# Mesophotic and Deep Sea Corals in the Gulf of Mexico – Impacts from Deepwater Horizon

## *Bibliography*

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## Background & Scope

NOAA's Office of Habitat Protection (OHP) in the National Marine Fisheries Service is participating in an Open Ocean Trustee Implementation Group studying marine life in the Gulf of Mexico and the impact of the Deepwater Horizon (DWH) oil spill on that life. The NOAA Central Library was consulted to create this annotated bibliography to provide OHP with literature on the mesophotic and deep sea corals in the Gulf of Mexico. In particular this bibliography covers the impacts of the DWH oil spill, mapping and restoration techniques for those coral communities. The literature presented here is intended to cover the most recent research in these areas, and also covers the status of the mesophotic and deep sea corals in the Gulf of Mexico prior to the DWH oil spill. The literature on the mapping and restoration techniques is from all over the world, not just the Gulf of Mexico. Additionally, all research presented here is from primarily the last ten years, though some – especially that of Section II – is from the last twenty years.

### Section I – Mesophotic and Deep Sea Corals after Deepwater Horizon

This section covers research on the impacts of the Deepwater Horizon oil spill on the mesophotic and deep sea corals of the Gulf of Mexico, including their larger environmental communities.

### Section II – Status of Mesophotic and Deep Sea Corals in the Gulf of Mexico prior to Deepwater Horizon

This section covers the status of the mesophotic and deep sea corals in the Gulf of Mexico prior to Deepwater Horizon oil spill. It includes literature from after the spill that also records data about the status of corals in that area.

### Section III – Mapping Mesophotic and Deep Sea Corals

This section covers techniques for mapping mesophotic and deep sea corals from all over the world, including the Gulf of Mexico.

### Section IV – Restoring Mesophotic and Deep Sea Corals

This section covers techniques for restoring mesophotic and deep sea corals from all over the world, including the Gulf of Mexico.

## Sources Reviewed

The following databases were used to identify sources: Clarivate Analytics' Web of Science: Science Citation Index Expanded and Social Science Index; JSTOR; ProQuest's Aquatic Sciences and Fisheries Abstracts; EBSCO's Academic Search Complete and EconLit; and NOAA's Institutional Repository. Only English language materials were included.

## Section I: Mesophotic and Deep Sea Corals after Deepwater Horizon

Buskey, E. J., White, H. K., & Esbaugh, A. J. (2016). Impact of Oil Spills on Marine Life in the Gulf of Mexico: effects on plankton, nekton, and deep-sea benthos *Oceanography*, 29(3), 174-181 https://doi.org/10.5670/oceanog.2016.81.

The Deepwater Horizon (DWH) oil spill was the largest accidental release of crude oil into the sea in history, and represents the most extensive use of chemical dispersants to treat an oil spill. Following the spill, extensive studies were conducted to determine the potential acute and sublethal toxic effects of crude oil and dispersants on a range of planktonic, nektonic, and benthic marine organisms. Organisms such as phytoplankton, zooplankton, and fish were examined via controlled laboratory studies, while others, such as deep-sea benthic invertebrates, which are difficult to sample, maintain, and study in the laboratory, were assessed through field studies. Laboratory studies with marine fishes focused on the sublethal effects of oil and dispersants, and early life history stages were generally found to be more sensitive to these toxins than adults. Field studies in the vicinity of the DWH spill indicate a significant reduction in abundance and diversity of benthic meiofauna and macrofauna as well as visual damage to deep-sea corals. Overall, studies indicate that while the responses of various marine species to oil and dispersants are quite variable, a general picture is emerging that chemical dispersants may be more toxic to some marine organisms than previously thought, and that small oil droplets created by dispersant use and directly consumed by marine organisms are often more toxic than crude oil alone.

Cordes, E., Auscavitch, S., Baums, I. B., Fisher, C. R., Girard, F., Gomez, C., . . . Weinheimer, A. (2016). ECOGIG: Oil Spill Effects on Deep-Sea Corals Through the Lenses of Natural Hydrocarbon Seeps and Long Time Series. *Oceanography*, 29(1, Supplement), 28-29 Retrieved from https://tos.org/oceanography/issue/volume-29-issue-01-supplement.

The 2015 Ecosystem Impacts of Oil and Gas Inputs to the Gulf(ECOGIG) expedition was a continuation of a three-year partnership between our Gulf of Mexico Research Institute-funded research consortium and the Ocean Exploration Trust to study the effects of oil and dispersant on corals and closely related communities affected by the 2010 Deepwater Horizon oil spill (White et al., 2012, 2014; Hsing et al., 2013; Fisher et al., 2014a,b; Figure 1A– C). As part of our analysis, we explored a new site to the west of the Macondo well in lease block Mississippi Canyon (MC) 462 where we examined 50 new corals for impact from the spill (Figure 1D). A total of over 250 corals were re-imaged in 2015 for this ongoing time-series study. Another goal was to initiate a study to determine how proximity to natural seeps affects corals and infauna in these communities.

Cordes, E. E., Berlet, S. P., Cardman, Z., Dannenberg, R., Demopoulos, A. W. J., Georgian, S. E., . . . Ramos, D. R. (2014). Exploring Deep-Sea Coral Communities and the Effects of Oil and Gas Inputs to the Gulf of Mexico. *Oceanography*, 27(1, Supplement), 28-29 Retrieved from https://tos.org/oceanography/issue/volume-27-issue-01-supplement.

The deep Gulf of Mexico is home to some of the most active natural oil and gas seeps in the world. It is estimated that over 1,000 natural seeps release more than 140,000 tonnes of oil per year into the Gulf of Mexico (MacDonald et al., 1993; NRC, 2003). These seeps support different types of communities, from microbes with diverse metabolic capabilities, to chemosynthetic organisms and numerous species of associated fauna.

DeLeo, D. M., Herrera, S., Lengyel, S. D., Quattrini, A., Kulathinal, R. J., & Cordes, E. E. (2018). Gene expression profiling reveals deep-sea coral response to the Deepwater Horizon oil spill. *Molecular Ecology*, 27(20), 4066-4077 https://doi.org/10.1111/mec.14847.

Deep-sea coral communities are key components of the Gulf of Mexico ecosystem and were adversely affected by the Deepwater Horizon (DWH) oil spill. Coral colonies exposed to oil and dispersant exhibited mortality, damage and physiological signatures of stress. Understanding how corals respond to oil and dispersant exposure at the molecular level is important to elucidate the sublethal effects of the DWH disaster and reveal broader patterns of coral stress responses. Gene expression profiles from RNAseq data were compared between corals at an impacted site and from a reference site. A total of 1,439 differentially expressed genes (twofold) were shared among impacted Paramuricea biscaya colonies. Genes involved in oxidative stress, immunity, wound repair, tissue regeneration and metabolism of xenobiotics were significantly differentially expressed in impacted corals. Enrichment among the overexpressed genes indicates the corals were enduring high metabolic demands associated with cellular stress responses and repair mechanisms. Underexpression of genes vital to toxin processing also suggests a diminished capacity to cope with environmental stressors. Our results provide evidence that deep-sea corals exhibited genome-wide cellular stress responses to oil and dispersant exposure and demonstrate the utility of next-generation sequencing for monitoring anthropogenic impacts in deep waters. These analyses will facilitate the development of diagnostic markers for oil and dispersant exposure in deep-sea invertebrates and inform future oil spill response efforts.

DeLeo, D. M., Ruiz-Ramos, D. V., Baums, I. B., & Cordes, E. E. (2016). Response of deep-water corals to oil and chemical dispersant exposure. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 129, 137-147 https://doi.org/10.1016/j.dsr2.2015.02.028.

Cold-water corals serve as important foundation species by building complex habitat within deep-sea benthic communities. Little is known about the stress response of these foundation species yet they are increasingly exposed to anthropogenic disturbance as human industrial presence expands further into the deep sea. A recent prominent example is the Deepwater Horizon oil-spill disaster and ensuing clean-up efforts that employed chemical dispersants. This study examined the effects of bulk oil-water mixtures, water-accommodated oil fractions, the dispersant Corexit 9500A (R), and the combination of hydrocarbons and dispersants on three species of corals living near the spill site in the Gulf of Mexico between 500 and 1100 m depths: Paramuricea type B3, Callogorgia delta and Leiopathes glaberrima. Following short-term toxicological assays (0-96 h), all three coral species examined showed more severe health declines in response to dispersant alone (2.3-3.4 fold) and the oil-dispersant mixtures (1.1-4.4 fold) than in the oil-only treatments. Higher concentrations of dispersant alone and the oil-dispersant mixtures resulted in more severe health declines. C delta exhibited somewhat less severe health declines than the other two species in response to oil and oil/dispersant mixture treatments, likely related to its increased abundance near natural hydrocarbon seeps. These experiments provide direct evidence for the toxicity of both oil and dispersant on deep-water corals, which should be taken into consideration in the development of strategies for intervention in future oil spills.

Demopoulos, A. W. J., Bourque, J. R., Cordes, E., & Stamler, K. M. (2016). Impacts of the Deepwater Horizon oil spill on deep-sea coral-associated sediment communities. *Marine Ecology Progress Series*, 561, 51-68 https://doi.org/10.3354/meps11905.

Cold-water corals support distinct populations of infauna within surrounding sediments that provide vital ecosystem functions and services in the deep sea. Yet due to their sedentary existence, infauna are vulnerable to perturbation and contaminant exposure because they are unable to escape disturbance events. While multiple deep-sea coral habitats were injured by the 2010 Deepwater Horizon (DWH) oil spill, the extent of adverse effects on coral-associated sediment communities is unknown. In 2011, sediments were collected adjacent to several coral habitats located 6 to 183 km from the wellhead in order to quantify the extent of impact of the DWH spill on infaunal communities. Higher variance in macrofaunal abundance and diversity, and different community structure (higher multivariate dispersion) were associated with elevated hydrocarbon concentrations and contaminants at sites closest to the wellhead (MC294, MC297, and MC344), consistent with impacts from the spill. In contrast, variance in meiofaunal diversity was not significantly related to distance from the wellhead and no other community metric (e.g. density or multivariate dispersion) was correlated with contaminants or hydrocarbon concentrations. Concentrations of polycyclic aromatic hydrocarbons (PAH) provided the best statistical explanation for observed macrofaunal community structure, while depth and presence of fine-grained mud best explained meiofaunal community patterns. Impacts associated with contaminants from the DWH spill resulted in a patchwork pattern of infaunal community composition, diversity, and abundance, highlighting the role of variability as an indicator of disturbance. These data represent a useful baseline for tracking post-spill recovery of these deep-sea communities.

Doughty, C. L., Quattrini, A. M., & Cordes, E. E. (2014). Insights into the population dynamics of the deep-sea coral genus Paramuricea in the Gulf of Mexico. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 99, 71-82 https://doi.org/10.1016/j.dsr2.2013.05.023.

Species in the genus Paramuricea are among the most common corals in deep waters ( >200 m) of the Gulf of Mexico. Paramuricea spp. increase habitat heterogeneity and provide substrate for numerous faunal associates, including ophiuroids that occur on the majority of coral colonies. In light of the Deepwater Horizon oil spill in the Gulf of Mexico, it has become apparent that there is a critical need for data on population dynamics within this genus. To date, at least one species of Paramuricea (P. biscaya) is known to be negatively impacted by the spill. Using remotely operated vehicles from 2009 to 2011, we documented the density and size frequency distributions of Paramuricea across 21 sites at depths of 2502500 m. Molecular barcoding (mtCOI+igri-MutS) was used to delineate species boundaries among the specimens collected. Results suggested that seven haplotypes are present in the Gulf, and appear to be partially segregated by depth [(type H: <260 m) (type E: 278-445 m) (type A: 443-541 m) (types B1-B3: 800-2600 m)]. Densities of Paramuricea spp. determined by ROV surveys were mapped onto high-resolution bathymetric data, which confirmed the corals' preference for topographic highs composed of hard substrata. At any one site, densities ranged from 0.043 +/- 0.01 (VK906, 380 m) to 1.18 +/- 0.81 colonies/m(2) (GC852, 1410 m). Mortality and recruitment rates were estimated from size-frequency data combined with estimated growth rates. Mortality rate decreased with size, from approximately 20% and 70% in new recruits of Paramuricea B3 and P. biscaya respectively, to less than 10% in colonies over 40 cm in both species. Recruitment rates were estimated from less than one to over 30 individuals per year per site, but patterns in size-frequency histograms suggest that this process is highly variable at the different sites and at different times. These data illustrate that populations of the slow-growing

Paramuricea species are sparsely distributed and exhibit low recruitment rates, making them highly susceptible to anthropogenic threats.

Etnoyer, P. J., Wickes, L. N., Silva, M., Dubick, J. D., Balthis, L., Salgado, E., & MacDonald, I. R. (2016). Decline in condition of gorgonian octocorals on mesophotic reefs in the northern Gulf of Mexico: before and after the Deepwater Horizon oil spill. *Coral Reefs*, 35(1), 77-90 https://doi.org/10.1007/s00338-015-1363-2.

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

Fisher, C. R., Demopoulos, A. W. J., Cordes, E. E., Baums, I. B., White, H. K., & Bourque, J. R. (2014). Coral Communities as Indicators of Ecosystem-Level Impacts of the Deepwater Horizon Spill. *Bioscience*, 64(9), 796-807 https://doi.org/10.1093/biosci/biu129.

The Macondo oil spill released massive quantities of oil and gas from a depth of 1500 meters. Although a buoyant plume carried released hydrocarbons to the sea surface, as much as half stayed in the water column and much of that in the deep sea. After the hydrocarbons reached the surface, weathering processes, burning, and the use of a dispersant caused hydrocarbon-rich marine snow to sink into the deep sea. As a result, this spill had a greater potential to affect deep-sea communities than had any previous spill. Here, we review the literature on impacts on deep-sea communities from the Macondo blowout and provide additional data on sediment hydrocarbon loads and the impacts on sediment infauna in areas with coral communities around the Macondo well. We review the literature on the genetic connectivity of deep-sea species in the Gulf of Mexico and discuss the potential for wider effects on deep Gulf coral communities.

Fisher, C. R., Hsing, P. Y., Kaiser, C. L., Yoerger, D. R., Roberts, H. H., Shedd, W. W., . . . Brooks, J. M. (2014). Footprint of Deepwater Horizon blowout impact to deep-water coral communities.

*Proceedings of the National Academy of Sciences of the United States of America*, 111(32), 11744-11749 https://doi.org/10.1073/pnas.1403492111.

On April 20, 2010, the Deepwater Horizon (DWH) blowout occurred, releasing more oil than any accidental spill in history. Oil release continued for 87 d and much of the oil and gas remained in, or returned to, the deep sea. A coral community significantly impacted by the spill was discovered in late 2010 at 1,370 m depth. Here we describe the discovery of five previously unknown coral communities near the Macondo wellhead and show that at least two additional coral communities were impacted by the spill. Although the oil-containing flocullent material that was present on corals when the first impacted community was discovered was largely gone, a characteristic patchy covering of hydrozoans on dead portions of the skeleton allowed recognition of impacted colonies at the more recently discovered sites. One of these communities was 6 km south of the Macondo wellhead and over 90% of the corals present showed the characteristic signs of recent impact. The other community, 22 km southeast of the wellhead between 1,850 and 1,950 m depth, was more lightly impacted. However, the discovery of this site considerably extends the distance from Macondo and depth range of significant impact to benthic macro-faunal communities. We also show that most known deep-water coral communities in the Gulf of Mexico do not appear to have been acutely impacted by the spill, although two of the newly discovered communities near the wellhead apparently not impacted by the spill have been impacted by deep-sea fishing operations.

Fisher, C. R., Montagna, P. A., & Sutton, T. T. (2016). How Did the Deepwater Horizon Oil Spill Impact Deep-Sea Ecosystems? *Oceanography*, 29(3), 182-195 https://doi.org/10.5670/oceanog.2016.82.

Approximately 90% of the volume of the Gulf of Mexico is contained in water deeper than 200 m, a region where the Deepwater Horizon (DWH) blowout had more impact on ecosystems than any previous oil spill. The remoteness and relative inaccessibility of the deep sea makes documenting even acute impacts to the animals that live in this realm difficult. This article reviews Natural Resource Damage Assessment studies and follow-up work funded as part of the Gulf of Mexico Research Initiative that targeted deepwater pelagic and benthic fauna. Oil was incorporated into the pelagic food web, and a reduction in planktonic grazers led to phytoplankton blooms. Fish larvae were killed, and a generation may have been lost. Cetaceans were killed, and many avoided the area of the spill. In the benthic realm, there was a large loss of diversity of soft-bottom infauna, which were still not recovering a year after the DWH oil spill. Colonial octocorals that are anchored to the hard seafloor and are especially vulnerable to anthropogenic impact, died as a result of being covered with flocculent material containing oil and dispersant. Soft- and hard-bottom effects of the oil spill were found as much as 14 km away from the DWH wellhead site. Deep-sea communities in the Gulf of Mexico are diverse, play critical roles in the food web and carbon cycling, affect productivity, are sensitive to perturbations, and are at risk to contaminant exposure; thus, it is important to understand the effects on these natural resources.

Frometa, J., DeLorenzo, M. E., Pisarski, E. C., & Etnoyer, P. J. (2017). Toxicity of oil and dispersant on the deep water gorgonian octocoral Swiftia exserta, with implications for the effects of the Deepwater Horizon oil spill. *Marine Pollution Bulletin*, 122(1-2), 91-99 https://doi.org/10.1016/j.marpolbul.2017.06.009.

Benthic surveys of mesophotic reefs in the Gulf of Mexico post Deepwater Horizon (DWH) showed that Swiftia exserta octocorals exhibited significantly more injury than in years before the spill. To determine the vulnerability of S. exserta to oil and dispersants, 96 h toxicity assays of surrogate DWH oil water-accommodated fractions (WAF), Corexit (R) 9500 dispersant, and the combination of both (CEWAF) were conducted in the laboratory. Fragment mortality occurred within 48 h for some fragments in the dispersant-alone and oil-dispersant treatments, while the WAF group remained relatively unaffected. The 96 h LC50 values were 70.27 mg/L for Corexit-alone and 41.04 mg/L for Corexit in CEWAF. This study provides new information on octocoral sensitivity to toxins, and indicates that combinations of oil and dispersants are more toxic to octocorals than exposure to oil alone. These results have important implications for the assessment of effects of the DWH spill on deep water organisms.

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. *Elementa-Science of the Anthropocene*, 7, 19 [https://doi.org/10.1525/elementa.349](https://doi.org/10.1525/elementa.349).

Although the role of deep-sea corals in supporting biodiversity is well accepted, their ability to recover from anthropogenic impacts is still poorly understood. An important component of recovery is the capacity of corals to grow back after damage. Here we used data collected as part of an image-based long-term monitoring program that started in the aftermath of the Deepwater Horizon oil spill to develop a non-destructive method to measure in situ growth rates of Paramuricea spp. corals and characterize the impact of the spill on growth. About 200 individual coral colonies were imaged every year between 2011 and 2017 at five sites (three that were impacted by the spill and two that were not). Images were then used to test different methods for measuring growth. The most effective method was employed to estimate baseline growth rates, characterize growth patterns, estimate the age of every colony, and determine the effects of impact and coral size on growth. Overall growth rates were variable but low, with average annual growth rates per site ranging from 0.14 to 2.5 cm/year/colony. Based on coral size and growth rates, some colonies are estimated to be over two thousand years old. While coral size did not have an influence on growth, the initial level of total impact in 2011 had a significant positive effect on the proportion of new growth after 2014. However, growth was not sufficient to compensate for branch loss at one of the impacted sites where corals are expected to take an average of 50 years to grow back to their original size. The non-destructive method we developed could be used to estimate the in situ growth rates on any planar octocoral, and would be particularly useful to follow the recovery of corals after impact or assess the effectiveness of Marine Protected Areas.

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, 117-127 [https://doi.org/10.1016/j.biocon.2018.06.028](https://doi.org/10.1016/j.biocon.2018.06.028).

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.

Girard, F., Fu, B., & Fisher, C. R. (2016). Mutualistic symbiosis with ophiuroids limited the impact of the Deepwater Horizon oil spill on deep-sea octocorals. *Marine Ecology Progress Series*, 549, 89-98 Retrieved from https://www.int-res.com/abstracts/meps/v549/p89-98/.

Deep-water corals form structurally complex biological habitats in the deep-sea that are generally associated with a diverse fauna. Yet, little is known about the effect of symbionts on coral resilience to natural or anthropogenic impacts. This study focused on the influence of the ophiuroid symbiont Asteroschema clavigerum on the resilience of its octocoral host Paramuricea biscaya after the Deepwater Horizon oil spill in the Gulf of Mexico. Corals were imaged between 2011 and 2014 at 4 sites, 3 of which were impacted by the spill. Each colony was digitized to quantify the impact on corals. We developed a method to define an area under the influence of ophiuroids for each coral colony. The level of total visible impact, as well as recovery, was then compared within and outside this area. For the majority of colonies, recovery from visible impact and hydroid colonization was negatively correlated with distance from the ophiuroid. Total visible impact was lower within the area influenced by ophiuroids, and branches within this area were more likely to recover. These results indicate that P. biscaya benefits from its association with A. clavigerum, likely through the physical action of ophiuroids removing material depositing on polyps, and perhaps inhibiting the settlement of hydroids. Although the beneficial role of the ophiuroids was demonstrated on corals affected by an oil spill, we suggest that these benefits would also extend to corals in environments exposed to natural sedimentation events, perhaps allowing the corals to live in environments where sedimentation would otherwise limit their survival.

Girard, F., Shea, K., & Fisher, C. R. (2018). Projecting the recovery of a long-lived deep-sea coral species after the Deepwater Horizon oil spill using state-structured models. *Journal of Applied Ecology*, 55(4), 1812-1822 https://doi.org/10.1111/1365-2664.13141.

1. Deepwater coral communities are hotspots of diversity and biomass. Most deep-sea coral species are long-lived and slow-growing and are, thus, expected to recover slowly after disturbance. A better understanding of the recovery potential of these organisms is necessary to make appropriate management decisions. 2. We used data from high-resolution monitoring of individual coral colonies that were impacted by the Deepwater Horizon oil spill (April 2010) to parameterize and validate an annual, impact-dependent, state-structured matrix model to estimate the time to recovery for each coral colony. We projected the dynamics of three branch states: visibly healthy, unhealthy and hydroid-colonized. Although we implicitly included branch loss in the model, we focused on the short-term return of extant, damaged branches to a visibly healthy state and did not consider the far longer term regrowth of lost branches. 3. Our model estimates that, depending on the initial level of impact, corals

impacted by the spill will take up to three decades to recover to a state where all remaining branches appear healthy, though the majority of corals are projected to reach that state within a decade. By that time, some of these colonies will have lost a significant number of branches, leading to approximately 10% reduction in total biomass at all impacted sites. 4. Overall, our model overestimates recovery, but branch loss estimates were reliable. Thus, the available growth rate data suggest that hundreds of years may be necessary for impacted communities to grow back to their initial biomass. 5. Policy implications. Our study quantifies the very slow recovery rate of deep-sea corals impacted by the Deepwater Horizon oil spill and demonstrates the imperative of prioritizing a precautionary approach for deep-sea ecosystems over restoration after the fact. As anthropogenic pressure on the deep sea is likely to increase, we suggest the establishment of coral monitoring sites implemented as part of Marine Protected Areas to limit and detect impact to deep-sea corals. Furthermore, our model may be used to plan shorter-and longer-term monitoring programmes after impact and to provide a timeline for policy.

Goodbody-Gringley, G., Wetzel, D. L., Gillon, D., Pulster, E., Miller, A., & Ritchie, K. B. (2013). Toxicity of Deepwater Horizon Source Oil and the Chemical Dispersant, Corexit® 9500, to Coral Larvae. *PLOS ONE*, 8(1), https://doi.org/10.1371/journal.pone.0045574.

Acute catastrophic events can cause significant damage to marine environments in a short time period and may have devastating long-term impacts. In April 2010 the BP-operated Deepwater Horizon (DWH) offshore oil rig exploded, releasing an estimated 760 million liters of crude oil into the Gulf of Mexico. This study examines the potential effects of oil spill exposure on coral larvae of the Florida Keys. Larvae of the brooding coral, Porites astreoides, and the broadcast spawning coral, Montastraea faveolata, were exposed to multiple concentrations of BP Horizon source oil (crude, weathered and WAF), oil in combination with the dispersant Corexit® 9500 (CEWAF), and dispersant alone, and analyzed for behavior, settlement, and survival. Settlement and survival of P. astreoides and M. faveolata larvae decreased with increasing concentrations of WAF, CEWAF and Corexit® 9500, however the degree of the response varied by species and solution. P. astreoides larvae experienced decreased settlement and survival following exposure to 0.62 ppm source oil, while M. faveolata larvae were negatively impacted by 0.65, 1.34 and 1.5 ppm, suggesting that P. astreoides larvae may be more tolerant to WAF exposure than M. faveolata larvae. Exposure to medium and high concentrations of CEWAF (4.28/18.56 and 30.99/35.76 ppm) and dispersant Corexit® 9500 (50 and 100 ppm), significantly decreased larval settlement and survival for both species. Furthermore, exposure to Corexit® 9500 resulted in settlement failure and complete larval mortality after exposure to 50 and 100 ppm for M. faveolata and 100 ppm for P. astreoides. These results indicate that exposure of coral larvae to oil spill related contaminants, particularly the dispersant Corexit® 9500, has the potential to negatively impact coral settlement and survival, thereby affecting the resilience and recovery of coral reefs following exposure to oil and dispersants.

Hsing, P. Y., Fu, B., Larcom, E. A., Berlet, S. P., Shank, T. M., Govindarajan, A. F., . . . Fisher, C. R. (2013). Evidence of lasting impact of the Deepwater Horizon oil spill on a deep Gulf of Mexico coral community. *Elementa-Science of the Anthropocene*, 1, https://doi.org/10.12952/journal.elementa.000012.

A coral community 11 km southwest of the site of the Deepwater Horizon blowout at 1,370 m water depth was discovered 3.5 months after the well was capped on 3 November 2010. Gorgonian corals at the site were partially covered by a brown flocculent material (floc) that contained hydrocarbons fingerprinted to the oil spill. Here we quantify the visible changes to the corals at this site during five visits over 17 months by digitizing images of individual branches of each colony and categorizing their condition. Most of the floc visible in November 2010 was absent from the corals by the third visit in March 2011, and there was a decrease in the median proportions of the colonies showing obvious signs of impact after the first visit. During our second visit in 2010, about six weeks after the first, we documented the onset of hydroid colonization (a sign of coral deterioration) on impacted coral branches that increased over the remainder of the study. Hydroid colonization of impacted portions of coral colonies by the last visit in March 2012 correlated positively with the proportion of the colony covered by floc during the first two visits in late 2010. Similarly, apparent recovery of impacted portions of the coral by March 2012 correlated negatively with the proportion of the coral covered with floc in late 2010. A notable feature of the impact was its patchy nature, both within and among colonies, suggesting that the impacting agent was not homogeneously dispersed during initial contact with the corals. While the median level of obvious visible impact decreased over time, the onset of hydroid colonization and the probability of impacts that were not visually obvious suggest that future visits may reveal additional deterioration in the condition of these normally long-lived corals.

Joye, S. B., Bracco, A., Ozgokmen, T. M., Chanton, J. P., Grosell, M., MacDonald, I. R., . . . Passow, U. (2016). The Gulf of Mexico ecosystem, six years after the Macondo oil well blowout. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 129, 4-19 https://doi.org/10.1016/j.dsr2.2016.04.018.

The Gulf of Mexico ecosystem is a hotspot for biological diversity and supports a number of industries, from tourism to fishery production to oil and gas exploration, that serve as the economic backbone of Gulf coast states. The Gulf is a natural hydrocarbon basin, rich with stores of oil and gas that lie in reservoirs deep beneath the seafloor. The natural seepage of hydrocarbons across the Gulf system is extensive and, thus, the system's biological components experience ephemeral, if not, frequent, hydrocarbon exposure. In contrast to natural seepage, which is diffuse and variable over space and time, the 2010 Macondo oil well blowout, represented an intense, focused hydrocarbon infusion to the Gulf's deepwaters. The Macondo blowout drove rapid shifts in microbial populations and activity, revealed unexpected phenomena, such as deepwater hydrocarbon plumes and marine "oil snow" sedimentation, and impacted the Gulf's pelagic and benthic ecosystems. Understanding the distribution and fate of Macondo oil was limited to some degree by an insufficient ability to predict the physical movement of water in the Gulf. In other words, the available physical oceanographic models lacked critical components. In the past six years, much has been learned about the physical oceanography of the Gulf, providing transformative knowledge that will improve the ability to predict the movement of water and the hydrocarbons they carry in future blowout scenarios. Similarly, much has been learned about the processing and fate of Macondo hydrocarbons. Here, we provide an overview of the distribution, fate and impacts of Macondo hydrocarbons and offer suggestions for future research to push the field of oil spill response research forward.

Prouty, N. G., Campbell, P. L., Mienis, F., Duineveld, G., Demopoulos, A. W. J., Ross, S. W., & Brooke, S. (2016). Impact of Deepwater Horizon spill on food supply to deep-sea benthos communities. *Estuarine Coastal and Shelf Science*, 169, 248-264 https://doi.org/10.1016/j.ecss.2015.11.008.

Deep-sea ecosystems encompass unique and often fragile communities that are sensitive to a variety of anthropogenic and natural impacts. After the 2010 Deepwater Horizon (DWH) oil spill, sampling efforts documented the acute impact of the spill on some deep-sea coral colonies. To investigate the impact of the DWH spill on quality and quantity of biomass delivered to the deep-sea, a suite of geochemical tracers (e.g., stable and radio-isotopes, lipid biomarkers, and compound-specific isotopes) was measured from monthly sediment trap samples deployed near a high-density deep-coral site in the Viosca Knoll area of the north-central Gulf of Mexico prior to (Oct-2008 to Sept-2009) and after the spill (Oct-10 to Sept-11). Marine (e.g., autochthonous) sources of organic matter (OM) dominated the sediment traps in both years, however after the spill, there was a pronounced reduction in marine-sourced OM, including a reduction in marine-sourced sterols and n-alkanes and a concomitant decrease in sediment trap organic carbon and pigment flux. Results from this study indicate a reduction in primary production and carbon export to the deep-sea in 2010-2011, at least 6-18 months after the spill started. Whereas satellite observations indicate an initial increase in phytoplankton biomass, results from this sediment trap study define a reduction in primary production and carbon export to the deep-sea community. In addition, a dilution from a low-C-14 carbon source (e.g., petro-carbon) was detected in the sediment trap samples after the spill, in conjunction with a change in the petrogenic composition. The data presented here fills a critical gap in our knowledge of biogeochemical processes and sub-acute impacts to the deep-sea that ensued after the 2010 DWH spill.

Prouty, N. G., Fisher, C. R., Demopoulos, A. W. J., & Druffel, E. R. M. (2016). Growth rates and ages of deep-sea corals impacted by the Deepwater Horizon oil spill. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 129, 196-212 https://doi.org/10.1016/j.dsr2.2014.10.021.

The impact of the April 2010 Deepwater Horizon (DWH) spill on deep-sea coral communities in the Gulf of Mexico (GoM) is still under investigation, as is the potential for these communities to recover. Impacts from the spill include observation of corals covered with flocculent material, with bare skeleton, excessive mucous production, sloughing tissue, and subsequent colonization of damaged areas by hydrozoans. Information on growth rates and life spans of deep-sea corals is important for understanding the vulnerability of these ecosystems to both natural and anthropogenic perturbations, as well as the likely duration of any observed adverse impacts. We report radiocarbon ages and radial and linear growth rates based on octocorals (Paramuricea spp. and Chrysogorgia sp.) collected in 2010 and 2011 from areas of the DWH impact. The oldest coral radiocarbon ages were measured on specimens collected 11 km to the SW of the oil spill from the Mississippi Canyon (MC) 344 site: 599 and 55 cal yr BP, suggesting continuous life spans of over 600 years for Paramuricea biscaya, the dominant coral species in the region. Calculated radial growth rates, between 0.34 mu m yr(-1) and 14.20 mu m yr(-1), are consistent with previously reported proteinaceous corals from the GoM. Anomalously low radiocarbon (Delta C-14) values for soft tissue from some corals indicate that these corals were feeding on particulate organic carbon derived from an admixture of modern surface carbon and a low C-14 carbon source. Results from this work indicate fossil carbon could contribute 5-10% to the coral soft tissue Delta C-14 signal within the area of the spill impact. The influence of a low C-14 carbon source (e.g., petro-carbon) on the particulate organic carbon pool was observed at all sites within 30 km of the spill site, with the exception of MC118, which may have been outside of the dominant northeast-southwest zone of impact. The quantitatively assessed extreme longevity and slow growth rates documented here highlight the vulnerability of these long-lived deep sea coral species to disturbance.

Quattrini, A. M., Etnoyer, P. J., Doughty, C., English, L., Falco, R., Renion, N., . . . Cordes, E. E. (2014). A phylogenetic approach to octocoral community structure in the deep Gulf of Mexico. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 99, 92-102 https://doi.org/10.1016/j.dsr2.2013.05.027.

Deep-sea communities are becoming increasingly vulnerable to anthropogenic disturbances, as fishing, hydrocarbon exploration and extraction, and mining activities extend into deeper water. Negative impacts from such activities were recently documented in the Gulf of Mexico (GoM), where the Deepwater Horizon oil spill caused substantial damage to a deep-water octocoral community. Although a faunal checklist and numerous museum records are currently available for the entire GoM, local-scale diversity and assemblage structure of octocoral communities remains unknown, particularly in deep water. On a series of recent cruises (2008-2011) using remotely operated vehicles, 435 octocorals were collected from 33 deep-water sites (250-2500 m) in the northern GoM. To elucidate species boundaries, the extended mitochondrial barcode (COI+igr1+msh) was successfully amplified and sequenced for 422 of these specimens, yielding a total of 64 haplotypes representing at least 52 species. Further, at least 29% of the species collected were either previously not known to occur in the GoM (12 species) or represent new species (at least three species). Overall, species richness at each site was fairly low (1-12 spp.). The greatest species richness occurred at the shallowest ( <325 m: GC140, n=8 spp.) and the deepest (2100 2500 m: DC673, n=12 spp., DC583, n=10 spp.) sites, and minimum taxonomic and phylogenetic (Faith's Index) diversity was evident at 600-950 m. This pattern is the opposite of the typical pattern of deep-sea diversity in the GoM, which normally peaks at mid-slope depths. Sorensen's Index of taxonomic beta-diversity indicated that six distinct (65-95% dissimilarity) species assemblages corresponded with five depth breaks at similar to 325, 425, 600, 1100, and 2100 m. Further assemblage structure was observed within certain depth zones. Of note, within the 425-600 m depth range, species assemblages at the West Florida Slope differed from the other sites, corresponding to an established biogeographic barrier. The phylogenetic approach used in this study provided important insights into the species boundaries of many taxa while demonstrating that evolutionary history plays a critical role in community structure of deep-sea octocorals.

Ruiz-Ramos, D. V., Fisher, C. R., & Baums, I. B. (2017). Stress response of the black coral Leiopathes glaberrima when exposed to sub-lethal amounts of crude oil and dispersant. *Elementa-Science of the Anthropocene*, 5, 16 https://doi.org/10.1525/elementa.261.

The 2010 Deep Water Horizon oil well failure released billions of gallons of crude oil into the deep Gulf of Mexico, and, combined with chemical dispersants, this oil caused significant coral mortality. However, the mechanisms by which oil and dispersed oil impact deep marine fauna are not well understood. Here, we investigate the effects of oil and dispersed oil on a black coral common in the deep Gulf of Mexico, Leiopathes glaberrima. This coral occurs in several color morphs that show ecological and genetic differences. We hypothesized that dispersed oil would be more detrimental to coral health than oil alone and that this difference would be detectable in the gene expression response of the colonies even at sub-lethal concentrations. In two experiments, four and six colonies of red and white color morphs were exposed to oil, dispersant, and dispersed oil for a minimum of 96 hours. Visual assessment indicated that indeed dispersant and dispersed oil treatments were more damaging than oil alone, for target concentrations of 25 mg L-1. Decline in health was observed for all treatments, independently of color morphotype, but the decline was faster in the white colonies exposed to dispersant. The responses to the treatments were also investigated by monitoring gene expression after 24 hours of sub-lethal chemical exposure. Coral gene expression differed by chemical stressor. Interestingly, the polycyclic aromatic hydrocarbon biomarker gene, cytochrome P450, was only up-regulated in dispersed oil but not oil alone, suggesting that the dispersant increased the availability of such hydrocarbons in the tissue. The gene expression response was apparent at 24 hours when visual impacts were not (yet) detectable. The use of chemical dispersants in oil-spill remediation may cause health declines in deep-water corals and deserves further study.

Silva, M., Etnoyer, P. J., & MacDonald, I. R. (2016). Coral injuries observed at Mesophotic Reefs after the Deepwater Horizon oil discharge. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 129, 96-107 https://doi.org/10.1016/j.dsr2.2015.05.013.

Pathologies in over 400 octocoral and antipatharian colonies were quantified in the aftermath of the DWH oil discharge. Observations were made in September 2011 at water depths of 65-75 m in the Pinnacle Reef trend area offshore from Mississippi and Alabama, Gulf of Mexico, using a digital macro camera deployed from an ROV to examine the coral populations for injury at two principal sites: Alabama Alps Reef (AAR) and Roughtongue Reef (RTR). Taxa observed to exhibit injury included gorgonian octocorals Hypnogorgia pendula, Bebtyce spp., Thesea nivea, and Swiftia exserta, the antipatharian Anti-pathes atlantica, and the sea whips Stichopathes sp., and Ellisella barbadensis. The most common type of injury was a biofilm with a clumped or flake-like appearance covering sea-fan branches. Extreme injuries were characterized by bare skeletons, broken and missing branches. Comparing the 2011 results to previous photo surveys of the same study sites between 1997 and 1999, we found significantly more occurrences of injury in 2011 among taxa with growth forms > 0.5 m. We hypothesize that Tropical Storm Bonnie facilitated and accelerated the mixing process of dispersant-treated hydrocarbons into the water column, resulting in harmful contact with coral colonies at mesophotic depths. Analysis of total polycyclic aromatic hydrocarbon (tPAH) concentrations in sediments at AAR and RTR found levels elevated above pre-discharge values, but orders of magnitude below toxicity thresholds established for fauna in estuarine sediments. The tPAH concentrations measured in octocoral and echinoderm tissue samples from AAR and RTR were detectable (mean values ranged from 51 to 345 ppb); however, bioeffect thresholds do not currently exist with which to evaluate the potential harm these levels may cause. Our findings indicate that coral injuries observed in 2011 may have resulted from an acute, isolated event rather than ongoing natural processes.

Simister, R. L., Antzis, E. W., & White, H. K. (2016). Examining the diversity of microbes in a deep-sea coral community impacted by the Deepwater Horizon oil spill. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 129, 157-166 https://doi.org/10.1016/j.dsr2.2015.01.010.

Deep-sea surface sediments and flocculent material (floc) associated with corals containing oil originating from the Deepwater Horizon (DWH) oil spill were examined to determine the diversity of microbes and the presence of functional genes involved in oil degradation. For all samples, 16S rRNA clone libraries were constructed to obtain full-length sequences and Illumina amplicon sequencing was used to further probe the diversity of the microbial community. The 16S rRNA gene data obtained by Illumina amplicon sequencing revealed Proteobacteria (55-64%) as the dominant bacteria in both sediment and floc samples. The floc samples were comprised of mostly aerobic or facultative aerobic phylotypes including Rhizobiales, Rhodobacterales, Sphingomonadales, Rickettsiales, Alteromonadales, Pseudomonadales, whereas mixtures of the aforementioned aerobic species and anaerobic phylotypes such as Desulfobacterales, Desulfuromonadales and Desulfarculales were present in the sediment samples. Genera affiliated with oil-degrading bacteria were identified in both sediment and floc samples. To evaluate the potential of the microbial community to degrade oil, clone libraries were constructed for the alkB gene (one of the structural genes of alkane hydroxylase involved in the aerobic degradation of n-alkanes of chain length > C-5-C-16) and the alkylsuccinate synthase/benzylsuccinate synthases (assA/bssA) gene (involved in the anaerobic degradation of n-alkanes [via assA] and polycyclic aromatic hydrocarbons [PAHs; via bssA]). The alkB gene was present in all samples with the majority of sequences clustering to members of the Proteobacteria closely aligned to environmental sequences from hydrocarbon seep environments. The assA/bssA genes were only detected in sediment samples and were closely affiliated with delta-Proteobacteria previously detected in oil contaminated sediments and oil-enrichment cultures. These data provide insight into the differences between environments impacted by the DWH oil spill and highlight the functional diversity of oil degrading microbes associated with a deep-sea coral community.

White, H. K., Hsing, P. Y., Cho, W., Shank, T. M., Cordes, E. E., Quattrini, A. M., . . . Fisher, C. R. (2012). Impact of the Deepwater Horizon oil spill on a deep-water coral community in the Gulf of Mexico. *Proceedings of the National Academy of Sciences of the United States of America*, 109(50), 20303-20308 https://doi.org/10.1073/pnas.1118029109.

To assess the potential impact of the Deepwater Horizon oil spill on offshore ecosystems, 11 sites hosting deep-water coral communities were examined 3 to 4 mo after the well was capped. Healthy coral communities were observed at all sites >20 km from the Macondo well, including seven sites previously visited in September 2009, where the corals and communities appeared unchanged. However, at one site 11 km southwest of the Macondo well, coral colonies presented widespread signs of stress, including varying degrees of tissue loss, sclerite enlargement, excess mucous production, bleached commensal ophiuroids, and covering by brown flocculent material (floc). On the basis of these criteria the level of impact to individual colonies was ranked from 0 (least impact) to 4 (greatest impact). Of the 43 corals imaged at that site, 46% exhibited evidence of impact on more than half of the colony, whereas nearly a quarter of all of the corals showed impact to >90% of the colony. Additionally, 53% of these corals' ophiuroid associates displayed abnormal color and/or attachment posture. Analysis of hopanoid petroleum biomarkers isolated from the floc provides strong evidence that this material contained oil from the Macondo well. The presence of recently damaged and deceased corals beneath the path of a previously documented plume emanating from the Macondo well provides compelling evidence that the oil impacted deep-water ecosystems. Our findings underscore the unprecedented nature of the spill in terms of its magnitude, release at depth, and impact to deep-water ecosystems.

## Section II: Status of Mesophotic and Deep Sea Corals in the Gulf of Mexico prior to Deepwater Horizon

Ahlfeld, T. E., Boland, G. S., & Kendall, J. J. (2007). Protection of deep-water corals with the development of oil and gas resources in the U.S. Gulf of Mexico: an adaptive approach. *Bulletin of Marine Science*, 81(3), 59-64 Retrieved from https://www.ingentaconnect.com/content/umrsmas/bullmar/2007/00000081/a00103s1/art00008.

The occurrence of Lophelia pertusa (Linnaeus, 1758) in the northern Gulf of Mexico (GOM) was first documented by Louis de Pourtalès in the late 1860s. The coral specimens were found in dredge samples collected during U.S. Coast Survey cruises conducted in the Straits of Florida and between the Dry Tortugas and the Campeche Bank (Smith, 1954). An extensive deep-water reef in the GOM was discovered in the 1950s approximately 74 km east of the Mississippi River Delta (Moore and Bullis, 1960). This reef, in water depths of 420–512 m, was reported as being composed largely of L. pertusa with the largest portion of the reef extending to a width of 55 m and length of over 305 m (Moore and Bullis, 1960). These habitats have since been shown to be much more extensive and important to the support of diverse communities of associated fauna than previously known in the GOM. Schroeder (2002) reported observations of L. pertusa on the upper De Soto Slope in the northeastern GOM. Individual colonies measured from a few cm to over 1.5 m in diameter while aggregations of closely associated colonies ranged up to 1.5–2 m in height and width and 3–4 m in length (Schroeder, 2002).

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010). Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs*, 29(2), 309-327 https://doi.org/10.1007/s00338-009-0581-x.

Coral reefs in shallow-water environments (<30 m) are in decline due to local and global anthropogenic stresses. This has led to renewed interest in the 'deep reef refugia' hypothesis (DRRH), which stipulates that deep reef areas (1) are protected or dampened from disturbances that affect shallow reef areas and (2) can provide a viable reproductive source for shallow reef areas following disturbance. Using the Caribbean as an example, the assumptions of this hypothesis were explored by reviewing the literature for scleractinian corals—the reef framework builders on tropical reefs. Although there is evidence to support that deep reefs (>30 m) can escape the direct effects of storm-induced waves and thermal bleaching events, deep reefs are certainly not immune to disturbance. Additionally, the potential of deep reefs to provide propagules for shallow reef areas seems limited to 'depth-generalist' coral species, which constitute only ~25% of the total coral biodiversity. Larval connectivity between shallow and deep populations of these species may be further limited due to specific life history traits (e.g., brooding reproductive strategy and vertical symbiont acquisition mode). This review exposes how little is known about deep reefs and coral reproduction over depth. Hence, a series of urgent research priorities are proposed to determine the extent to which deep reefs may act as a refuge in the face of global reef decline.

Brooke, S., & Young, C. M. (2009). In situ measurement of survival and growth of Lophelia pertusa in the northern Gulf of Mexico. *Marine Ecology Progress Series*, 397, 153-161 Retrieved from https://www.int-res.com/abstracts/meps/v397/p153-161/.

Growth rates of Lophelia pertusa were directly measured using stained coral fragments, deployed in situ for more than 1 yr on small transplant units. Survival of the fragments was quantified after deployment (1) within dense coral areas (high coral) and (2) on exposed bare substrate (no coral) in the same area as the reef. Samples of L. pertusa were collected from Viosca Knoll (430 to 520 m depth), northern Gulf of Mexico in July 2004, stained with Alizarin red, photographed and secured onto transplant units for redeployment. The transplants were recovered in September 2005 and percent polyp survival, growth (mm of linear extension) and number of new polyps were recorded. Survival was high (>90%) for all transplant units and the average linear growth rate observed (~3.77 and 2.44 mm $yr^{-1}$ for high coral and no coral sites, respectively) fell at the lower end of the published range for this species. There was no significant difference between any of the survival or growth parameters between sites. The stain bands on the coral sections illustrated double growth centers, which introduces an additional level of complexity when assessing growth through lateral banding patterns. Growth rates of L. pertusa have been inferred using various direct and indirect methods; however, this study represents the first direct measurement of in situ growth for this species.

Brooke, S. D., Holmes, M. W., & Young, C. M. (2009). Sediment tolerance of two different morphotypes of the deep-sea coral Lophelia pertusa from the Gulf of Mexico. *Marine Ecology Progress Series*, 390, 137-144 https://doi.org/10.3354/meps08191.

On the upper slope of the northern Gulf of Mexico, topographic features are often associated with authigenic carbonate, which provides hard substrate for sessile benthic communities. At depths >300 m, large Lophelia pertusa colonies frequently occur on these carbonate outcroppings. Surficial sediments at these depths are dominated by fine-grained particulates, which are readily resuspended during the episodic high current events that have been documented for the Gulf of Mexico. Colonies of L. pertusa found in the deep Gulf of Mexico exhibit 2 distinct growth forms: the very heavily calcified 'brachycephala' and the more fragile 'gracilis'. The objective of this research was to determine the tolerance of these 2 morphotypes to suspended sediment and to complete burial, using sediment collected from the study region. Results demonstrated that, although both morphotypes of L. pertusa can tolerate fairly heavy sediment conditions, mortality increases rapidly with longer burial or higher sediment loads.

Brooks, J. M., Fisher, C. R., Cordes, E. E., Roberts, H. H., Baums, I., Bernard, B. B., . . . Wolff, G. A. (2013). *Exploration and Research of Northern Gulf of Mexico Deepwater Natural and Artificial Hard-Bottom Habitats with Emphasis on Coral Communities: Reefs, Rigs, and Wrecks—"Lophelia II" : Interim Report*. Retrieved from: https://repository.library.noaa.gov/view/noaa/18371

This document represents TDI-Brooks' Interim Report for the Lophelia II Project, Contract M08PC20038, issued by the U.S. Department of the Interior, Bureau of Ocean Energy Management, Regulation and Enforcement (now the Bureau of Ocean Energy Management [BOEM]) "Exploration and Research of Northern Gulf of Mexico Deepwater Natural and Artificial Hard Bottom Habitats with Emphasis on Coral Communities: Reef, Rigs, and Wrecks. This report provides detailed information regarding field sampling, sampling activity, and sample analyses. Results will possibly be revised. This report is a preliminary product of Contract M08PC20038.

Causey, B., Delaney, J., Diaz, E., Dodge, R. E., Garcia, J. R., Higgins, J., . . . Turgeon, D. D. (2002). Status of Coral Reefs in the US Caribbean and Gulf of Mexico: Florida, Texas, Puerto Rico, US Virgin Islands and Navassa. In *Status of Coral Reefs of the World*. Townsville, Australia: Australian Institute of Marine Science. https://nsuworks.nova.edu/occ_facreports/10/

The following report on the status of US Caribbean coral reef ecosystems has been summarised from more extensive reports submitted to the US Coral Reef Task Force (USCRTF) working group that implemented in 2000 'A National Program to Assess, Inventory, and Monitor US Coral Reef Ecosystems'. The more-lengthy reports are also the basis for the biennial-issued document, 'Status and Trends of US Coral Reef Ecosystems'. Each author is a recognised technical expert with responsibility for monitoring and/or managing aspects of their respective coral reef ecosystems.

Cordes, E. E., McGinley, M. P., Podowski, E. L., Becker, E. L., Lessard-Pilon, S., Viada, S. T., & Fisher, C. R. (2008). Coral communities of the deep Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers*, 55(6), 777-787 https://doi.org/10.1016/j.dsr.2008.03.005.

Habitat formation by foundation species is a major ecological force affecting community structure in numerous systems. On the upper continental slope of the Gulf of Mexico, the cold-water scleractinian coral Lophelia pertusa creates complex habitat on cold seep-associated carbonates. In this study, the communities associated with the cold-water coral L. pertusa are described from the Gulf of Mexico for the first time. A total of 68 taxa was identified in close association with the coral framework. Three species with specific relationships to L. pertusa were identified: Eunice sp., a polychaete which may facilitate colony formation in L. pertusa; Coralliophila sp., a species of corallivorous gastropod ; and Stenopus sp., a decapod crustacean which may act in a cleaner shrimp role in these habitats. Similarity among coral-associated communities was best explained by similarity in depth of collection and the proportion of live coral in the collections. These variables were somewhat confounded with location as the sites to the east were both shallower and contained higher proportions of live coral; however, distance between collections per se was not as significant in the analyses. The coral-associated communities also showed a low degree of similarity to communities inhabiting vestimentiferan tubeworm aggregations that occur nearby at the same sites. The increased habitat heterogeneity in the coral structure, differences in the niches constructed by the two foundation species, and different direct interspecific interactions between foundation species and members of the associated community contributed to the presence of dissimilar communities in these two biogenic habitats.

DeBose, J. L., Nuttall, M. F., Hickerson, E. L., & Schmahl, G. P. (2013). A high-latitude coral community with an uncertain future: Stetson Bank, northwestern Gulf of Mexico. *Coral Reefs*, 32(1), 255-267 https://doi.org/10.1007/s00338-012-0971-3.

Limited data exist that detail trends in benthic community composition of high-latitude coral communities. As anthropogenic stressors are projected to increase in number and intensity, long-term monitoring datasets are essential to understanding community stability and ecosystem resilience. In 1993, a long-term monitoring program was initiated at Stetson Bank, in the Gulf of Mexico. Over the course of this monitoring, a major shift in community structure occurred, in which the coral-sponge community was replaced by an algal-dominated community. During the initial years of this study, the coral community at Stetson Bank was relatively stable. Beginning in the late 1990s, sponge cover began a steady decline from over 30 % to less than 25 %. Then, in 2005, the benthic community underwent a further significant change when living coral cover declined from 30 % to less than 8 % and sponges declined to less than 20 % benthic cover. This abrupt shift corresponded with a Caribbean-wide bleaching event in 2005 that caused major mortality of Stetson Bank corals. Previous bleaching events at

Stetson Bank did not result in wide-scale coral mortality. Several environmental parameters may have contributed to the rapid decline in this benthic community. We suggest that the combined effects of coastal runoff and elevated temperatures contributed to the observed shift. We present an analysis of 15 years of monitoring data spanning from 1993 to 2008; this dataset provides both a biological baseline and a multiyear trend analysis of the community structure for a high-latitude coral-sponge community in the face of changing climatic conditions.

Demopoulos, A. W. J., Bourque, J. R., & Frometa, J. (2014). Biodiversity and community composition of sediment macrofauna associated with deep-sea Lophelia pertusa habitats in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers*, 93, 91-103 https://doi.org/10.1016/j.dsr.2014.07.014.

Scleractinian corals create three-dimensional reefs that provide sheltered refuges, facilitate sediment accumulation, and enhance colonization of encrusting fauna. While heterogeneous coral habitats can harbor high levels of biodiversity, their effect on the community composition within nearby sediments remains unclear, particularly in the deep sea. Sediment macrofauna from deep-sea coral habitats (Lophelia pertusa) and non-coral, background sediments were examined at three sites in the northern Gulf of Mexico (VK826, VK906, MC751, 350–500m depth) to determine whether macrofaunal abundance, diversity, and community composition near corals differed from background soft-sediments. Macrofaunal densities ranged from 26 to 125 individuals 32cm−2 and were significantly greater near coral versus background sediments only at VK826. Of the 86 benthic invertebrate taxa identified, 16 were exclusive to near-coral habitats, while 14 were found only in background sediments. Diversity (Fisher's α) and evenness were significantly higher within near-coral sediments only at MC751 while taxon richness was similar among all habitats. Community composition was significantly different both between near-coral and background sediments and among the three primary sites. Polychaetes numerically dominated all samples, accounting for up to 70% of the total individuals near coral, whereas peracarid crustaceans were proportionally more abundant in background sediments (18%) than in those near coral (10%). The reef effect differed among sites, with community patterns potentially influenced by the size of reef habitat. Taxon turnover occurred with distance from the reef, suggesting that reef extent may represent an important factor in structuring sediment communities near L. pertusa. Polychaete communities in both habitats differed from other Gulf of Mexico (GOM) soft sediments based on data from previous studies, and we hypothesize that local environmental conditions found near L. pertusa may influence the macrofaunal community structure beyond the edges of the reef. This study represents the first assessment of L. pertusa-associated sediment communities in the GOM and provides baseline data that can help define the role of transition zones, from deep reefs to soft sediments, in shaping macrofaunal community structure and maintaining biodiversity; this information can help guide future conservation and management activities.

Díaz, M. C., & Pomponi, S. A. (2018). New Poecilosclerida from mesophotic coral reefs and the deep-sea escarpment in the Pulley Ridge region, eastern Gulf of Mexico: Discorhabdella ruetzleri n.sp. (Crambeidae) and Hymedesmia (Hymedesmia) vaceleti n.sp. (Hymedesmiidae). *Zootaxa*, 4466(1), 229 https://doi.org/10.11646/zootaxa.4466.1.17.

Pulley Ridge, a limestone ridge that extends nearly 300 km along the southwestern Florida shelf in the eastern Gulf of Mexico, supports a mesophotic coral ecosystem (59 to 94 m deep), surrounded by deeper waters. An ongoing evaluation of Porifera biodiversity observed and collected during expeditions by Harbor Branch Oceanographic Institute (2003–2015) have shown the existence of approximately 102 sponge species, with at least 20 species new to science. The present paper describes two novel Poecilosclerida from mesophotic reefs and deep escarpments in the Pulley Ridge Region, Eastern Gulf of Mexico, namely Discorhabdella ruetzleri n.sp. (Crambeidae, Poecilosclerida) and Hymedesmia (Hymedesmia) vaceleti n. sp. (Hymedesmiidae, Poecilosclerida). This is the first record of Discorhabdella for the greater Caribbean and the Central West Atlantic. The skeleton of D. ruetzleri n.sp. includes the unique pseudoastrose acanthostyles of the genus, and it is distinct from congeners in the size ranges of the megascleres and in the occurrence of predominantly smooth instead of tuberose choanosomal and ectosomal subtylostyles. The intense blue color and the spicule combination of Hymesdesmia (H.) vaceleti n.sp. makes this species unique among other Hymedesmia spp. from the western Atlantic. The discovery represents a considerable expansion in the known biogeographical distribution of the genus Discorhabdella which is represented now by six species with a discrete geographic distribution (New Zealand, Azores, Western Mediterranean Sea, Eastern Pacific in Panama). This work is the first contribution to an ongoing effort to discover and document the importance of sponge biodiversity on mesophotic reefs and associated deep-water habitats in the Gulf of Mexico and the Caribbean.

Etnoyer, P. J., Wagner, D., Fowle, H. A., Poti, M., Kinlan, B., Georgian, S. E., & Cordes, E. E. (2018). Models of habitat suitability, size, and age-class structure for the deep-sea black coral Leiopathes glaberrima in the Gulf of Mexico. *Deep-Sea Research Part II-Topical Studies in Oceanography*, 150, 218-228 https://doi.org/10.1016/j.dsr2.2017.10.008.

Deep-sea corals are important components of the benthos in the Gulf of Mexico, because they provide structural complexity to associated species of fish and invertebrates, and they serve as proxies for environmental conditions on millennial time scales. In the Gulf of Mexico, large colonies of the black coral Leiopathes glaberrima have been estimated to be over 2000 years old. As such, they are vulnerable to disturbance and slow to recover from adverse interactions with anchors, fishing gear, sedimentation, oil and gas extraction, and sampling. There is a growing need for non-lethal scientific collections and new information on the distribution, ecology, and population connectivity of L. glaberrima aggregations to support management decisions. A large number of remotely operated vehicle (ROV) surveys have been conducted in the Gulf of Mexico deep sea since 2008, including telepresence cruises that broadcast live seafloor images to shore. Visual observations from these surveys were collated and geo-referenced in a regional database with national museum records in order to: (1) map the distribution of L. glaberrima throughout the U.S. Gulf of Mexico, (2) predict the distribution of L. glaberrima based upon environmental correlates using maximum entropy (MaxEnt) modeling, and (3) correlate the size-class structure to the age-class structure using growth rate estimates from previous radiocarbon studies. We found that L. glaberrima has a broad distribution in the U.S. Gulf of Mexico, with suitable habitat spanning depths between 200 and 1000 m that are concentrated near the Mississippi Canyon and along the West Florida Shelf. On average, L. glaberrima colonies had a height of 34.2 cm and a basal diameter of 0.42 cm, which correlates to an age of similar to 143 yrs. Future efforts should focus on calibrating the size and growth relationships of black corals and other corals, in order to add value to telepresence-based exploration and promote non-invasive sampling techniques.

Georgian, S. E., DeLeo, D., Durkin, A., Gomez, C. E., Kurman, M., Lunden, J. J., & Cordes, E. E. (2016). Oceanographic patterns and carbonate chemistry in the vicinity of cold-water coral reefs in the Gulf of Mexico: Implications for resilience in a changing ocean. *Limnology and Oceanography*, 61(2), 648-665 https://doi.org/10.1002/lno.10242.

To accurately assess the threat that global climate change poses to marine systems, a detailed baseline of the current carbonate chemistry and other oceanographic conditions is required. Despite the heightened vulnerability of deep-sea communities to ocean acidification, there have been relatively few studies investigating the carbonate chemistry immediately above cold-water coral reefs. Here, we present data collected during five cruises from 2010 to 2014 in the northern Gulf of Mexico and quantify the carbonate system and other oceanographic parameters in offshore surface-waters, the water column, and at deep benthic sites. Benthic sites containing the scleractinian cold-water coral L. pertusa occurred in waters with a relatively wide temperature range (6.8–13.6°C), low potential density ($\sigma\theta$ = 26.9 ± 0.3 kg m−3), low dissolved oxygen concentration (111.3 ± 2.0 µmol kg−1), low pHT (7.87 ± 0.04), low ΩARAG (1.31 ± 0.14), and a low availability of carbonate ions (94.4 ± 9.2 µmol kg−1) compared with L. pertusa habitats in other regions. Based on previous modelling and experimental results, these values place L. pertusa at the edge of its viable niche in the deep Gulf of Mexico. However, significantly elevated total alkalinity (+39–44 µmol kg−1) was detected above large L. pertusa mounds, suggesting that carbonate dissolution within the mounds may be partially ameliorating the direct effects of ocean acidification. Together, these results provide an important baseline for assessing future oceanographic changes in the Gulf of Mexico and for predicting the resilience of cold-water coral reefs to global climate and ocean change.

Georgian, S. E., Shedd, W., & Cordes, E. E. (2014). High-resolution ecological niche modelling of the cold-water coral Lophelia pertusa in the Gulf of Mexico. *Marine Ecology Progress Series*, 506, 145-161 https://doi.org/10.3354/meps10816.

The niche of many deep-sea species remains poorly resolved despite decades of seafloor exploration. Without better information on the distribution and habitat preference of key species, a complete understanding of the ecology of deep-sea communities will remain unattainable. It is increasingly apparent that cold-water corals are among the dominant foundation species in the deep sea, providing both structurally complex habitat and significant ecosystem services. In this study, the niche and distribution of the cold-water coral Lophelia pertusa in the Gulf of Mexico was evaluated using the maximum entropy (Maxent) approach. Ecological niche models were constructed for a broad region of the northern Gulf of Mexico using data gridded at a spatial resolution of 25 m, including bathymetry, substrate type, export productivity, and aragonite saturation state at depth. Fine-scale models were constructed at a resolution of 5 m using only remotely sensed bathymetric and surface reflectivity data. The broad-scale model performed well, with an area under the curve (AUC) of 0.981. All fine-scale models performed well when verified using training data (average AUC of 0.963) and when validated using independent occurrence data from a new geographic region (average AUC of 0.937). The distribution of L. pertusa in the Gulf of Mexico was found to be controlled primarily by depth, local topography, and availability of hard substrate. While these factors have long been associated with the success of cold-water corals, their relative importance has never been quantified in the Gulf of Mexico, making it historically difficult to precisely delineate L. pertusa’s niche and predict its distribution in unexplored regions. Given these results, we suggest that future expeditions combine remotely sensed data with niche modelling techniques to increase the efficiency of deep-sea exploration.

Hickerson, E. L., Schmahl, G. P., & Weaver, D. C. (2006). Patterns of Deep Coral Communities on Reefs and Banks in the Northwestern Gulf of Mexico. 87. [no URL available].

Dozens of reefs and banks rise from the depths of the continental shelf margin off the coast of Texas and Louisiana in the northwestern Gulf of Mexico. The East and West Flower Garden Banks are two such features, which harbor some of the healthiest shallow water coral reefs in the continental United States. However, most of the area of the Flower Garden Banks as well as numerous other banks in this region lie below the depth range of active scleractinian coral reef development. In spite of important baseline scientific investigations conducted in the late 1970's and early 1980's, the extent and nature of these communities are still not well known. Recent surveys by the authors and collaborators have further characterized a number of the reefs and banks in this vicinity. The collection of high resolution multibeam survey data has been instrumental in the planning and execution of hundreds of remotely operated vehicles (ROV) and manned submersibles surveys. These areas, occurring in depths from 50 to 200 meters, contain rich deep coral communities, comprised of a variety of antipatharians, solitary and branching corals, octocorals and associated species, and provide important habitat for a variety of fish species of commercial and recreational importance. A description and preliminary patterns of zonation and community structure of these communities will be provided.

Jarrett, B. D., Hine, A. C., Halley, R. B., Naar, D. F., Locker, S. D., Neumann, A. C., . . . Ciembronowicz, K. (2005). Strange bedfellows—a deep-water hermatypic coral reef superimposed on a drowned barrier island; southern Pulley Ridge, SW Florida platform margin. *Marine Geology*, 214(4), 295-307 https://doi.org/10.1016/j.margeo.2004.11.012.

The southeastern component of a subtle ridge feature extending over 200 km along the western ramped margin of the south Florida platform, known as Pulley Ridge, is composed largely of a non-reefal, coastal marine deposit. Modern biostromal reef growth caps southern Pulley Ridge (SPR), making it the deepest hermatypic reef known in American waters. Subsurface ridge strata are layered, lithified, and display a barrier island geomorphology. The deep-water reef community is dominated by platy scleractinian corals, leafy green algae, and coralline algae. Up to 60% live coral cover is observed in 60–75 m of water, although only 1–2% of surface light is available to the reef community. Vertical reef accumulation is thin and did not accompany initial ridge submergence during the most recent sea-level rise. The delayed onset of reef growth likely resulted from several factors influencing Gulf waters during early stages of the last deglaciation (∼14 kyr B.P.) including; cold, low-salinity waters derived from discrete meltwater pulses, high-frequency sea-level fluctuations, and the absence of modern oceanic circulation patterns. Currently, reef growth is supported by the Loop Current, the prevailing western boundary current that impinges upon the southwest Florida platform, providing warm, clear, low-nutrient waters to SPR. The rare discovery of a preserved non-reefal lowstand shoreline capped by rich hermatypic deep-reef growth on a tectonically stable continental shelf is significant for both accurate identification of late Quaternary sea-level position and in better constraining controls on the depth limits of hermatypic reefs and their capacity for adaptation to extremely low light levels.

Johnston, M. A., Embesi, J. A., Eckert, R. J., Nuttall, M. F., Hickerson, E. L., & Schmahl, G. P. (2016). Persistence of coral assemblages at East and West Flower Garden Banks, Gulf of Mexico. *Coral Reefs*, 35(3), 821-826 https://doi.org/10.1007/s00338-016-1452-x.

Since 1989 a federally supported long-term coral reef monitoring program has focused on two study sites atop East and West Flower Garden Banks in the northwestern Gulf of Mexico. We examined 25 yr of benthic cover data to provide a multi-decadal baseline and trend analysis of the community structure for this coral reef system. Despite global coral reef decline in recent decades, mean coral cover at East and West Flower Garden Banks was above 50% for the combined 25 yr of continuous monitoring, and represented a stable coral community. However, mean macroalgal cover increased significantly between 1998 and 1999, rising from approximately 3 to 20%, and reaching a maximum above 30% in 2012. In contrast to many other shallow water reefs in the Caribbean region, increases in mean macroalgal cover have not been concomitant with coral cover decline at the Flower Garden Banks.

Lunden, J. J., Georgian, S. E., & Cordes, E. E. (2013). Aragonite saturation states at cold-water coral reefs structured by Lophelia pertusa in the northern Gulf of Mexico. *Limnology and Oceanography*, 58(1), 354-362 https://doi.org/10.4319/lo.2013.58.1.0354.

Ocean acidification, the reduction in pH and calcium carbonate saturation states of seawater, is likely to exhibit its most immediate effects on cold-water corals in deep waters with the shoaling of the aragonite saturation horizon. However, empirical data describing the carbonate chemistry at cold-water coral reefs are very rare. Regions of the upper slope of the Northern Gulf of Mexico harbor several deep-water reefs structured by the scleractinian Lophelia pertusa. We collected discreet water samples at a range of depths in the Gulf of Mexico, including eight Lophelia reefs, and measured total alkalinity and pH to calculate the aragonite saturation state ($\Omega$arag). The deep waters of the Gulf of Mexico (> 300 m depth) were at aragonite saturation states between 0.98 and 1.69. L. pertusa was present at sites with $\Omega$arag between 1.25 and 1.69, and carbonate ion concentrations between 92 and 123 µmol $kg^{-1}$. These data provide a critical baseline for detecting future changes in carbonate chemistry in the water column (i.e., aragonite saturation horizon shoaling), as well as at the sites of well-developed cold-water coral structures threatened by ongoing ocean acidification.

Lunden, J. J., McNicholl, C. G., Sears, C. R., Morrison, C. L., & Cordes, E. E. (2014). Acute survivorship of the deep-sea coral Lophelia pertusa from the Gulf of Mexico under acidification, warming, and deoxygenation. *Frontiers in Marine Science*, 1(78), https://doi.org/10.3389/fmars.2014.00078.

Changing global climate due to anthropogenic emissions of $CO_2$ are driving rapid changes in the physical and chemical environment of the oceans via warming, deoxygenation, and acidification. These changes may threaten the persistence of species and populations across a range of latitudes and depths, including species that support diverse biological communities that in turn provide ecological stability and support commercial interests. Worldwide, but particularly in the North Atlantic and deep Gulf of Mexico, Lophelia pertusa forms expansive reefs that support biological communities whose diversity rivals that of tropical coral reefs. In this study, L. pertusa colonies were collected from the Viosca Knoll region in the Gulf of Mexico (390 to 450 m depth), genotyped using microsatellite markers, and exposed to a series of treatments testing survivorship responses to acidification, warming, and deoxygenation.

All coral nubbins survived the acidification scenarios tested, between pH of 7.67 and 7.90 and aragonite saturation states of 0.92 and 1.47. However, calcification generally declined with respect to pH, though a disparate response was evident where select individuals net calcified and others exhibited net dissolution near a saturation state of 1. Warming and deoxygenation both had negative effects on survivorship, with up to 100% mortality observed at temperatures above 14ºC and oxygen concentrations of approximately 1.5 ml·l-1. These results suggest that, over the short-term, climate change and OA may negatively impact L. pertusa in the Gulf of Mexico, though the potential for acclimation and the effects of genetic background should be considered in future research.

Morrison, C. L., Eackles, M. S., Johnson, R. L., & King, T. L. (2008). Characterization of 13 microsatellite loci for the deep-sea coral, Lophelia pertusa (Linnaeus 1758), from the western North Atlantic Ocean and Gulf of Mexico. *Molecular Ecology Resources*, 8(5), 1037-1039 https://doi.org/10.1111/j.1755-0998.2008.02147.x.

Abstract A suite of 13 polymorphic tri- and tetranucleotide microsatellite loci were isolated from the ahermatypic deep-sea coral, Lophelia pertusa. Among 51 individuals collected from three disjunct oceanic regions, allelic diversity ranged from six to 38 alleles and averaged 9.1 alleles per locus. Observed heterozygosity ranged from 9.1 to 96.8% and averaged 62.3% in the Gulf of Mexico population. For some loci, amplification success varied among collections, suggesting regional variation in priming site sequences. Four loci showed departures from Hardy?Weinberg equilibrium in certain collections which may reflect nonrandom mating.

Morrison, C. L., Johnson, R. L., King, T. L., Ross, S. W., & Nizinski. (2008). Molecular Assessment of Deep-sea Scleractinian Coral Biodiversity and Population Structure of Lophelia Pertusa in the Gulf of Mexico. In K. J. Sulak, M. Randall, K. E. Luke, A. D. Norem, & J. M. Miller (Eds.), *Characterization of Northern Gulf of Mexico Deepwater Hard Bottom Communities with Emphasis on Lophelia Coral - Lophelia Reef Megafaunal Community Structure, Biotopes, Genetics, Microbial Ecology, and Geology (2004–2006)*. Reston, VA: U.S. Department of the Interior. Retrieved from: https://pubs.er.usgs.gov/publication/ofr20081148

Geographic patterns of genetic diversity in Lophelia pertusa were examined by quantifying genetic diversity present in populations, and assessing levels of genetic differentiation within the Gulf of Mexico (5 sampling locations, Lophelia were compared to Lophelia populations from the Southeastern U.S. continental slope (6 sampling locations, 18-990 km apart) and with Europe (5400-7900 km away from sampled U.S. populations). A suite of nine microsatellite markers for Gulf of Mexico Lophelia were developed; 190 individuals have been genotyped. The microsatellite markers were highly variable, ranging from 11-53 alleles per locus with an average of 27.4 alleles per locus. Eighteen (9%) individuals with identical multi-locus genotypes were identified as clones. Populations of Lophelia harbored substantial genetic diversity. The majority of populations had unique alleles indicative of little gene flow. Pairwise chord distances were high among all populations (0.42 - 0.62), and regional groupings of populations resulted from a neighbor-joining clustering analysis. North versus south areas of Viosca Knoll 826, the most intensively sampled area, had fixation index estimates significantly greater than zero, suggesting little larval mixing. Comparisons of all Gulf Lophelia populations with the shallowest site, VK862, produced significant fixation indices. Quantitative estimates of hierarchical gene diversity

(AMOVA) indicated significant population structure at every level: between the three regions examined; between Gulf and southeastern U.S. regions; and within the Gulf and southeastern U.S. regions. Mantel tests identified significant correlations between geographic and genetic distance (an isolation-by-distance pattern) at larger spatial scales, but not within regions. Thus, dispersal of Lophelia larvae is generally localized, with occasional long distance dispersal occurring such that some genetic cohesion is retained regionally within the Gulf and Southeastern U.S. Genetic differentiation observed between these regions suggests more restricted gene flow than expected, suggesting that the most effective management plan for Lophelia may be regional reserve networks. Gulf of Mexico deep-sea scleractinian coral biodiversity was put into a phylogenetic framework by comparison of 16S mitochondrial DNA sequences. Four basal lineages were revealed, including the 'complex' and 'robust' corals, the genus Anthemiphyllia, plus several species belonging to the family Caryophylliidae. The latter basal coral lineage appears diverse since three Gulf species grouped within this clade. Members of the family Caryophylliidae were not monophyletic, but appeared in six clades; the majority of which were in the 'robust' coral group. The high estimate of genetic distance reported previously between Lophelia in different oceanic regions was not supported.

Prouty, N. G., Roark, E. B., Buster, N. A., & Ross, S. W. (2011). Growth rate and age distribution of deep-sea black corals in the Gulf of Mexico. *Marine Ecology Progress Series*, 423, 101-115 https://doi.org/10.3354/meps08953.

Black corals (order Antipatharia) are important long-lived, habitat-forming, sessile, benthic suspension feeders that are found in all oceans and are usually found in water depths greater than 30 m. Deep-water black corals are some of the slowest-growing, longest-lived deep-sea corals known. Previous age dating of a limited number of black coral samples in the Gulf of Mexico focused on extrapolated ages and growth rates based on skeletal $^{210}$Pb dating. Our results greatly expand the age and growth rate data of black corals from the Gulf of Mexico. Radiocarbon analysis of the oldest Leiopathes sp. specimen from the upper De Soto Slope at 300 m water depth indicates that these animals have been growing continuously for at least the last 2 millennia, with growth rates ranging from 8 to 22 µm $yr^{-1}$. Visual growth ring counts based on scanning electron microscopy images were in good agreement with the $^{14}$C-derived ages, suggestive of annual ring formation. The presence of bomb-derived $^{14}$C in the outermost samples confirms sinking particulate organic matter as the dominant carbon source and suggests a link between the deep-sea and surface ocean. There was a high degree of reproducibility found between multiple discs cut from the base of each specimen, as well as within duplicate subsamples. Robust $^{14}$C -derived chronologies and known surface ocean $^{14}$C reservoir age constraints in the Gulf of Mexico provided reliable calendar ages with future application to the development of proxy records.

Quattrini, A. M., Georgian, S. E., Byrnes, L., Stevens, A., Falco, R., & Cordes, E. E. (2013). Niche divergence by deep-sea octocorals in the genus Callogorgia across the continental slope of the Gulf of Mexico. *Molecular Ecology*, 22(15), 4123-4140 https://doi.org/10.1111/mec.12370.

Environmental variables that are correlated with depth have been suggested to be among the major forces underlying speciation in the deep sea. This study incorporated phylogenetics and ecological niche models (ENM) to examine whether congeneric species of Callogorgia (Octocorallia: Primnoidae) occupy different ecological niches across the continental slope of the Gulf of Mexico (GoM) and whether this niche divergence could be important in the evolution of these closely related species. Callogorgia americana americana, Callogorgia americana delta and Callogorgia gracilis were documented at 13 sites in the GoM (250–1000 m) from specimen collections and extensive video observations. On a first order, these species were separated by depth, with C. gracilis occurring at the shallowest sites, C. a. americana at mid-depths and C. a. delta at the deepest sites. Callogorgia a. delta was associated with areas of increased seep activity, whereas C. gracilis and C. a. americana were associated with narrow, yet warmer, temperature ranges and did not occur near cold seeps. ENM background and identity tests revealed little to no overlap in ecological niches between species. Temporal calibration of the phylogeny revealed the formation of the Isthmus of Panama was a vicariance event that may explain some of the patterns of speciation within this genus. These results elucidate the potential mechanisms for speciation in the deep sea, emphasizing both bathymetric speciation and vicariance events in the evolution of a genus across multiple regions.

Reed, J. K., Weaver, D. C., & Pomponi, S. A. (2006). Habitat and fauna of deep-water Lophelia pertusa coral reefs off the southeastern U.S.: Blake plateau, Straits of Florida, and Gulf of Mexico. *Bulletin of Marine Science*, 78(2), 343-375 Retrieved from https://www.ingentaconnect.com/content/umrsmas/bullmar/2006/00000078/00000002/art00009.

Expeditions from 1999 to 2004 for biomedical research explored various deep-sea coral ecosystems (dSCE) off the southeastern U.S. (Blake Plateau, Straits of Florida, and eastern Gulf of Mexico). Habitat and benthos were documented from 57 dives with human occupied submersibles and three with a remotely operated vehicle (ROV), and resulted in ∼100 hrs of videotapes, 259 in situ digital images, 621 museum specimens, and > 400 microbial isolates. These were the first dives to document the habitat, benthic fauna, and fish diversity of some of these poorly known deep-water reefs. Fifty-eight fish species and 142 benthic invertebrate taxa were identified. High-definition topographic SEABEAM maps and echosounder profiles were also produced. Sites included in this report range from South Carolina on the Blake Plateau to the southwestern Florida slope: 1) Stetson Lophelia reefs along the eastern Blake Plateau off South Carolina; 2) Savannah Lophelia lithoherms along the western Blake Plateau off Georgia; 3) east Florida Lophelia reefs, 4) Miami Terrace escarpment in the Straits of Florida; 5) Pourtalès Terrace off the Florida keys; and 6) west Florida Lophelia lithoherms off the southwestern Florida shelf in the Gulf of Mexico. These are contrasted with the azooxanthellate deep-water oculina reefs at the shelf-edge off central eastern Florida. The fisheries and biopharmaceutical resource potential of these deep-water habitats remain relatively unknown. Although these habitats are not currently designated as marine protected areas (MPAs) or coral habitat areas of particular concern (HAPCs), they are ecologically diverse, vulnerable to physical destruction, and irreplaceable resources. Activities involving bottom trawling, pipelines, or oil/gas production could negatively impact these reefs. National Oceanic and Atmospheric Administration (NOAA) Fisheries and the South Atlantic Fishery Management Council are currently developing priority mapping sites of the dSCEs within this region, and these data may provide potential targets for new MPAs and HAPCs.

Ross, S. W., Brooke, S., Quattrini, A. M., Rhode, M., & Watterson, J. C. (2015). A deep-sea community, including Lophelia pertusa, at unusually shallow depths in the western North Atlantic Ocean off

northeastern Florida. *Marine Biology*, 162(3), 635-648 https://doi.org/10.1007/s00227-015-2611-2.

Living colonies of the cold-water scleractinian coral Lophelia pertusa and other typically deep-water organisms were discovered in unusually shallow depths (180–250 m) off northeastern Florida. Observations of L. pertusa on rocky substrata and coral-built mounds represent the shallowest records of large colonies of this coral in the western Atlantic Ocean. Bioherms up to 30 m tall, extensive areas of eroded L. pertusa rubble, and a well-developed cold-water community indicated that these sites are long-term features, rather than short-term opportunistic responses to temporary shifts in environmental conditions. Species that are commonly observed on deeper reefs off the southeastern USA were abundant at the shallow sites. The most abundant fishes on reef habitats were Helicolenus dactylopterus, Laemonema barbatulum, Dysommina rugosa, and Anthias spp. In addition to L. pertusa, the most common macroinvertebrates on hard substrata were Eumunida picta, Chaceon fenneri, octocorals, cup corals, and glass sponges. Bottom and near-bottom temperatures (7–10 °C) and nutrient concentrations at the shallow sites were similar to those normally encountered at 500–600 m in this region. The shallow reef sites occur in an area known for frequent Gulf Stream-driven upwelling of deep, nutrient-rich water. However, the upwelling must be persistent or permanent in order to maintain deep-sea communities at such shallow depths. Based on these data, this area is under final review by the US Department of Commerce for inclusion in one of the regional Coral Habitat Areas of Particular Concern.

Ross, S. W., Rhode, M., & Brooke, S. (2017). Deep-sea coral and hardbottom habitats on the west Florida slope, eastern Gulf of Mexico. *Deep-Sea Research Part I-Oceanographic Research Papers*, 120, 14-28 https://doi.org/10.1016/j.dsr.2016.12.005.

Until recently, benthic habitats dominated by deep-sea corals (DSC) appeared to be less extensive on the slope of the Gulf of Mexico (GOM) than in the northeast Atlantic Ocean or off the southeastern US. There are relatively few bioherms (i.e., coral-built mounds) in the northern GOM, and most DSCs are attached to existing hard substrata (e.g., authigenically formed carbonate). The primary structure-forming, DSC in the GOM is Lophelia pertusa, but structure is also provided by other living and dead scleractinians, antipatharians (black corals), octocorals (gorgonians, soft corals), hydrocorals and sponges, as well as abundant rocky substrata. The best development of DSCs in the GOM was previously documented within Viosca Knoll oil and gas lease blocks 826 and 862/906 (north-central GOM) and on the Campeche Bank (southern GOM in Mexican waters). This paper documents extensive deer; reef ecosystems composed of DSC and rocky hard-bottom recently surveyed on the West Florida Slope (WFS, eastern GOM) during six research cruises (2008-2012). Using multibeam sonar, CTD casts, and video from underwater vehicles, we describe the physical and oceanographic characteristics of these deep reefs and provide size or area estimates of deep coral and hardground habitats. The multibeam sonar analyses revealed hundreds of mounds and ridges, some of which were subsequently surveyed using underwater vehicles. Mounds and ridges in < 525 m depths were usually capped with living coral colonies, dominated by L. pertusa. An extensive rocky scarp, running roughly north-south for at least 229 km, supported lower abundances of scleractinian corals than the mounds and ridges, despite an abundance of settlement substrata. Areal comparisons suggested that the WFS may exceed other parts of the GOM slope in extent of living deep coral coverage and other deep-reef habitat (dead coral and rock). The complex WFS region warrants additional studies to better understand the influences of oceanography and geology on the occurrence of DSC and associated organisms. Protection measures are being considered to ensure the long-term integrity of this diverse ecosystem.

Schroeder, W. W. (2002). Observations of Lophelia pertusa and the surficial geology at a deep-water site in the northeastern Gulf of Mexico. *Hydrobiologia*, 471(1), 29-33 https://doi.org/10.1023/A:1016580632501.

Authigenic carbonate, precipitated in conjunction with biogeochemical activity associated with hydrocarbon and related fluid seepage, provides exposed and buried hard substrate on the crest and flanks of a low-relief mound located on the upper De Soto Slope in the northeastern Gulf of Mexico. Lophelia pertusa has successfully colonized some of this carbonate material. Individual colonies range in size from a few centimeters to over 1.5 m in diameter while aggregations of closely associated colonies with linear orientations were observed to attain 1.5–2 m in height and width and 3–4 m in length. Many of the aggregated colonies appear to be in the first phase of the `thicket' building stage described by Squires (1964). Colonies less than 50–75 cm in diameter were nearly always completely pure white. Larger colonies and the aggregated colonies are often light to dark brown in coloration at their base and center with many having only white terminal branches and some with no white corallum at all.

Schroeder, W. W. (2007). Seabed characteristics and Lophelia pertusa distribution patterns at sites in the northern and eastern Gulf of Mexico. *Bulletin of Marine Science*, 81(3), 315-323 Retrieved from https://www.ingentaconnect.com/content/umrsmas/bullmar/2007/00000081/a00103s1/art00026.

The often patchy, discontinuous distribution of Lophelia pertusa (Linnaeus, 1758) was unequivocally established by Wilson (1979a,b) during his investigations of Rockall Bank and other sites in the north-east Atlantic. This work corroborated earlier findings by Joubin (1922) in the Bay of Biscay, Stetson et al. (1962) on Blake Plateau, and Squires (1964) in Wairarapa, New Zealand. Two decades later, Rogers (1999), in his review of the biology of L. pertusa and other deep-water reef-forming corals, concluded that factors influencing the distribution of deep-water corals by and large continued to be poorly understood. However, he goes on to state that over small scales topography and hydrographic conditions play important roles in structuring distribution patterns. In their study off Norway, Mortensen et al. (2001) found that although L. pertusa reefs were not evenly distributed over the seabed they did occur in geographic and bathymetric patterns that appeared to be regulated by external factors such as: (1) presence of suitable substrate; (2) topography; (3) physical and chemical properties of water masses; and (4) availability of food. Even in the most recent literature uncertainties remain as to exactly which factors play controlling roles in determining distribution patterns (Roberts et al., 2003; Taviani et al., 2005).

Schroeder, W. W. (2007). *Seafloor Characteristics and Distribution Patterns of Lophelia pertusa and Other Sessile Megafauna at Two Upper-Slope Sites in the Northeastern Gulf of Mexico*. Retrieved from: https://www.boem.gov/ESPIS/4/4256.pdf

Habitat-forming deep-water (a.k.a. cold-water) coral ecosystems are known to serve as important components of the world's oceans and seas. One of the principal species of branching scleractinian corals that form deep-water assemblages is the tuft coral Lophelia pertusa. Generally, these corals are very slow to develop and fragile. As a result they are vulnerable to sustaining damage that if extensive can require years for recovery, if at all. Unfortunately this situation is already occurring globally principally due to destructive fishing practices and secondarily as a consequence of activities associated with exploration and extraction of fossil fuels. In light of the continuing expansion of oil and gas activities into the deep Gulf of Mexico (GoM), there is a crucial need to understand the basic biology and functional ecology of these unique systems, and ultimately to determine appropriate management strategies for their protection.

Schroeder, W. W., Brooke, S. D., Olson, J. B., Phaneuf, B., McDonough, J. J., & Etnoyer, P. (2005). Occurrence of deep-water Lophelia pertusa and Madrepora oculata in the Gulf of Mexico. In A. Freiwald & J. M. Roberts (Eds.), *Cold-Water Corals and Ecosystems* (pp. 297-307). Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/3-540-27673-4_14

One of the critical information needs identified at the 2003 Deep-Sea Corals Workshop in Galway, Ireland, was to locate and chart deep-sea corals in order to develop reliable estimates of their distribution and abundance. While reports of deep-sea corals from the Gulf of Mexico date back to the 1860s, relatively little is known about their distribution or abundance. This paper attempts to provide a current assessment of the occurrence of Lophelia pertusa and Madrepora oculata in water depths greater than 200 m in the Gulf of Mexico by summarizing records from (1) published material, (2) the 2003 National Museum of Natural History Taxonomic Database, (3) findings obtained during the September-October 2003 NOAA-OE RV Ronald H. Brown cruise RB-03-07-leg-2 in the northern Gulf, and (4) from various unpublished sources.

## Section III: Mapping Mesophotic and Deep Sea Corals

Bullimore, R. D., Foster, N. L., & Howell, K. L. (2013). Coral-characterized benthic assemblages of the deep Northeast Atlantic: defining “Coral Gardens” to support future habitat mapping efforts. *ICES Journal of Marine Science*, 70(3), 511-522 https://doi.org/10.1093/icesjms/fss195.

Providing statistically robust maps of habitat distributions on which to base spatial planning and management of the marine area is reliant upon established and agreed descriptions and definitions of habitats. “Coral Gardens” is an Oslo–Paris Convention (OSPAR) listed habitat, which currently cannot be reliably mapped as a result of poorly developed deep-sea habitat classification systems and habitat definitions. The aim of this study is to assess and inform development of the current definition of this habitat to support future mapping efforts. This study uses multivariate community analysis of video data to identify deep-sea benthic assemblages characterized by coral taxa and thus constituting a potential “coral gardens” habitat. Assemblages are assessed against a set of qualifying criteria, derived from current definitions of “coral gardens”, first at the assemblage level then sample by sample. The current definition of “coral gardens” captures a range of benthic assemblages, thus “Coral Gardens” cannot be considered a single “habitat”. While 19 assemblages are identified as being characterized by one or more coral garden taxa, only 8 meet the qualifying criteria. It is suggested that the current definition incorporates descriptions of the different "Coral Gardens" assemblages together with guidance on threshold densities for coral species specific to each assemblage type.

Clark, R. D., Siceloff, L., & Winship, A. J. (2018). *Mapping bottom-contact fishing intensity in the Gulf of Mexico in relation to predicted suitable habitats for deep sea corals*. Retrieved from https://repository.library.noaa.gov/view/noaa/18065

In 2013, NCCOS completed predictive habitat suitability models for 21 species and complexes of deep corals in the Gulf ofMexico, including framework-forming deep cor als. In addition to internal cross-validation, these models wer e field-tested and validated during the Okeanos Explorer EC1402L3 mission in April 2014. These models are being used to advise the Gulf of Mexico Fishery Management Council on possible deep coral protection zones, and have also been used by BOEM, NOAA OR&R and academic partners. However, no effort to date has assessed the degree of overlapbetween fishing intensity with bottom-contact gear and predicted habitat suitability of key deep coral groups. NOAA's Deep Sea Coral Research and Technology Program has identified the need to know more about where bottom contact commercial fishing takes place and how it may impact deep coral communities. This report examines two bottom contact fishing gears, shrimp trawls and bottom longlines, and potential conflicts with specific predicted coral communities.

*Cold-Water Corals and Ecosystems*. (2005). (A. Freiwald & J. M. Roberts Eds.). Berlin, Germany: Springer-Verlag Berlin Heidelberg. https://doi.org/10.1007/3-540-27673-4

Following the exciting exploration of hot vent and cold seep ecosystems, the rediscovery of cold-water coral ecosystems with high-technology instrumentation is currently another hot topic in multidisciplinary marine research. Conventionally, coral reefs are regarded as restricted to warm and well-illuminated tropical seas, not associated with cold and dark waters of higher latitudes. However, ongoing scientific missions have shed light on the global significance of this overlooked ecosystem. Cold-water coral ecosystems are involved in the formation of large seabed structures such as reefs and giant carbonate mounds, and they represent unexploited paleo-environmental archives of earth history. Like their tropical cousins, cold-water coral ecosystems harbour rich species diversity. Despite the great water depths, commercial interests overlap more and more with the coral occurrences. Human activities already impinge directly on cold-water coral reefs causing severe damage to this vulnerable ecosystem. In this volume, the current key institutions involved in cold-water coral research have contributed 62 state-of-the-art articles from geology and oceanography to biology and conservation.

Conti, L. A., Lim, A., & Wheeler, A. J. (2019). High resolution mapping of a cold water coral mound. *Scientific Reports*, 9, 15 https://doi.org/10.1038/s41598-018-37725-x.

Cold-water coral (CWC) mounds are biogenic, long-lived morphostructures composed primarily by scleractinian CWC's and hemipelagic sediments that form complex deep-sea microhabitats found globally but specifically along the European-Atlantic margin. In this work, high-resolution mapping was applied to identify individual organismal distribution and zonation across a CWC Piddington Mound within the Porcupine Seabight, Ireland Margin. Marine Object-Based Image Analysis (MOBIA) and different machine learning classification methods (decision tree, logistic regression, and deep neural network) were applied to a high-resolution (2 mm) reef-scale video mosaic and ROV-mounted multibeam data in order to provide new insights into the spatial organization of coral frameworks and environmental factors on CWC mounds. The results showed an accurate quantification of the amount of Coral Framework (14.5%; similar to 2% live and similar to 12.5% dead) and sponges (similar to 3.5%) with heterogeneous distribution, restricted to a certain portion of the mound. This is the first object level quantification of live and dead coral framework facies and individual sponges across an entire CWC mound. This approach has application for habitat and conservation studies, provides a quantification tool for carbon budget assessments and can provide a baseline to assess CWC mound change. The approach can also be modified for application in other habitats.

Davies, A. J., Duineveld, G. C. A., Lavaleye, M. S. S., Bergman, M. J. N., van Haren, H., & Roberts, J. M. (2009). Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral Lophelia pertusa (Scleractinia) at the Mingulay Reef Complex. *Limnology and Oceanography*, 54(2), 620-629 https://doi.org/10.4319/lo.2009.54.2.0620.

In 2006 and 2007, multiple deployments of current meters and optical sensors on landers and moorings were made in the first detailed in situ study of the particle supply to the coral community in the Mingulay Reef complex in the Sea of Hebrides at 140-m water depth. Two distinct and predictable supply mechanisms were resolved. One mechanism consisted of the rapid downwelling of surface water caused by hydraulic control of tidal flow that transports particles from the surface to the corals in less than an hour. The rapid downwelling was recorded on the reef top as a pulse of warm, fluorescent, and relatively clear water at the onset of the flood and ebb tides. The pulse was strongest after flood tide and lasted for up to 3 h. The second mechanism consisted of advection onto the reef of deep bottom water with a high suspended matter load. This advection occurred during peak tides and was combined with topographical current acceleration on the reef top, enhancing delivery of particles to the corals.

De Mol, L., Van Rooij, D., Pirlet, H., Greinert, J., Frank, N., Quemmerais, F., & Henriet, J.-P. (2011). Cold-water coral habitats in the Penmarc'h and Guilvinec Canyons (Bay of Biscay): Deep-water versus shallow-water settings. *Marine Geology*, 282(1), 40-52 https://doi.org/10.1016/j.margeo.2010.04.011.

In 1948, Le Danois reported for the first time the occurrence of living cold-water coral reefs, the so-called “massifs coralliens”, along the European Atlantic continental margin. In 2008, a cruise with R/V Belgica was set out to re-investigate these cold-water corals in the Penmarc'h and Guilvinec Canyons along the Gascogne margin of the Bay of Biscay. During this cruise, an area of 560km2 was studied using multibeam swath bathymetry, CTD casts, ROV observations and USBL-guided boxcoring. Based on the multibeam data and the ROV video imagery, two different cold-water coral reef settings were distinguished. In water depths ranging from 260 to 350m, mini mounds up to 5m high, covered by dead cold-water coral rubble, were observed. In between these mounds, soft sediment with a patchy distribution of gravel was recognised. The second setting (350–950m) features hard substrates with cracks, spurs, cliffs and overhangs. In water depths of 700 to 950m, both living and dead cold-water corals occur. Occasionally, they form dense coral patches with a diameter of about 10–60m, characterised by mostly stacked dead coral rubble and a few living specimens. U/Th datings indicate a shift in cold-water coral growth after the Late Glacial Maximum (about 11.5ka BP) from shallow to deep-water settings. The living cold-water corals from the deeper area occur in a water density (sigma–theta) of 27.35–27.55kgm$^{-3}$, suggested to be a prerequisite for the growth and distribution of cold-water coral reefs along the northern Atlantic margin. In contrast, the dead cold-water coral fragments in the shallow area occur in a density range of 27.15–27.20kgm$^{-3}$ which is slightly outside the density range where living cold-water corals normally occur. The presented data suggest that this prerequisite is also valid for coral growth in the deeper canyons (>350m) in the Bay of Biscay.

Dolan, M. F. J., Grehan, A. J., Guinan, J. C., & Brown, C. (2008). Modelling the local distribution of cold-water corals in relation to bathymetric variables: Adding spatial context to deep-sea video data. *Deep Sea Research Part I: Oceanographic Research Papers*, 55(11), 1564-1579 https://doi.org/10.1016/j.dsr.2008.06.010.

Video data and high-resolution multibeam bathymetry were acquired using a Remotely Operated Vehicle (ROV) on the flank of a carbonate mound (~850m depth) in the Porcupine Seabight, SW Ireland. The ROV-mounted multibeam system revealed details of bathymetry that were not resolved by ship-borne multibeam survey, but appear to be important in structuring the distribution of the cold-water corals Lophelia pertusa and Madrepora oculata. Quantitative measures of slope, orientation, roughness and curvature were calculated from the ROV multibeam bathymetry data across a range of spatial scales. These parameters were analysed for their ecological relevance to the distribution of the corals and used in an Ecological Niche Factor Analysis (ENFA) to identify the most suitable areas for coral colonisation within the extent of our ROV multibeam data. The suitability map covers an area nine times the size of the area imaged directly by video. Cross-validation of the results with video data indicates that the predictions are reliable. This combined survey and modelling approach offers a comprehensive method for ground-truthing discrete seabed features such as mounds. It provides spatial context to high-resolution deep-water video observations and highlights the importance of bathymetric variables in influencing coral distribution.

Foglini, F., Grande, V., Marchese, F., Bracchi, V. A., Prampolini, M., Angeletti, L., . . . Taviani, M. (2019). Application of Hyperspectral Imaging to Underwater Habitat Mapping, Southern Adriatic Sea. *Sensors*, 19(10), 18 https://doi.org/10.3390/s19102261.

Hyperspectral imagers enable the collection of high-resolution spectral images exploitable for the supervised classification of habitats and objects of interest (OOI). Although this is a well-established technology for the study of subaerial environments, Ecotone AS has developed an underwater hyperspectral imager (UHI) system to explore the properties of the seafloor. The aim of the project is to evaluate the potential of this instrument for mapping and monitoring benthic habitats in shallow and deep-water environments. For the first time, we tested this system at two sites in the Southern Adriatic Sea (Mediterranean Sea): the cold-water coral (CWC) habitat in the Bari Canyon and the Coralligenous habitat off Brindisi. We created a spectral library for each site, considering the different substrates and the main OOI reaching, where possible, the lower taxonomic rank. We applied the spectral angle mapper (SAM) supervised classification to map the areal extent of the Coralligenous and to recognize the major CWC habitat-formers. Despite some technical problems, the first results demonstrate the suitability of the UHI camera for habitat mapping and seabed monitoring, through the achievement of quantifiable and repeatable classifications.

Grasmueck, M., Eberli, G. P., Viggiano, D. A., Correa, T., Rathwell, G., & Luo, J. (2006). Autonomous underwater vehicle (AUV) mapping reveals coral mound distribution, morphology, and oceanography in deep water of the Straits of Florida. *Geophysical Research Letters*, 33(23), https://doi.org/10.1029/2006GL027734.

To make progress in understanding the distribution and genesis of coral mounds in cold and dark water, maps of morphology and oceanographic conditions resolving features at the 1?10 m scale are needed. An autonomous underwater vehicle (AUV) cruising 40 m above the seafloor surveyed a 48 km2 coral mound field in 600-800 m water depth at the base of slope of Great Bahama Bank. The AUV acquired 1?3 meter resolution acoustic backscatter and bathymetry together with current vectors, salinity, and temperature. The multibeam bathymetry resolved more than 200 coral mounds reaching up to 90 m height. Mound morphology is surprisingly diverse and mound distribution follows E-W oriented off-bank ridges. Bottom currents reverse every 6 hours indicating tidal flow decoupled from the north flowing surface current. The AUV data fill the gap between low-resolution surface-based mapping and visual observations on the seafloor, revealing the dynamic environment and spatial relationships of an entire coral mound field.

Guinan, J., Brown, C., Dolan, M. F. J., & Grehan, A. J. (2009). Ecological niche modelling of the distribution of cold-water coral habitat using underwater remote sensing data. *Ecological Informatics*, 4(2), 83-92 https://doi.org/10.1016/j.ecoinf.2009.01.004.

Despite a growing appreciation of the need to protect sensitive deep sea ecosystems such as cold-water corals, efforts to map the extent of their distribution are limited by their remoteness. Here we develop ecological niche models to predict the likely distributions of cold-water corals based on occurrence records and data describing environmental parameters (e.g. seafloor terrain attributes and oceanographic conditions). This study has used bathymetric data derived from ship-borne multibeam swath systems, species occurrence data from remotely operated vehicle video surveys and oceanographic parameters from hydrodynamic models to predict coral locations in regions where there is a paucity of direct observations. Predictions of the locations of the scleractinian coral, Lophelia pertusa are based primarily upon ecological niche modelling using a genetic algorithm. Its accuracy has been quantified at local (~25 km2) and regional scales (~4000 km2) along the Irish continental slope using a variety of error assessment techniques and a comparison with another ecological niche modelling technique. With appropriate choices of parameters and scales of analyses, ecological niche modelling has been effective in predicting the distributions of species at local and regional scales. Refinements of this approach have the potential to be particularly useful for ocean management given the need to manage areas of sensitive habitat where survey data are often limited.

Hovland, M., Jensen, S., & Indreiten, T. (2012). Unit pockmarks associated with Lophelia coral reefs off mid-Norway: more evidence of control by 'fertilizing' bottom currents. *Geo-Marine Letters*, 32(5), 545-554 https://doi.org/10.1007/s00367-012-0284-0.

High-resolution topographic mapping of Norwegian deep-water Lophelia coral reefs and their immediate surrounding seafloor has disclosed striking associations with small (<5 m diameter) 'unit' pockmarks. A total of four study areas with Lophelia reefs and unit pockmarks are here described and discussed. At the large Fauna reef, which spans 500 m in length and 100 m in width (25 m in height), there is a field of 184 unit pockmarks occurring on its suspected upstream side. Three other, intermediate-sized Morvin reefs are associated with small fields of unit pockmarks situated upstream of live Lophelia colonies. For two of the latter locations, published data exist for geochemical and microbial analyses of sediment and water samples. Results indicate that these unit pockmarks are sources of light dissolved hydrocarbons for the local water mass, together with nutrient-rich pore waters. It is suggested that the 'fertilized' seawater flows with the prevailing bottom current and feeds directly into the live portion of the Lophelia reefs. With an estimated growth rate of ~1 cm per year for the Morvin Lophelia corals, it would take between 1,000 and 2,000 years for the reefs to colonize the closest unit pockmarks, currently occurring 10–20 m from their leading (live) edges.

Howell, K. L., Holt, R., Endrino, I. P., & Stewart, H. (2011). When the species is also a habitat: Comparing the predictively modelled distributions of Lophelia pertusa and the reef habitat it forms. *Biological Conservation*, 144(11), 2656-2665 https://doi.org/10.1016/j.biocon.2011.07.025.

Internationally there is political momentum to establish networks of marine protected areas for the conservation of threatened species and habitats. Practical implementation of such networks requires an understanding of the distribution of these species and habitats. Predictive modelling provides a method by which continuous distribution maps can be produced from limited sample data. This method is particularly useful in the deep sea where a number of biological communities have been identified as vulnerable 'habitats', including Lophelia pertusa reefs. Recent modelling efforts have focused on predicting the distribution of this species. However the species is widely distributed where as reef habitat is not. This study uses Maxent predictive modelling to investigate whether the distribution of the species acts as a suitable proxy for the reef habitat. Models of both species and habitat distribution across Hatton Bank and George Bligh Bank are constructed using multibeam bathymetry, interpreted substrate and geomorphology layers, and derived layers of bathymetric position index (BPI), rugosity, slope and aspect. Species and reef presence records were obtained from video observations. For both models performance is fair to excellent assessed using AUC and additional threshold dependant metrics. 7.17% of the study area is predicted as highly suitable for the species presence while only 0.56% is suitable for reef presence, using the sensitivity–specificity sum maximisation approach to determine the appropriate threshold. Substrate is the most important variable in the both models followed by geomorphology in the RD model and fine scale BPI in the SD model. The difference in the distributions of reef and species suggest that mapping efforts should focus on the habitat rather than the species at fine (100m) scales.

Huvenne, V. A. I., Tyler, P. A., Masson, D. G., Fisher, E. H., Hauton, C., Hühnerbach, V., . . . Wolff, G. A. (2011). A Picture on the Wall: Innovative Mapping Reveals Cold-Water Coral Refuge in Submarine Canyon. *PLOS ONE*, 6(12), e28755 https://doi.org/10.1371/journal.pone.0028755.

Cold-water corals are azooxanthellate species found throughout the ocean at water depths down to 5000 m. They occur in patches, reefs or large mound structures up to 380 m high, and as ecosystem engineers create important habitats for a diverse fauna. However, the majority of these habitats are now within reach of deep-sea bottom trawling. Many have been severely damaged or are under threat, despite recent protection initiatives. Here we present a cold-water coral habitat type that so far has been overlooked – quite literally – and that has received minimal impact from human activities. Vertical and overhanging cliffs in deep-sea canyons, revealed using an innovative approach to marine habitat mapping, are shown to provide the perfect substratum for extensive cold-water coral-based communities. Typical canyon-related processes, including locally enhanced internal tides and focussed downslope organic carbon transport, provide favourable environmental conditions (current regime, food input) to sustain the communities, even outside the optimal depth and density envelopes reported elsewhere in the NE Atlantic. Our findings show that deep-sea canyons can form natural refuges for faunal communities sensitive to anthropogenic disturbance, and have the potential to fulfil the crucial role of larval sources for the recolonisation of damaged sites elsewhere on the margin.

Price, D. M., Robert, K., Callaway, A., Lo lacono, C., Hall, R. A., & Huvenne, V. A. I. (2019). Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. *Coral Reefs*, https://doi.org/10.1007/s00338-019-01827-3.

Fine-scale structural complexity created by reef-building coral in shallow-water environments is influential on biodiversity, species assemblage and functional trait expression. Cold-water coral reefs are also hotspots of biodiversity, often attributed to the hard surface and structural complexity provided by the coral. However, that complexity has seldom been quantified on a centimetric scale in cold-water coral reefs, unlike their shallow-water counterparts, and has therefore never been linked in a similar way to the reef inhabitant community. Structure from motion techniques which create high-resolution 3D models of habitats from sequences of photographs is being increasingly utilised, in tandem with 3D spatial analysis to create useful 3D metrics, such as rugosity. Here, we demonstrate the use of ROV video transect data for 3D reconstructions of cold-water coral reefs at depths of nearly 1000 m in the Explorer Canyon, a tributary of Whittard Canyon, NE Atlantic. We constructed 40 3D models of approximately 25-m-length video transects using Agisoft Photoscan software, resulting in sub-centimetre resolution reconstructions. Digital elevation models were utilised to derive rugosity metrics, and orthomosaics were used for coral coverage assessment. We found rugosity values comparable to shallow-water tropical coral reef rugosity. Reef and nearby non-reef communities differed in assemblage composition, which was driven by depth and rugosity. Species richness, epifauna abundance and fish abundance increased with structural complexity, being attributed to an increase in niches, food, shelter and alteration of physical water movement. Biodiversity plateaued at higher rugosity, illustrating the establishment of a specific reef community supported by more than 30% coral cover. The proportion of dead coral to live coral had limited influence on the community structure; instead, within-reef patterns were explained by depth and rugosity, though our results were confounded to a certain extent by multi-collinearity. Fine-scale structural complexity appeared to be integral to local-scale ecological patterns in cold-water coral reef communities.

Purser, A., Bergmann, M., Lundälv, T., Ontrup, J., & Nattkemper, T. W. (2009). Use of machine-learning algorithms for the automated detection of cold-water coral habitats: a pilot study. *Marine Ecology Progress Series*, 397, 241-251 https://doi.org/10.3354/meps08154.

Cold-water coral reefs are recognised as important biodiversity hotspots on the continental margin. The location of terrain features likely to be associated with living reef has been made easier by recent developments in acoustic sensing technology. For accurate assessment and fine-scale mapping of these newly identified coral habitats, analysis of video data is still required. In the present study we explore the potential of manual and automatic abundance estimation of cold-water corals and sponges from still image frames extracted from video footage from Tisler Reef (Skagerrak, Norway). The results and processing times from 3 standard visual assessment methods (15-point quadrat, 100-point quadrat and frame mapping) are compared with those produced by a new computer vision system. This system uses machine-learning algorithms to detect species within frames automatically. Cold-water coral density estimates obtained from the automated method were similar to those gained by the other methods. The automated method slightly underestimated (by 10 to 20%) coral coverage in frames which lacked a uniform seabed illumination. However, it did much better in the detection of small live coral fragments than the 15-point method. For assessing sponge coverage, the automated system did not perform as satisfactorily. It mistook a percentage of the seabed for sponge (0.1 to 2% of most frames) and underestimated sponge coverage in frames that contained many sponges. Results indicate that the machine-learning approach is appropriate for estimating live cold-water coral density, but further work is required before the system can be applied to sponges within the reef environment.

Reed, J. K., Shepard, A. N., Koenig, C. C., Scanlon, K. M., & Gilmore, R. G. (2005). Mapping, habitat characterization, and fish surveys of the deep-water Oculina coral reef Marine Protected Area: a review of historical and current research. In A. Freiwald & J. M. Roberts (Eds.), *Cold-Water Corals and Ecosystems* (pp. 443-465). Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/3-540-27673-4_22

Deep-water Oculina coral reefs, which are similar in structure and development to deep-water Lophelia reefs, stretch 167 km (90 nm) at depths of 60–100 m along the eastern Florida shelf of the United States. These consist of numerous pinnacles and ridges, 3–35 m in height, that are capped with thickets of living and dead coral, Oculina varicosa. Extensive areas of dead Oculina rubble are due in part to human impacts (e.g., fish and shrimp trawling, scallop dredging, anchoring, bottom longlines, and depth charges) but also may be due in part to natural processes such as bioerosion, disease, or global warming. In the 1970s, the reefs were teeming with fish. By the early 1990s, both commercial and recreational fisheries had taken a toll on the reefs, especially on the coral habitat and populations of grouper and snapper. In 1984, 315 km2 (92 nm2) was designated the Oculina Habitat of Particular Concern (OHAPC), prohibiting trawling, dredging, bottom longlines and anchoring, and establishing the first deep-sea coral marine protected area in the world. In 2000, the Oculina Marine Protected Area (MPA) was expanded to 1029 km2 (300 nm2). Despite these protective measures, manned submersible and ROV observations in the Oculina MPA between 1995 and 2003 suggest that portions of the coral habitat have been reduced to rubble since the 1970s, grouper spawning aggregations may be absent, and illegal trawling continues. This paper is a review of the results of the mapping, habitat characterization, and fish surveys from the early historical studies (1960–1980s) to the more recent surveys (1995–2003).

Rengstorf, A. M., Grehan, A., Yesson, C., & Brown, C. (2012). Towards High-Resolution Habitat Suitability Modeling of Vulnerable Marine Ecosystems in the Deep-Sea: Resolving Terrain Attribute Dependencies. *Marine Geodesy*, 35(4), 343-361 https://doi.org/10.1080/01490419.2012.699020.

Recent habitat suitability models used to predict the occurrence of vulnerable marine species, particularly framework building cold-water corals, have identified terrain attributes such as slope and bathymetric position index as important predictive parameters. Due to their scale-dependent nature, a realistic representation of terrain attributes is crucial for the development of reliable habitat suitability models. In this paper, three known coral areas and a noncoral control area off the west coast of Ireland were chosen to assess quantitative and distributional differences between terrain attributes derived from bathymetry grids of varying resolution and information content. Correlation analysis identified consistent changes of terrain attributes as grain size was altered. Response characteristics and dimensions depended on terrain attribute types and the dominant morphological length-scales within the study areas. The subsequent effect on habitat suitability maps was demonstrated by preliminary models generated at different grain sizes. This study demonstrates that high resolution habitat suitability models based on terrain parameters derived from multibeam generated bathymetry are required to detect many of the topographical features found in Irish waters that are associated with coral. This has implications for marine spatial planning in the deep sea. Supplemental materials are available for this article. Go to the publisher's online edition of Marine Geodesy to view the free supplemental file.

Rengstorf, A. M., Yesson, C., Brown, C., & Grehan, A. J. (2013). High-resolution habitat suitability modelling can improve conservation of vulnerable marine ecosystems in the deep sea. *Journal of Biogeography*, 40(9), 1702-1714 https://doi.org/10.1111/jbi.12123.

Aim The distribution of vulnerable marine ecosystems in the deep sea is poorly understood. This has led to the emergence of modelling methods to predict the occurrence of suitable habitat for conservation planning in data-sparse areas. Recent global analyses for cold-water corals predict a high probability of occurrence along the slopes of continental margins, offshore banks and seamounts in the north-eastern Atlantic, but tend to overestimate the extent of the habitat and do not provide the detail needed for finer-scale assessments and protected area planning. Using Lophelia pertusa reefs as an example, this study integrates multibeam bathymetry with a wide range of environmental data to produce a regional high-resolution habitat suitability map relevant for marine spatial planning. Location Irish continental margin (extended continental shelf claim). Methods Maximum entropy modelling was used to predict L. pertusa reef distribution at a spatial resolution of 0.002°. Coral occurrences were assembled from public databases, publications and video footage, and filtered for quality. Environmental predictor variables were produced by re-sampling of global oceanographic data sets and a regional ocean circulation model. Multi-scale terrain parameters were computed from multibeam bathymetry. Results Suitable habitat was predicted on mound features and in canyon areas along a narrow band following the slopes of the Irish continental margin, the Rockall Bank and the Porcupine Bank. Standard deviation of the seabed slope (54%), temperature (28%) and bottom shear stress (9%) were the most important variables to predict coral distribution. Main conclusions This is the first regional coral habitat suitability modelling study to incorporate full coverage multibeam bathymetry in the deep sea. The use of high-resolution environmental data and quality-controlled distribution data significantly reduces habitat overestimation demonstrated by global-scale analyses and produces detailed maps to support marine protected area network design. The strong response of the corals to local-scale terrain variability highlights the need to protect the seabed from anthropogenic impacts that may reduce its complexity, such as bottom trawling.

Roberts, J. M., Brown, C. J., Long, D., & Bates, C. R. (2005). Acoustic mapping using a multibeam echosounder reveals cold-water coral reefs and surrounding habitats. *Coral Reefs*, 24(4), 654-669 https://doi.org/10.1007/s00338-005-0049-6.

Multibeam surveys were carried out in four areas to the west of Scotland where the coral Lophelia pertusa had previously been recorded. Distinctive seabed mounds were found in one area; video images from the mounds showed coral reef formation, and grab samples recovered L. pertusa reef framework and rubble. Skeleton samples were dated to 3,800 years BP. Grab samples contained 123 species of fauna. The reef structures, termed the Mingulay Reef Complex, were identified as topographic mound-like structures from the bathymetric data and were also visible on the backscatter images. The location of the reefs coincides with Atlantic bottom waters, close to a primary productivity centre and mixing zone, in an area where currents are likely to be accelerated by rocky seafloor ridges. This study shows that multibeam echosounders are powerful tools to locate and map deep-water coral reefs irrespective of water depth.

Roberts, J. M., Davies, A. J., Henry, L. A., Dodds, L. A., Duineveld, G. C. A., Lavaleye, M. S. S., . . . van Haren, H. (2009). Mingulay reef complex: an interdisciplinary study of cold-water coral habitat, hydrography and biodiversity. *Marine Ecology Progress Series*, 397, 139-151 https://doi.org/10.3354/meps08112.

The Mingulay reef complex in the Sea of the Hebrides west of Scotland was first mapped in 2003 with a further survey in 2006 revealing previously unknown live coral reef areas at 120 to 190 m depth. Habitat mapping confirmed that distinctive mounded bathymetry was formed by reefs of Lophelia pertusa with surficial coral debris dating to almost 4000 yr. Benthic lander and mooring deployments revealed 2 dominant food supply mechanisms to the reefs: a regular rapid downwelling of surface water delivering pulses of warm fluorescent water, and periodic advection of high turbidity bottom waters. Closed chamber respirometry studies suggest that L. pertusa responds to seawater warming, such as that seen during the rapid downwelling events, with increases in metabolic rate. Lipid biomarker analysis implies that corals at Mingulay feed predominantly on herbivorous calanoid copepods. Integrating geophysical and hydrographical survey data allowed us to quantify the roles of these environmental factors in controlling biodiversity of attached epifaunal species across the reefs. Longitudinal structuring of these communities is striking: species richness (α) and turnover (β) change significantly west to east, with variation in community composition largely explained by bathymetric variables that are spatially structured on the reef complex. Vibro-cores through the reef mounds show abundant coral debris with significant hiatuses. High resolution side-scan sonar revealed trawl marks in areas south of the coral reefs where vessel monitoring system data showed the highest density of local fishing activity. The interdisciplinary approach in this study allowed us to record the food supply and hydrographic environment experienced by L. pertusa and determine how it may be ecophysiologically adapted to these conditions. Improved basic understanding of cold-water coral biology and biodiversity alongside efforts to map and date these long-lived habitats are vital to development of future conservation policies.

Savini, A., Vertino, A., Marchese, F., Beuck, L., & Freiwald, A. (2014). Mapping Cold-Water Coral Habitats at Different Scales within the Northern Ionian Sea (Central Mediterranean): An Assessment of Coral Coverage and Associated Vulnerability. *PLOS ONE*, 9(1), e87108 https://doi.org/10.1371/journal.pone.0087108.

In this study, we mapped the distribution of Cold-Water Coral (CWC) habitats on the northern Ionian Margin (Mediterranean Sea), with an emphasis on assessing coral coverage at various spatial scales over an area of 2,000 km2 between 120 and 1,400 m of water depth. Our work made use of a set of data obtained from ship-based research surveys. Multi-scale seafloor mapping data, video inspections, and previous results from sediment samples were integrated and analyzed using Geographic Information System (GIS)-based tools. Results obtained from the application of spatial and textural analytical techniques to acoustic meso-scale maps (i.e. a Digital Terrain Model (DTM) of the seafloor at a 40 m grid cell size and associated terrain parameters) and large-scale maps (i.e. Side-Scan Sonar (SSS) mosaics of 1 m in resolution ground-truthed using underwater video observations) were integrated and revealed that, at the meso-scale level, the main morphological pattern (i.e. the aggregation of mound-like features) associated with CWC habitat occurrences was widespread over a total area of 600 km2. Single coral mounds were isolated from the DTM and represented the geomorphic proxies used to model coral distributions within the investigated area. Coral mounds spanned a total area of 68 km2 where different coral facies (characterized using video analyses and mapped on SSS mosaics) represent the dominant macro-habitat. We also mapped and classified anthropogenic threats that were identifiable within the examined videos, and, here, discuss their relationship to the mapped distribution of coral habitats and mounds. The combined results (from multi-scale habitat mapping and observations of the distribution of anthropogenic threats) provide the first quantitative assessment of CWC coverage for a Mediterranean province and document the relevant role of seafloor geomorphology in influencing habitat vulnerability to different types of human pressures.

Somoza, L., Ercilla, G., Urgorri, V., León, R., Medialdea, T., Paredes, M., . . . Nombela, M. A. (2014). Detection and mapping of cold-water coral mounds and living Lophelia reefs in the Galicia Bank, Atlantic NW Iberia margin. *Marine Geology*, 349, 73-90 https://doi.org/10.1016/j.margeo.2013.12.017.

We report, for first time, the occurrence of cold-water coral mounds and large number of living Lophelia reefs along the Galicia Bank (Atlantic NW Iberian margin). Detection and mapping of living coral reefs and mounds have been carried out by means of multibeam bathymetry, backscatter images, ultra-high resolution and high-resolution multichannel seismic reflection data and sampling. In addition, profiling CTDs have been made to characterise environmental conditions as temperature, salinity and dissolved oxygen contents of the coral sites. Based on these dataset, two main provinces of cold-water coral mounds and reefs have been identified in the Galicia Bank at water depths between 620 and 1125m. The Breogham Mound Province along the western flank of the Galicia Bank shows a sequence of well-developed mounds composed of: (1) Stepped semi-buried elongated mounds, the tallest mounds with heights up 70m and widths of 450m lined up in along-slope trending ridges and intercalated with upslope migrating sediment drifts at water depths from 1125 to 826m; (2) Single and composite seabed mounds show heights of 10–12m and average widths of 100m at 825 and 780m water depths and (3) Lophelia reefs forming mini-mounds 2–4m high and 80–100m width growing on a flat erosional surface at the summit of the bank at 780–750m water depths. Otherwise, the Castelao Mound Province at the eastern flank of the bank is mainly constituted by cluster of mini-mounds hosting living Lophelia pertusa and Madrepora oculata reefs. These living reefs are detected based on ultra-high resolutions parametric echosounders as mini-mounds with an acoustically transparent interior. Otherwise, semi-buried and exposed mounds are mapped with a combination of multibeam and backscatter images identified by their high strength values and seabed expression. We conclude that the initiation, growth and distribution of cold-water coral mounds on the Galicia Bank have been controlled by the following environmental forcing factors: (i) water masses with a potential density resulted of the turbulent boundary between the Mediterranean Outflow and the intermediate Atlantic water masses which allowed the transport of coral larvae along the NE Atlantic margins (ii) the formation of a hard substrate, possibly related to subsurface fluid flow, necessary for the initial settle of coral larvae and (iii) the turbulences created by the Mediterranean flow impinging the topography of the bank creating suitable currents that favour intrusion of the nutrient afflux from the Atlantic mass waters to deep waters allowing to coral colonies to growth.

Trotter, J. A., Pattiaratchi, C., Montagna, P., Taviani, M., Falter, J., Thresher, R., . . . McCulloch, M. T. (2019). First ROV Exploration of the Perth Canyon: Canyon Setting, Faunal Observations, and Anthropogenic Impacts. *Frontiers in Marine Science*, 6, 24 https://doi.org/10.3389/fmars.2019.00173.

This study represents the first ROV-based exploration of the Perth Canyon, a prominent submarine valley system in the southeast Indian Ocean offshore Fremantle (Perth), Western Australia. This multi-disciplinary study characterizes the canyon topography, hydrography, anthropogenic impacts, and provides a general overview of the fauna and habitats encountered during the cruise. ROV surveys and sample collections, with a specific focus on deep-sea corals, were conducted at six sites extending from the head to the mouth of the canyon. Multi-beam maps of the canyon topography show near vertical cliff walls, scarps, and broad terraces. Biostratigraphic analyses of the canyon lithologies indicate Late Paleocene to Late Oligocene depositional ages within upper bathyal depths (200-700 m). The video footage has revealed a quiescent 'fossil canyon' system with sporadic, localized concentrations of mega- and macrobenthos (similar to 680-1,800 m), which include corals, sponges, molluscs, echinoderms, crustaceans, brachiopods, and worms, as well as plankton and nekton (fish species). Solitary (Desmophyllum dianthus, Caryophyllia sp., Vaughanella sp., and Polymyces sp.) and colonial (Solenosmilia variabilis) scleractinians were sporadically distributed along the walls and under overhangs within the canyon valleys and along its rim. Gorgonian, bamboo, and proteinaceous corals were present, with live Corallium often hosting a diverse community of organisms. Extensive coral graveyards, discovered at two disparate sites between similar to 690-720 m and 1,560-1,790 m, comprise colonial (S. variabilis) and solitary (D. dianthus) scleractinians that flourished during the last ice age (similar to 18 ka to 33 ka BP). ROV sampling (674-1,815 m) spanned intermediate (Antarctic Intermediate Water) and deep waters (Upper Circumpolar Deep Water) with temperatures from similar to 2.5 to 6 degrees C.

Seawater CTD profiles of these waters show consistent physical and chemical conditions at equivalent depths between dive sites. Their carbonate chemistry indicate supersaturation (Omega(calcite) similar to 1.3-2.2) with respect to calcite, but mild saturation to undersaturation (Omega(aragonite) similar to 0.8-1.4) of aragonite; notably some scleractinians were found living below the aragonite saturation horizon (similar to 1,000 m). Seawater delta C-13 and nuclear bomb produced Delta C-14 compositions decrease in the upper canyon waters by up to similar to 0.8 parts per thousand (<800 m) and 95 parts per thousand (<500 m), respectively, relative to measurements taken nearby in 1978, reflecting the ingress of anthropogenic carbon into upper intermediate waters.

Veit, H., Blondel, P., Huvenne, V. A. I., & Freiwald, A. (1996). Habitat mapping on a deep-water coral reef off Norway, with a comparison of visual and computer-assisted sonar imagery interpretation. In B. J. Todd & H. G. Greene (Eds.), *Geological Association of Canada Special Paper, 47* (pp. 287-298). St. Johns, Canada: Geological Association of Canada. http://oceanrep.geomar.de/39030/

The Sula Ridge Reef complex, a large cold-water coral reef structure on the mid-Norwegian shelf built mainly by Lophelia pertusa, was mapped entirely using a high-resolution sidescan sonar. In addition, a dense echosounding grid, underwater vide observations and dives using the manned research submersible Jago, provided precise high-quality ground-truthing, and allowed a detailed interpretation of the reef structure and its surrounding geological features. The result of this visual sidescan sonar interpretation is a facies map that delineates different potential habitats within the coral reef environment, e.g. live coral reef, dead coral structure and sediment-covered coral/rubble, etc. In an attempt to improve this interpretation, computer-assisted image analysis was applied to a representative section of the sonar data to try to reveal patterns 'invisible' to the human eye (using the TexAn software). Texture analysis uses Grey-Level Cooccurrence Matrices (GLCMs) to calculate statistical indices quantifying the distribution of grey levels and their spatial relationship within the image. For example, regions of rough textures (coral mounds) can be distinguished from areas of smooth background sediment or zones of heterogeneous texture resulting from sediment-covered coral debris and dropstones colonized by sponges. The results of the computer-assisted approach were carefully compared with the earlier visual interpretation ro identify the differences and to see where the interpretation could be improved. Overall, it shows that texture analysis is a useful tool to make facies/habitat mapping from sidescan sonar easier and faster, revealing details overlooked during visual interpretation. However, validation of certain details by an experienced interpreter is still necessary, and therefore visual and computer-assisted interpretation should be used as complementary tools.

## Section IV: Restoring Mesophotic and Deep Sea Corals

Boch, C. A., DeVogelaere, A., Burton, E., King, C., Lord, J., Lovera, C., . . . Barry, J. P. (2019). Coral Translocation as a Method to Restore Impacted Deep-Sea Coral Communities. *Frontiers in Marine Science*, 6(540), https://doi.org/10.3389/fmars.2019.00540.

Corals and sponges in rocky deep-sea environments are foundation species postulated to enhance local diversity by increasing biogenic habitat heterogeneity and enriching local carbon cycling. These key groups are highly vulnerable to disturbances (e.g., trawling, mining, and pollution) and are threatened by expansive changes in ocean conditions linked to climate change (acidification, warming, and deoxygenation). Once damaged by trawling or other disturbances, recolonization and regrowth may require centuries or longer, highlighting the need for stewardship of these deep-sea coral and sponge communities (DSCSCs). To this end, the sustainability of DSCSCs may be enhanced not only by protecting existing communities, but also repopulating disturbed areas using active restoration methods. Here, we report one of the first studies to explore methods to restore deep-sea coral populations by translocating coral fragments of multiple coral species. Branches of deep-sea corals were collected by ROV from 800–1300 m depth off central California and propagated into multiple fragments once at the surface. These fragments were then attached to "coral pots" using two different methods and placed in the same habitat to assess their survivorship (n=113 total fragments, n=7 taxa, n=7 deployment groups). Mean survivorship for all translocated coral fragments observed within the first 365 days was ~52%, with the highest mortality occurring in the first 3 months. In addition to an initial temporal sensitivity, survival of coral fragments varied by attachment method and among species. All coral fragments attached to coral pots using zip ties died, while those attached by cement resulted in differential survivorship over time. The latter method resulted in 80–100% fragment survivorship after one year for Corallium sp., Lillipathes sp., and Swiftia kofoidi, 12–50% for the bamboo corals Keratoisis sp. and Isidella tentaculum, and 0–50% for the bubblegum corals Paragorgia arborea and Sibogagorgia cauliflora. These initial results indicate differences in sensitivities to transplanting methods among coral species, but also suggest that repopulation efforts may accelerate the recovery of disturbed DSCSCs.

Bruno, J. F., & Bertness, M. D. (2001). Habitat modification and facilitation in benthic marine communities. In M. D. Bertness, S. D. Gaines, & M. E. Hay (Eds.), *Marine Community Ecology* (pp. 201-218). Sunderland: Sinauer Associates.

In this chapter we argue that the biological generation of habitats and the positive interactions that occur within them are fundamental processes across a wide range of benthic marine environments. Although we recognize that positive interactions play an important role in evolutionary processes such as speciation and extinction, our focus will be on their role in generating patterns that occur on ecological time scales. We begin by attempting to clarify definitions and by discussing semantic controversies related to habitat modification and facilitation. Next, we present a brief historical perspective of studies on this topic and ask why such research is less common than investigations of negative interactions such as predation. We then introduce some conceptual issues and models that make predictions about the conditionalities of facilitation. Some of these models are largely untested, so this section presents possible directions for future research. We conclude by suggesting how ecologists can apply what is known about habitat modification to marine conservation issues.

*Cold-Water Corals and Ecosystems*. (2005). (A. Freiwald & J. M. Roberts Eds.). Berlin, Germany: Springer-Verlag Berlin Heidelberg.

Following the exciting exploration of hot vent and cold seep ecosystems, the rediscovery of cold-water coral ecosystems with high-technology instrumentation is currently another hot topic in multidisciplinary marine research. Conventionally, coral reefs are regarded as restricted to warm and well-illuminated tropical seas, not associated with cold and dark waters of higher latitudes. However, ongoing scientific missions have shed light on the global significance of this overlooked ecosystem. Cold-water coral ecosystems are involved in the formation of large seabed structures such as reefs and giant carbonate mounds, and they represent unexploited paleo-environmental archives of earth history. Like their tropical cousins, cold-water coral ecosystems harbour rich species diversity. Despite the great water depths, commercial interests overlap more and more with the coral occurrences. Human activities already impinge directly on cold-water coral reefs causing severe damage to this vulnerable ecosystem. In this volume, the current key institutions involved in cold-water coral research have contributed 62 state-of-the-art articles from geology and oceanography to biology and conservation.

Huvenne, V. A. I., Bett, B. J., Masson, D. G., Le Bas, T. P., & Wheeler, A. J. (2016). Effectiveness of a deep-sea cold-water coral Marine Protected Area, following eight years of fisheries closure. *Biological Conservation*, 200, 60-69 https://doi.org/10.1016/j.biocon.2016.05.030.

Pressure on deep-sea ecosystems continues to increase as anthropogenic activities move into ever deeper waters. To mitigate impacts on vulnerable habitats, various conservation measures exist, such as the designation of Marine Protected Areas (MPAs). So far, however, little evidence is available about their effectiveness. This paper presents a unique follow-up study assessing the status and recovery of a deep-sea fisheries closure and MPA at similar to 1000 m water depth in the NE Atlantic, eight years after designation. The Darwin Mounds cold-water coral ecosystem was discovered in 1998, and closed to all bottom contact fisheries, especially trawling, in 2003. Our repeat survey in 2011 used both high-resolution sidescan sonar data collected by Autonomous Underwater Vehicle (AUV) and video footage from a Remotely Operated Vehicle (ROV) to evaluate recovery. The results demonstrate that (1) protection was successful and fishing impact was largely avoided in the Western Darwin Mounds, which contained similar proportions of live cold-water coral occurrence in 2011 as observed in 1998-2000; however (2) the Eastern Darwin Mounds suffered severe damage pre-closure, and by 2011 showed no coral recolonisation and very little re-growth. These results are further evidence for the low resilience and slow recovery potential of deep-sea ecosystems, and underline once again the importance of the precautionary principle in deep-sea conservation.

Jaap, W. C. (2000). Coral reef restoration. *Ecological Engineering*, 15(3), 345-364 https://doi.org/10.1016/S0925-8574(00)00085-9.

Coral reefs are widely recognized for concentration of biological activity, fisheries and tourism, coastal protection, geological processes, and aesthetic wonder. A principal cause of reef damage in Florida is ships running into reefs. The other major human impact on Florida's reefs is dredging for beach renourishment and channel maintenance. In response to chronic reef damage, federal and state agencies and consultants have developed techniques to restore, as best possible, reefs impacted by human disturbance. These efforts include salvaging sponges and corals, removing loose debris from the reef, rebuilding three-dimensional (3-D) structures onto leveled-scarified reef surfaces, and transplanting sponges and corals back on the cleared reef surfaces. This paper presents an overview of restoration approaches; a discussion on legal and administration to both damage and restoration of these essential fish habitats; a brief review of some case studies; and a discussion of restoration success criteria. Salvage of corals and sponges is critical to the success of any reef restoration effort. If a living surface is allowed to sit on the sand for a few days, that surface will die. Often the grounded vessel will have crushed the reef, excavating sediments and rubble that end up as a berm of material behind the ship's resting position. Dealing with massive amounts of rubble debris is challenging. The options include leaving it in place and stabilizing it with cements; moving it a long way from the site and dumping it in deep water; or reconfiguring it by moving it off reef and building piles where it can do no harm. After the debris is moved off the reef platform, corals and other sessile benthic organisms (salvaged resources) can be transplanted on the damaged area. Monitoring is important to determine the success of the restoration and to look for ways to improve future projects. Sampling sites for monitoring should include restored areas plus a reference area (undamaged habitat of a relatively similar nature that is in close proximity) for comparison. The following questions should be addressed for any reef restoration project: are the transplanted organisms still secured to the reef? Is the vitality (color, disease, algal competition) of the transplanted organisms equivalent to the organisms in the reference sites? Is recruitment (settlement of juvenile organisms) similar in the restored areas and the reference areas? Monitoring should be tied to decision making so corrections can be made.

Macreadie, P. I., Fowler, A. M., & Booth, D. J. (2011). Rigs-to-reefs: will the deep sea benefit from artificial habitat? *Frontiers in Ecology and the Environment*, 9(8), 455-461 https://doi.org/10.1890/100112.

As a peak in the global number of offshore oil rigs requiring decommissioning approaches, there is growing pressure for the implementation of a "rigs-to-reefs" program in the deep sea, whereby obsolete rigs are converted into artificial reefs. Such decommissioned rigs could enhance biological productivity, improve ecological connectivity, and facilitate conservation/restoration of deep-sea benthos (eg cold-water corals) by restricting access to fishing trawlers. Preliminary evidence indicates that decommissioned rigs in shallower waters can also help rebuild declining fish stocks. Conversely, potential negative impacts include physical damage to existing benthic habitats within the "drop zone", undesired changes in marine food webs, facilitation of the spread of invasive species, and release of contaminants as rigs corrode. We discuss key areas for future research and suggest alternatives to offset or minimize negative impacts. Overall, a rigs-to-reefs program may be a valid option for deep-sea benthic conservation.

Maier, C. (2008). High recovery potential of the cold-water coral Lophelia pertusa. *Coral Reefs*, 27(4), 821-821 https://doi.org/10.1007/s00338-008-0398-z.

Lophelia pertusa (Linnaeus 1758) is one of the few coldwater coral species capable of constructing reef-like frameworks, which are the basis for cold-water coral bioherms (recently reviewed by Roberts et al. 2006). Live L. pertusa colonies were collected from cold-water coral bioherms at Rockall Bank, Mingulay, and Skagerrak, eastern Atlantic Ocean. Due to sampling procedures some of the corallites were severely fragmented (Fig. 1). Fragments were maintained in aquaria and inspection over several months revealed an astonishing recovery potential.

Rinkevich, B. (2014). Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? *Current Opinion in Environmental Sustainability*, 7, 28-36 https://doi.org/10.1016/j.cosust.2013.11.018.

The coral reefs worldwide are exposed to multiple anthropogenic threats and persisting global change impacts, causing continuous degradation, also calling for the development of novel restoration methodologies. Of the most promising emerging approaches, deriving its rationale from silviculture, is the low-cost ‘gardening concept’, guided by a two-step restoration operation: (a) mid-water nursery phase, where coral-nubbins are farmed and (b) transplantation of nursery-farmed colonies. Tested worldwide, at least 86 coral-species and over 100000 colonies were successfully farmed in different archetype nurseries, and several novel transplantation methodologies were developed. A number of unanticipated emerged outcomes were the immediate establishment of coral infaunal biodiversity in nurseries, the development of nurseries into ‘larval dispersion hubs’ and the enhanced reproduction of transplanted coral colonies. Altogether, and in addition to envisaged results (e.g., high survivorship, fast coral growth), results attest that the gardening-toolbox could serve as a ubiquitous ecological engineering platform for restoration on a global scale.

Roberts, J. M., Wheeler, A. J., Freiwald, A., & Cairns, S. D. (2009). Impacts and Conservation. In *Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats*: Cambridge University Press. https://www.cambridge.org/us/academic/subjects/life-sciences/ecology-and-conservation/cold-water-corals-biology-and-geology-deep-sea-coral-habitats?format=AR&isbn=9780511537233

The ecosystems at the bottom of the deep sea are out of sight beneath the impenetrable grey of the waves. Any marine ecosystem, especially those of the deep sea, are remote from people’s daily experience and may therefore be of little general interest. One of the greatest challenges facing deep-sea conservation is raising awareness of the hidden diversity and vulnerability of this, the largest and least-known environment on Earth. What is out of sight can all too often also be out of mind, but public perception of the threats facing some marine ecosystems, such as shallow-water tropical coral reefs, is relatively high – they are highly visual and popular holiday destinations for many people. But although out of sight and sometimes thousands of miles from the nearest land, cold-water corals and other deep-sea benthic ecosystems have been affected by human activity. Many, if not most, marine ecosystems have been affected by fishing and researchers regularly report deep-water trawl damage to cold-water coral and sponge habitats. Here we will describe present-day impacts, consider emerging threats and review what can and is being done to ensure their conservation.

Strömberg, S. M., Lundälv, T., & Goreau, T. J. (2010). Suitability of mineral accretion as a rehabilitation method for cold-water coral reefs. *Journal of Experimental Marine Biology and Ecology*, 395(1), 153-161 https://doi.org/10.1016/j.jembe.2010.08.028.

Extensive areas of the cold-water scleractinian Lophelia pertusa have been damaged due to the impact of bottom-trawling and natural recovery is slow or absent. Here we evaluate a method for coral reef rehabilitation intended to enhance coral transplant survival and growth, i.e. mineral accretion by electrolysis in seawater. Electrolysis in seawater produces a semi-natural substrate in the form of aragonite ($CaCO_3$). The method has been used in coral reef rehabilitation programmes in tropical coral habitats but has so far not been tested in temperate deep-water habitats. A controlled laboratory experiment was performed to test the effect of the substrate per se and different levels of applied current densities (0.00–2.19Am−2), including galvanic elements (Fe|Zn), on coral fragments attached to the cathodes. The studied responses were; growth rate, budding frequency, mortality, and general health status (degree of polyp activity). We found that the budding frequency differed significantly between treatments, with higher frequencies in low current density treatments. Significant differences were also found in the frequency distribution of calices displaying a growth of ≥2mmyr−1, with higher frequencies in the lowest applied current density (LI), controls, and galvanic elements. Growth rates were slightly higher in LI, although non-significant. Zero mortality was observed in the control group as well as in LI. The degree of polyp activity was not affected by the treatments. These results are in part congruent with earlier studies and the method is found suitable for L. pertusa. The positive effects were mainly restricted to the lowest applied current density treatment (0.06Am−2). The optimal current density level is hereby found to be considerably lower than levels used in previous studies and provide new guidelines for what levels to use in rehabilitation programmes with this method.

Van Dover, C. L., Aronson, J., Pendleton, L., Smith, S., Arnaud-Haond, S., Moreno-Mateos, D., . . . Warner, R. (2014). Ecological restoration in the deep sea: Desiderata. *Marine Policy*, 44, 98-106 https://doi.org/10.1016/j.marpol.2013.07.006.

An era of expanding deep-ocean industrialization is before us, with policy makers establishing governance frameworks for sustainable management of deep-sea resources while scientists learn more about the ecological structure and functioning of the largest biome on the planet. Missing from discussion of the stewardship of the deep ocean is ecological restoration. If existing activities in the deep sea continue or are expanded and new deep-ocean industries are developed, there is need to consider what is required to minimize or repair resulting damages to the deep-sea environment. In addition, thought should be given as to how any past damage can be rectified. This paper develops the discourse on deep-sea restoration and offers guidance on planning and implementing ecological restoration projects for deep-sea ecosystems that are already, or are at threat of becoming, degraded, damaged or destroyed. Two deep-sea restoration case studies or scenarios are described (deep-sea stony corals on the Darwin Mounds off the west coast of Scotland, deep-sea hydrothermal vents in Manus Basin, Papua New Guinea) and are contrasted with on-going saltmarsh restoration in San Francisco Bay. For these case studies, a set of socio-economic, ecological, and technological decision parameters that might favor (or not) their restoration are examined. Costs for hypothetical restoration scenarios in the deep sea are estimated and first indications suggest they may be two to three orders of magnitude greater per hectare than costs for restoration efforts in shallow-water marine systems.