were square-root transformed and the Morisita-Horn resemblance measure was used to assess ecological dissimilarity among samples.

The PERMANOVA results indicated that there was a non-random difference (*F* = 37.85; *p* = 0.0001; *dfRx* = 1, *dfTotal* = 34) between the megafaunal communities sampled in 2010 vs. those in 2017. Calculations of multivariate dispersions using PERMDISP showed that the variability in beta-diversity (i.e., variability in megafaunal community variability) declined significantly (*F* = 94.01; *p* = 0.0001; *dfRx* = 1, *dfTotal* = 34) by 77% between 2010 (disp. = 0.4955) and 2017 (disp. = 0.1110). This implies that the post-DWH period’s megafaunal communities were becoming homogenized after DWH. When examining the IndVal table for this faunal group (Table S4), it becomes clear that two taxa in particular (*P. armatus*, *G. aculeata*) are strongly associated with the 2017 samples and, in fact, are essentially “perfect” indicators for that period displaying high fidelity to the 2017 samples exclusively, as well as high specificity within that group’s samples (i.e., found in a very high proportion of the factor level’s observations). The PERMANOVA results were visualized via CAP for all taxa included in these analyses (Figure S5).

# Supplementary Tables

# Supplementary Table S1. Vulnerability (V) and resilience (R) rankings (H=high, M=medium, L=low) of each representative taxon organized by hierarchical group including the factors contributing to the ranking and associated references.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Hierarchical  Group** | **Taxon** | **V** | **R** | **Contributing Factors** | **Associated Reference(s)** |
| **Microbes** | Alpha proteobacteria | M | M | Overlap of habitat and MOSSFA,  short-life span, abundance, life span, frequency of reproduction, ability to respond to hydrocarbons, detoxifying capacity, co-varying stressors | Mason et al., 2014; Kleindienst et al., 2016; Yang et al., 2016 A,B; Overholt et al., 2019 |
|  | Beta proteobacteria | L | L |  |  |
|  | Gamma proteobacteria | L | H |  |  |
|  | Delta proteobacteria | M | H |  |  |
|  | Epsilon Proteobacteria | L | H |  |  |
|  | (AOA) Archaea | L | L |  |  |
| **Foraminifera** | *Bulimiina* spp. | L | H | Ability to avoid hydrocarbons, spatial overlap of populations with toxic components, duration of exposure, abundance, lifespan, co-varying stressors  Opportunistic in low Oxygen  environments | Mojtahid et al., 2006; Schwing et al., 2015; Schwing et al., 2017B  Schwing et al., 2018: Schwing et al., 2020B,C |
|  | *Bolivina* spp. | M | M | Low densities during DWH,  tolerant of high organic deposition, higher abundances following DWH |  |
|  | *Globocassidulina* spp. | L | H | Opportunistic in low Oxygen environments |  |
|  | *Uvigerina* spp. | M | M | Low densities during DWH,  tolerant of high organic deposition, higher abundances following DWH |  |
| **Meiofauna** | Harpacticoida | H | L | Ability to avoid hydrocarbons, life span, co-varying stressors  Sensitive to pollution | Montagna et al., 2013; Baguley et al., 2015;  Reuscher et al., 2017; Montagna and Girard 2020; |
|  | Nematoda | L | H | Opportunistic in polluted environments |  |
| **Macrofauna** | Cirratulidae | M | M | Ability to avoid hydrocarbons, spatial overlap of populations with toxic components, duration of exposure, abundance, life span, co-varying stressors | Montagna et al., 2013;Washburn et al., 2016; Montagna et al., 2017; Reuscher et al., 2017; Washburn et al., 2017; Montagna and Girard 2020; |
|  | Dorvilleidae | L | H |  |  |
|  | Nannastacidae | H | L |  |  |
|  | Nemertea | M | M |  |  |
|  | Oedicerotidae | H | L |  |  |
|  | Prochaetodermatidae | M | M |  |  |
|  | Sphyrapidae | L | H |  |  |
|  | Syllidae | M | M |  |  |
|  | Thyasiridae | L | H |  |  |
|  | Typhlotanaidae | H | L |  |  |
| **Megafauna** | *Chacion* spp. | H | M | Ability to avoid hydrocarbons, spatial overlap of populations with toxic components, duration of exposure, abundance, life span, co-varying stressors  high abundance at wellhead  (associated with oil chemical cues), post-DWH homogeneity between sites | Valentine and Benfield, 2013; McClain et al., 2019 |
|  | Cucumbers | H | M |  |  |
|  | Giant isopods | L | M |  |  |
|  | Ophiuroids | H | L |  |  |
|  | Seep mussels | L | M |  |  |
|  | Seep tubeworms | L | M |  |  |
| **Corals** | *Callogorgia* spp. | L | M | Ability to avoid hydrocarbons, spatial overlap of populations with toxic components, duration of exposure, abundance, life span, co-varying stressors, modularity  Branch loss, hyrdozoan colonization,  slow branch regrowth | White et al., 2012; Hsing et al., 2013;  Fisher et al., 2014A,B; White et al., 2014;  DeLeo et al., 2015; Girard and Fisher, 2018;  Girard et al., 2019; Montagna and Girard, 2020) |
|  | *Leiopathes* spp. | M | L |  |  |
|  | *Lophelia* spp. | M | H |  |  |
|  | *Paramuricea* spp. | H | L |  |  |
|  | *Swiftia* spp. | H | M |  |  |
| **Fish** | Ophidiidae | M | M | Small size, likely MOSSFA coverage  of habitat, short life span, ability to avoid hydrocarbons, co-varying stressors | Powell et al., 2013; Limouzy-Paris et al., 1994 |

**Supplementary Table S2.** Each column represents a sediment core sampled for foraminifera (Schwing et al., 2018), and they are labeled with the two-digit month and year of collection, along with the site ID (format: MMYY-SampID). Years were estimated from samples’ depth increments (mm), and which were converted to dates using short-lived radioisotope sediment-dating methods (Brooks et al., 2015; Larson et al., 2018). The two samples from 2010 denoted by \* were removed for multivariate analyses of “before” and “after” the DWH event.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Number of Samples Analyzed | | | | |  |
| **Year** | **0814-DSH08** | **0814-DSH10** | **0814-PCB06** | **0815-DWH01** | **0815-SW01** | **Total** |
| *2015* | - | - | 1 | 2 | 2 | **5** |
| *2014* | 1 | 3 | 1 | 2 | 1 | **8** |
| *2013* | 1 | 2 | 1 | 1 | 2 | **7** |
| *2012* | 2 | 1 | 1 | - | - | **4** |
| *2011* | 1 | - | - | - | - | **1** |
| *2010* | - | 1\* | 1\* | - | - | **2** |
| *2009* | - | - | 1 | - | - | **1** |
| *2008* | - | 1 | - | 1 | - | **2** |
| *2007* | - | - | - | - | 1 | **1** |
| *2006* | - | - | - | - | - | **0** |
| *2005* | 1 | 1 | - | - | 1 | **3** |
| *2004* | - | - | - | - | - | **0** |
| *2003* | - | - | - | - | - | **0** |
| *2002* | - | - | - | - | - | **0** |
| *2001* | - | - | 1 | - | - | **1** |
| *2000* | 1 | - | - | - | 1 | **2** |
|  |  |  |  |  |  |  |
| *1994* | 1 | - | - | - | - | **1** |
|  |  |  |  |  |  |  |
| *1991* | - | - | 1 | - | - | **1** |
|  |  |  |  |  |  |  |
| *1985* | - | - | - | 1 | - | **1** |
|  | - | - | - | - | - | **0** |
| *1981* | - | - | 1 | - | - | **1** |
|  | - | - | - | - | - | **0** |
| *1977* | - | - | - | 1 | - | **1** |
| **Total** | **8** | **9** | **9** | **8** | **8** | **42** |

# Supplementary Table S3: Indicator Values (IndVal) for the top 20 benthic foraminifera taxa selected to represent the time periods before and after the DWH event. Indicator values range from 0-100, and are interpreted as percentages where IndVal = 100 represents a “perfect” indicator for a particular factor level.

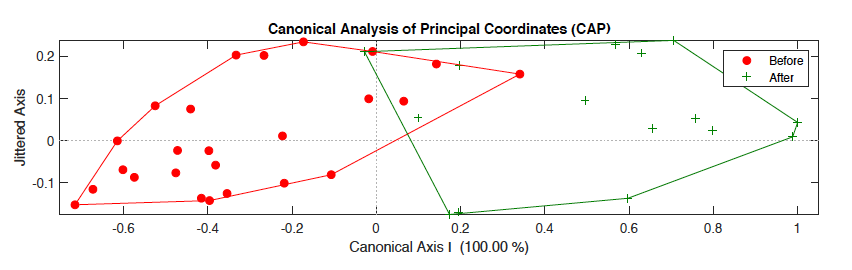
|  |  |  |  |
| --- | --- | --- | --- |
| **Representative Taxa** | **IndVal** | ***p*-Value** | **Group** |
| *'Cibicidoides pachyderma'* | 62.2 | 0.0031 | Before |
| *'Chilostomella oolina'* | 61.0 | 0.0020 | Before |
| *'Osangularia culter'* | 59.7 | 0.0078 | Before |
| *'Bulimina striata mexicana'* | 57.3 | 0.0273 | Before |
| *'Bolivina lowmani'* | 55.6 | 0.0017 | Before |
| *'Lenticulina convergens'* | 55.0 | 0.0015 | Before |
| *'Cassidulina reniforme'* | 54.9 | 0.0108 | Before |
| *'Oridorsalis tenerus'* | 54.7 | 0.0119 | Before |
| *'Nuttalides rugosus'* | 53.1 | 0.0121 | Before |
| *'Laticarinina pauperata'* | 42.8 | 0.0426 | Before |
| *'Sigmoilopsis schlumbergeri'* | 36.1 | 0.0175 | Before |
| *'Bolivina barbata'* | 20.0 | 0.0463 | Before |
| *'Cribrostomoides subglobosum'* | 63.1 | 0.0038 | After |
| *'Subreophax monile'* | 58.7 | 0.0106 | After |
| *'Veleroninoides wiesneri'* | 56.6 | 0.0252 | After |
| *'Trochammina ochracea'* | 53.4 | 0.0089 | After |
| *'Testulosiphon indivisus'* | 44.3 | 0.0461 | After |
| *'Rhizammina algaeformis'* | 42.5 | 0.0229 | After |
| *'Adercotryma glomerata'* | 40.9 | 0.0260 | After |
| *'Reophax scorpiurus'* | 31.5 | 0.0485 | After |

**Supplementary Table S4.** Indicator Values (IndVal) for the top 11 megafauna taxa selected to represent the sampling periods 2010 (Valentine and Benfield, 2013) and 2017 (McClain et al., 2019). Indicator values range from 0-100, and are interpreted as percentages where IndVal = 100 represents a “perfect” indicator for a particular factor level.

|  |  |  |  |
| --- | --- | --- | --- |
| **Representative Taxa** | **IndVal** | ***p*-Value** | **Group** |
| *'Asteroidea\_spp'* | 57.9 | 0.0001 | 2010 |
| *'Nematocarcinus\_rotundus'* | 47.4 | 0.0010 | 2010 |
| *'Elpididae\_spp'* | 26.3 | 0.0457 | 2010 |
| *'Plesiopenaeus\_armatus'* | **100.0** | 0.0001 | 2017 |
| *Glyphocrangon\_aculeata'* | **94.1** | 0.0001 | 2017 |
| *'Galatheoidea'* | 61.5 | 0.0002 | 2017 |
| *Trachonurus\_villosus'* | 52.9 | 0.0002 | 2017 |
| *Dicrolene\_introniger'* | 47.1 | 0.0017 | 2017 |
| *'Zoarcidae\_sp\_K'* | 47.1 | 0.0015 | 2017 |
| *'Chaceon\_fenneri'* | 35.3 | 0.0058 | 2017 |
| *'Paguroidea\_sp\_A'* | 25.7 | 0.0481 | 2017 |

# Supplementary Figures

Macintosh HD:Users:Patty:Documents:BP:Manuscripts:2020 Benthic Core 3 synthesis :Figures:Figure S1_Foram Time Series.pdf**Supplementary Figure S1.** A time-series of total benthic foraminifera mean values for richness (A), Shannon diversity (B) and evenness (C) utilizing data from five DWH-impacted sites included in Schwing et al., (2018A) and short-lived radioisotope dates from Brooks et al., (2015) and Larson et al., (2018).



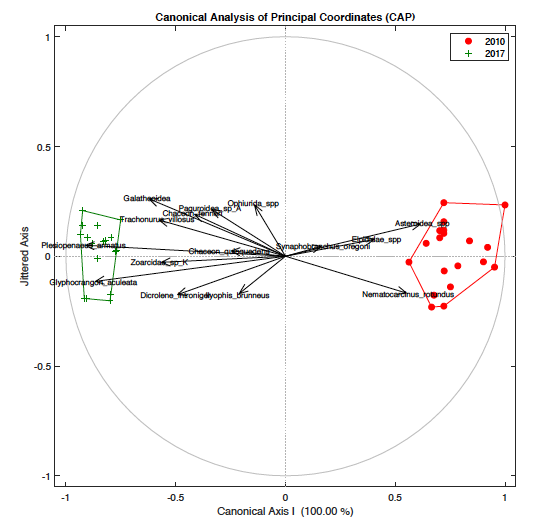
**Supplementary Figure S2.** Canonical analysis of principal coordinates (CAP) of total benthic foraminifera beta-diversity from sediment core layers collected at 5 DWH-impacted sites using a before (pre-DWH; red) and after (post-DWH: green) treatment. Data were from Schwing et al. (2018), Brooks et al. (2015) and Larson et al. (2018). Black vectors represent the relative contribution of each taxa to the separation of groups along the horizontal axis. The vertical axis is jittered (i.e., arbitrary) to aid in visualization, and the borders of each data cloud were drawn using convex-hulls.

Macintosh HD:Users:Patty:Documents:BP:Manuscripts:2020 Benthic Core 3 synthesis :Figures:Figure S3.pdf

**Supplementary Figure S3.** A time series of mean values for meiofauna abundance (A), Shannon diversity (B), nematode:copepod ratio (C), and evenness (D). Error bars represent standard deviation. Data were utilized from the northern Gulf of Mexico Continental Slope Study (NGOMCSS, Pequagnat et al. 1990), the Deep Gulf of Mexico Benthos Program (DGoMB; Baguley et al. 2006; Rowe and Kennicutt 2008), and post-DWH, Natural Resource Damage Assessment (NRDA; (Montagna et al. 2013; Reuscher et al. 2017).

Macintosh HD:Users:Patty:Documents:BP:Manuscripts:2020 Benthic Core 3 synthesis :Figures:Figure S4 Macrofauna Time series.pdf

**Supplementary Figure S4.** A time series of mean values for macrofauna abundance (A), Shannon diversity (B) and evenness (C). Data were utilized from the NGOMCSS (Gallaway 1988), DGoMB (Haedrich et al. 2008; Rowe and Kennicutt 2008) and post-DWH, Natural Resource Damage Assessment (Montagna et al. 2013; Washburn et al. 2017).



**Supplementary Figure 5.** Canonical analysis of principal coordinates (CAP) of benthic megafauna from 2010 (red; Valentine and Benfield, 2013) and 2017 (green; McClain et al., 2019). Black vectors represent the relative contribution of each taxa to the separation of groups along the horizontal axis. The vertical axis is jittered (i.e., arbitrary) to aid in visualization, and the borders of each data cloud were drawn using convex-hulls.

**LITERATURE CITED**

1. Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32-46.
2. Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245-253.
3. Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecol. Lett. 9, 683-693.
4. Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol. Monogr. 83, 557-574.
5. Anderson, M.J., Willis, T.J., 2003. Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. Ecology 84, 511-525.
6. Baguley, J. G., Montagna, P. A., Hyde, L. J., Kalke, R. D., & Rowe, G. T. (2006). Metazoan meiofauna abundance in relation to environmental variables in the northern Gulf of Mexico deep sea, *53*, 1344–1362. https://doi.org/10.1016/j.dsr.2006.05.012
7. Baguley, J., Montagna, P., Cooksey, C., Hyland, J., Bang, H., Morrison, C., … Ricci, M. (2015). Community response of deep-sea soft-sediment metazoan meiofauna to the Deepwater Horizon blowout and oil spill. *Marine Ecology Progress Series*, *528*, 127–140. https://doi.org/10.3354/meps11290
8. Brooks GR, Larson RA, Schwing PT, Romero I, Moore C, Reichart GJ, Jilbert T, Chanton JP, Hastings DW, Overholt WA, Marks KP, Kostka JE, Holmes CW, Hollander D (2015). Sediment Pulse in the NE Gulf of Mexico Following the 2010 DWH Blowout. PLoS ONE, 10(7): e0132341. doi:10.1371/journal.pone.013234
9. Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8, 148-159.
10. Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.J., 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. Biometrics 62, 361-371.
11. DeLeo DM, Ruiz-Ramos DV, Baums IB, Cordes EE (2015) Response of deep-water corals to oil and chemical dispersant exposure. Deep-Sea Res II Top Stud Oceanogr 129:137–147. https://doi.org/10.1016/j.dsr2.2015.02.028
12. Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345-366.
13. Fisher CR, Demopoulos AWJ, Cordes EE, Baums IB, White HK et al (2014A) Coral communities as indicators of ecosystem-level impacts of the Deepwater Horizon Spill. Bioscience 64:796–807. <https://doi.org/10.1093/biosci/biu129>
14. Fisher CR, Hsing P-Y, Kaiser CL, Yoerger DR, Roberts HH, Bourque JR (2014B) Footprint of Deepwater Horizon blowout impact to deep-water coral communities. Proc Natl Acad Sci 111:11744–11749.
15. Gallaway BJ (ed.). (1988) Northern Gulf of Mexico Continental Slope Study, Final Report: Year 4 . Volume II: Synthesis Report. Final report submitted to the Minerals Management Service, New Orleans, LA . Contract No. 14-12-0001-30212 . OCS Study/MMS 88-0053 . 318 p.
16. Girard, F., & Fisher, C. R. (2018). Long-term impact of the Deepwater Horizon oil spill on deep-sea corals detected after seven years of monitoring. *Biological Conservation*, *225*(June), 117–127. https://doi.org/10.1016/j.biocon.2018.06.028
17. Girard, F., Cruz, R., Glickman, O., Harpster, T., & Fisher, C. R. (2019). In situ growth of deep-sea octocorals after the Deepwater Horizon oil spill. Elem Sci Anth, 7: 12. DOI: https://doi.org/10.1525/elementa.349
18. Haedrich RL, Devine JA, Kendall VJ (2008) Predictors of species richness in the deep-benthic fauna of the northern Gulf of Mexico. Deep-Sea Research II 55: 2650–2656.
19. Hsing P-Y, Fu B, Larcom E, Berlet SP, Shank TM, Govindarajan AF, Lukasiewiccz AJ, Dixson PM, Fisher CR (2013) Evidence of lasting impact of the Deepwater Horizon oil spill on a deep Gulf of Mexico coral community. Elementa: Sci Anthropocene 1:000012. https://doi.org/10.12952/journal.elementa.000012
20. Jones, D.L., 2017. The Fathom Toolbox for MATLAB: Software for multivariate ecological and oceanographic analysis. University of South Florida, College of Marine Science, St. Petersburg, FL, USA. Available from: <https://www.marine.usf.edu/research/matlab-resources/>.
21. Kilborn, J.P., 2020. The Darkside Toolbox for MATLAB. University of South Florida, College of Marine Science, St. Petersburg, FL.
22. Kleindienst, S., Grim, S., Sogin, M. *et al.* Diverse, rare microbial taxa responded to the *Deepwater Horizon* deep-sea hydrocarbon plume. *ISME J* **10,**400–415 (2016). https://doi.org/10.1038/ismej.2015.121
23. Larson, R.A., Brooks, G.R., Schwing, P.T., Carter, S., Hollander, D.J. (2018). High Resolution Investigation of Event-Driven Sedimentation: Northeastern Gulf of Mexico. Anthropocene, 24, 40–50, 10.1016/j.ancene.2018.11.002.Legendre, P., Legendre, L., 2012. Numerical Ecology, Third English edition ed. Elsevier, Amsterdam, The Netherlands.
24. Limouzy-Paris, C., M. F. McGowan, W. J. R., & J. P. Umaran, and S. S. C. (1994). DIVERSITY OF FISH LARVAE IN THE FLORIDA KEYS: RESULTS FROM SEFCAR. *Bulletin of Marine Science*, *54*(3), 857–870.
25. Mason, O. U., Scott, N. M., Gonzalez, A., Robbins-Pianka, A., Bælum, J., Kimbrel, J., … Jansson, J. K. (2014). Metagenomics reveals sediment microbial community response to Deepwater Horizon oil spill. *The ISME Journal*, *8*(7), 1464–1475. <https://doi.org/10.1038/ismej.2013.254>
26. McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82, 290-297.
27. Mcclain, C. R., Nunnally, C., & Benfield, M. C. (2019). Persistent and substantial impacts of the Deepwater Horizon oil spill on deep-sea megafauna. R. Soc. open sci. 6: 191164. http://dx.doi.org/10.1098/rsos.191164
28. Mojtahid M, Jorissen F, Durrieu J, Galgani F, Howa H, Redois F, Camps R (2006). Benthic foraminifera as bio-indicators of drill cutting disposal in tropical east Atlantic outer shelf environments. Marine Micropaleontology 61:58-75.
29. Montagna P, Baguley JG, Cooksey C, Hartwell I, Hyde LJ, Hyland JL, Kalke RD, Kracker LM, Reuscher M, Rhodes ACE (2013) Deep-sea benthic footprint of the Deepwater Horizon blowout. PLoS One 8(8):e70540. https://doi.org/10.1371/journal.pone.0070540
30. Montagna PA, Baguley JG, Cooksey C, Hyland JL (2017B) Persistent impacts to the deep soft-bottom benthos one year after the Deepwater Horizon event. Integr Environ Assess Manag 13:342–351. https://doi.org/10.1002/ieam.1791
31. Montagna PA, Girard F (2020) Deep-sea benthic faunal impacts and community evolution before, during and after the Deepwater Horizon event (Chap. 22). In: Murawski SA, Ainsworth C, Gilbert S, Hollander D, Paris CB, Schlüter M, Wetzel D (eds) Deep oil spills: facts, fate, effects. Springer, Cham
32. Overholt, W. A., Schwing, P., Raz, K. M., Hastings, D., Hollander, D. J., & Kostka, J. E. (2019). The core sea floor microbiome in the Gulf of Mexico is remarkably consistent and shows evidence of recovery from disturbance caused by major oil spills. *Environmental Microbiology*, *21*(11), 4316–4329. https://doi.org/10.1111/1462-2920.14794
33. Pequengnat WE, Gallaway BJ, Pequegnat LH (1990) Aspects of the ecology of the deep-water fauna of the Gulf of Mexico. American Zoologist 30:45-64.
34. Powell, S. M., Haedrich, R. L., & McEachran, J. D. (2017). The Deep-sea Demersal Fish Fauna of the Northern Gulf of Mexico. *Journal of the Northwest Atlantic Fisheries Society*, *31*(December), 19–33. https://doi.org/10.2960/J.v31.a2
35. Rowe GT, Kennicutt MC (2008) Introduction to the Deep Gulf of Mexico Benthos Program Deep Sea Research II 55:2536-2540.
36. Reuscher MG, Baguley JG, Conrad-Forrest N, Cooksey C, Hyland JL, Lewis C, Montagna PA, Ricker RW, Rohal M, Washburn T (2017) Temporal patterns of the Deepwater Horizon impacts on the benthic infauna of the northern Gulf of Mexico continental slope. PLoS One 12(6):e0179923. https://doi.org/10.1371/journal.pone.0179923
37. Schwing PT, O’Malley BJ, Hollander DJ (2018A) Resilience of Benthic Foraminifera in the Northern Gulf of Mexico Following the Deepwater Horizon Event (2011-2015). Ecological Indicators 84:753-764, <http://dx.doi.org/10.1016/j.ecolind.2017.09.044>.
38. Valentine, M. M., & Benfield, M. C. (2013). Characterization of epibenthic and demersal megafauna at Mississippi Canyon 252 shortly after the Deepwater Horizon Oil Spill. *Marine Pollution Bulletin*, *77*(1–2), 196–209. https://doi.org/10.1016/j.marpolbul.2013.10.004
39. Washburn T, Rhodes ACE, Montagna PA (2016) Benthic taxa as potential indicators of a deep-sea oil spill. Ecol Indic 71:587–597. https://doi.org/10.1016/j.ecolind.2016.07.045
40. Washburn T, Reuscher MG, Montagna PA, Cooksey C, Hyland JL (2017) Macrobenthic community structure in the deep Gulf of Mexico one year after the Deepwater Horizon blowout. Deep-Sea Res I 127:21–30. https://doi.org/10.1016/j.dsr.2017.06.001
41. White HK, Hsing PY, Cho W, Shank TM, Cordes EE, Quattrinni AM, Nelson RK, Camilli R, Demopoulos AWJ, German CR, Brooks JM, Robert HH, Shedd W, Reddy AM, Fisher CR (2012) Impact of the Deepwater Horizon oil spill on a deep-water coral community in the Gulf of Mexico. Proc Natl Acad Sci 109:20303–20308. <https://doi.org/10.1073/pnas.1118029109>
42. White HK, Lyons SL, Harrison SJ, Findley DM, Liu Y, Kujawinski EB (2014) Long-term persistence of dispersants following the Deepwater Horizon oil spill. Environ Sci Technol Lett 1:295–299. https://doi.org/10.1021/ez500168r
43. Yang, T., Nigro, L. M., Gutierrez, T., Ambrosio, L. D., Joye, S. B., Highsmith, R., & Teske, A. (2016A). Deep-Sea Research II Pulsed blooms and persistent oil-degrading bacterial populations in the water column during and after the Deepwater Horizon blowout. *Deep-Sea Research Part II*, *129*, 282–291. <https://doi.org/10.1016/j.dsr2.2014.01.014>
44. Yang, T., Speare, K., McKay, L., MacGregor, B.J., Joye, S.B., Teske, A. (2016B). Distinct bacterial communities in surficial seafloor sediments following the 2010 Deepwater Horizon Blowout. Frontiers in Microbiology, 7, 1-18, doi: 10.3389/fmicb.2016.01384