# The first decade of scientific insights from the Deepwater Horizon oil release

Elizabeth B. Kujawinski[1]✉, Christopher M. Reddy[1], Ryan P. Rodgers[2], J. Cameron Thrash[3], David L. Valentine[4] and Helen K. White[5]

Abstract | The 2010 Deepwater Horizon disaster remains the largest single accidental release of oil and gas into the ocean. During the 87-day release, scientists used oceanographic tools to collect wellhead oil and gas samples, interrogate microbial community shifts and activities, and track the chemical composition of dissolved oil in the ocean's interior. In the decade since the disaster, field and laboratory investigations studied the physics and chemistry of irrupted oil and gas at high pressure and low temperature, the role of chemical dispersants in oil composition and microbial hydrocarbon degradation, and the impact of combined oil, gas and dispersants on the flora and fauna of coastal and deep-sea environments. The multi-faceted, multidisciplinary scientific response to the released oil, gas and dispersants culminated in a better understanding of the environmental factors that influence the short-term and long-term fate and transport of oil in marine settings. In this Review, we summarize the unique aspects of the Deepwater Horizon release and highlight the advances in oil chemistry and microbiology that resulted from novel applications of emerging technologies. We end with an outlook on the applicability of these findings to possible oil releases in future deep-sea drilling locations and newly-opened high-latitude shipping lanes.

[1]Department of Marine Chemistry & Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, MA, USA.

[2]National High Magnetic Field Laboratory, Florida State University, Tallahassee, FL, USA.

[3]Department of Biological Sciences, University of Southern California, Los Angeles, CA, USA.

[4]Department of Earth Science and Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA, USA.

[5]Departments of Chemistry and Environmental Studies, Haverford College, Haverford, PA, USA.

✉e-mail: ekujawinski@whoi.edu

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The explosion of the Deepwater Horizon (DWH) drilling rig in the northern Gulf of Mexico on 20 April 2010 caused the deaths of 11 crew members and marked the onset of an uncontrolled oil and natural gas release from the damaged Macondo well, located 80 km off the coast of Louisiana in the US Bureau of Ocean Energy Management's Mississippi Canyon lease block 252 (MC-252) at a water depth of 1,500 m (FIG. 1a). The well was finally capped on 15 July 2010 by a team of academic and industrial engineers (FIG. 1b). Over the 87-day period, the uncapped well released $5.3 \times 10^{11}$ g of oil (defined as hydrocarbons with ≥6 carbons that are liquid at 1 atm)[1] and $1.7 \times 10^{11}$ g of natural gas (hydrocarbons with ≤5 carbons that are gases at 1 atm)[1] at high pressure ($1.5 \times 10^4$ kPa) into the overlying water column, leading to extensive dissolution of hydrocarbons in the deep sea[2,3], referred to as the subsurface intrusion. The remainder of the hydrocarbons travelled to the sea surface, where $1.4–2.0 \times 10^{11}$ g of the volatile compounds ($\leq n$-$C_{16}$ compounds) evaporated into the atmosphere within 3–10 h of surfacing[4–6] and $3.3–3.6 \times 10^{11}$ g of the less-volatile compounds ($> n$-$C_{16}$ compounds)[4–6] spread over $11 \pm 5 \times 10^3$ km$^2$ (REF.[7]), reaching a total of $2 \times 10^3$ km of coastline along five Gulf of Mexico states[8] (FIG. 1a). Approximately 2–20% of the total released hydrocarbons were deposited on the sea floor[9], primarily as oil residue. In response to the disaster, $2.9 \times 10^6$ and $4.1 \times 10^6$ l of chemical dispersants were applied at the wellhead and to the sea surface, respectively[10], in efforts to reduce surface oil slicks and sequester oil in the deep sea, more than any other known application in history. In total, the DWH oil release was unprecedented by almost any metric of marine oil discharge disasters, including volume and scale of hydrocarbon release, depth of the discharge, and application of surface and subsurface dispersants.

The DWH disaster posed several scientific and logistical challenges, including where the oil and gas would travel after irruption from the wellhead, whether chemical dispersants could alter the oil and gas fate and transport without significant environmental impact, and how affected ecosystems — from the deep sea to the coastal marshes — would respond to discharged oil and gas and applied dispersants. The unique location (deep sea) and oil-and-gas volume released during this disaster rendered previous models and predictions of oil and gas fate poorly applicable, thus requiring a rapid shift in response planning and execution. Within weeks of the DWH explosion, researchers and responders realized that four

### Key points

- The Deepwater Horizon (DWH) disaster was the largest single accidental release of oil and gas to the ocean. Over 87 days, oil, gas and dispersants impacted 11,000 km$^2$ of ocean surface and 2,000 km of coastline.
- The application of subsurface dispersants was unique to the DWH disaster. Empirical observations, laboratory data and modelling efforts offer conflicting conclusions as to whether dispersants reduced the sea surface expression of released oil.
- The DWH disaster was the first wide-scale environmental application of emerging systems biology tools based on microbial gene analysis. These tools provided unprecedented insights into the identity, structure, growth dynamics, succession and overall response of microbial communities to oil, gas and dispersant release to marine ecosystems.
- Advanced analytical chemistry technologies provided novel information regarding source oil composition, biodegradation, photochemical oxidation, water-column processes, accurate measurements of biomarkers and identification of oil weathering products.
- The Gulf of Mexico coastline and deep ocean were contaminated with oil, gas and dispersants to differing degrees. In many cases, coastal ecosystems recovered as predicted based on previous oil release studies, whereas, in others, the disaster combined with other stressors to deleterious effect. Examination of the disaster's impacts on the deep sea, and its ongoing recovery, continue.
- Insights from the first decade of DWH-related research underscore the need for integrated analytical platforms and data synthesis to understand the complexities of the environmental responses to oil, gas and dispersant release. The spill science community must be ready to work collaboratively across academia, industry and government during possible future oil releases in the deep sea and high latitudes.

**Dispersants**
Chemical mixtures used during oil spill response to break up and decrease the size of oil slicks or oil droplets so that they more easily mix with water.

zones would need to be examined for released oil, gas and dispersants: the subsurface where dissolved oxygen anomalies indicated a large intrusion of hydrocarbons was degraded by oxygen-consuming bacteria[3,11,12]; the surface where oil sheens and emulsions extended over 11,000 km$^2$ (REF. 7); the atmosphere where volatilized oil and gas were rapidly transported away from the crippled oil rig[13]; and the sea floor, where oil might sink due to weathering or ballasting[14,15].

These overarching challenges required observing and sampling the earliest stages of the oil discharge, which is difficult, as such disasters progress more quickly than most research can be mobilized[16]. Furthermore, the challenges could not be addressed using the standard technologies at the time, which were mostly prescribed by the Oil Pollution Act of 1990 (legislated partly in response to the 1989 Exxon Valdez spill) and were obsolete because academic research on oil spills had stagnated. Nevertheless, the scientific community responded quickly to the DWH disaster by altering field plans and, as a result, research expeditions in the Gulf of Mexico were the first to detect[17,18] and map[3,12,19,20] the subsurface intrusions of oil and gas travelling away from the wellhead. Academic and government scientists mobilized tools and techniques repurposed from basic science applications, such as those used when studying natural oil and gas seeps and the biogeochemical cycling of methane and other gases[21–24] (FIG. 2). Oceanographic instrumentation was deployed to track and sample oil and gas flowing from the damaged well[1] and to measure oil droplet sizes[25] and dissolved low-molecular weight components within the subsurface intrusion[19,26]. During the DWH event, additional research expeditions collected surface and deep water to assess microbial community dynamics[3,11], explore chemical transformations in oil and gas components[2] and track the fate of chemical dispersants[27]. Government scientists at the US National Oceanic and Atmospheric Administration (NOAA) mobilized overflights to assess air quality and measure hydrocarbons that had volatilized to the atmosphere[13]. While early analyses of these samples and the follow-up field, laboratory and modelling studies were funded initially by a combination of BP, the US National Science Foundation (NSF; 'RAPID' grants), the US Department of Energy (DOE) and the US NOAA, BP and other responsible parties paid US$19 billion towards post-disaster research and recovery[28], including US$500 M for the Gulf of Mexico Research Initiative (GoMRI). Scientific investigation following the DWH disaster has collectively culminated in over 5,000 publications to date (April 2020, based on Google Scholar search with 'Deepwater Horizon' and 'oil spill'), with research still ongoing. The breadth and diversity of scientific inquiry into the DWH disaster enabled significant advances in oil chemistry and microbiology, and highlighted the need for the integration of complementary datasets to understand the complexity of environmental perturbations.

In this Review, scientific questions raised by and results from the DWH disaster are discussed, with a focus on the chemical and microbiological aspects of the disaster and ongoing recovery. The irruption, dissolution, and microbial degradation of oil and gas in the deep sea, which is inaccessible to typical oil response procedures[3,5,12,19], are detailed. We then explore the previously unpredictable impacts of subsurface dispersant applications on oil composition, the extent of hydrocarbon biodegradation and deep-water ecosystems. Finally, we review environmental factors that led to extensive weathering of the oil and gas over the 87-day duration of the discharge, the broader environmental impacts of the event, and future directions for oil disaster science.

## Subsurface oil, gas and dispersants

During a deep-sea oil well blowout like the DWH disaster, 100 °C hydrocarbon gas and oil irrupts at high pressure into much colder water[1]. Components of the released oil and gas follow different paths from the wellhead, with some rising to the surface, and the remainder forming deep-sea intrusions of oil and gas at 1,100 m water depth due to natural buoyancy[17,19]. Predicting the partitioning of irrupted oil and gas between the subsurface intrusion layer and the sea surface is difficult, as the distance and speed of the transport depends on the physical properties of the surrounding seawater (which were known), the oil-to-gas ratio and flow dynamics at the release point, and oil composition, droplet size, and buoyancy. Existing models of oil droplet size distribution were based on surface water models and lab experiments, and thus did not reflect deep-sea conditions; as a result, in situ observations were needed to constrain the oil's fate. In one example, holographic imaging equipment developed for studying the morphologies and distributions of marine microplankton and mesozooplankton (the Video Plankton Recorder and the Holocam)[29–31] was adapted. Starting in early June (approximately six weeks after the DWH well blowout began), oil droplets and plankton at depth were successfully imaged with this equipment a few kilometres away from the Macondo wellhead[25,31,32], providing oil droplet size distribution data that were previously unattainable and highlighting a technology that can be used in future deep-sea oil releases[28]. However, imaging data did not capture the oil droplet size distribution at the wellhead, so subsequent modelling[33,34] and laboratory[35,36] efforts have focused on understanding the role of oil-to-gas ratio, source geometry conditions and dispersant application on release trajectories and droplet-size distributions.

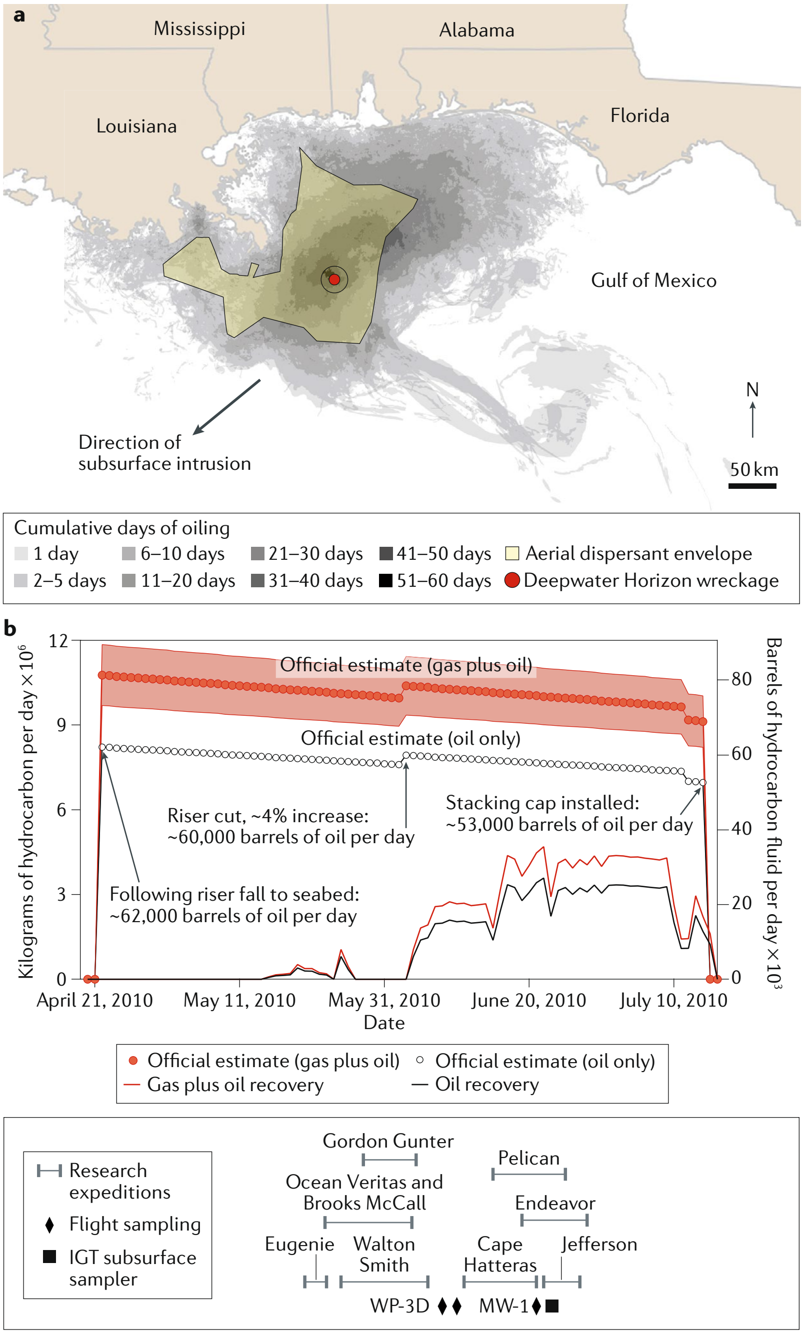

Fig. 1 | **Oil and gas release in the Gulf of Mexico during the Deepwater Horizon disaster. a** | Map of oiled area between April and July 2010 (grey shading) with surface dispersant application (yellow overlay). Research expeditions to assess the extent of the subsurface intrusion occurred between May and July 2010, within the region denoted by the black circle around the Deepwater Horizon wreckage site (red dot). Oiling data were derived from satellite data produced by the National Oceanic and Atmospheric Administration's National Environmental Satellite, Data and Information Service. **b** | The timeline of daily hydrocarbon release from the MC-252 wellhead (according to official estimates), sampling from research vessels (as listed in REFS[5,20]), aerial surveys and the isobaric gas tight (IGT) subsurface sampler between 20 April 2010, and the closure of the wellhead. Data for panel **a** adapted from maps produced using the ERMA GIS tool (www.erma.noaa.gov). Panel **b** adapted with permission from REF.[5], PNAS.

Oil droplets released during the DWH disaster can be categorized into three size categories, each with different buoyancies, but with overlapping chemical compositions[5]. The largest oil droplets (greater than 0.3 mm diameter) exhibited sufficient buoyancy to rise to the ocean surface, with rise times below 4 h[5], transporting a mixture of soluble and insoluble compounds to the sea surface where some volatilized into the atmosphere[13,37] (FIG. 3a). The medium-sized droplets (0.1–0.3 mm) ascended more slowly (rise times below 10 h), and their composition was very sensitive to initial oil composition and release dynamics. For example, moderately soluble hydrocarbons such as toluene, xylene, naphthalene and (methyl)cyclopentane partitioned to the aqueous phase from all droplet sizes as a function of the droplet exposure time and surface area-to-volume ratio, as well as their relative concentration in the source oil[5] (FIG. 3a–c). By contrast, the smallest droplets (smaller than 0.1 mm) and soluble gases (methane, ethane, propane) lacked the buoyancy to rise after being emplaced in deep-sea intrusions, although the degree of hydrocarbon dissolution could not be measured due to challenges in separating oil droplets from the surrounding waters[5]. A substantial fraction of the released oil and gas (by mass) was retained in the deep-sea intrusions because of the relatively high proportion of gases in the DWH irruption (FIG. 3d). However, reducing the sea surface expression of released oil was a high priority during DWH mitigation efforts and thus responders were motivated to disrupt the larger, faster-rising size classes of oil droplets into small droplets that would remain in the deep sea. At the same time, reducing droplet sizes and maximizing dissolution should make oil and gas more accessible to microbial degradation in the absence of any physiological limitation[38].

Chemical dispersants were used by the DWH disaster responders to decrease the size of oil droplets[38]. Dispersants (parenthetical values refer to Corexit 9500, the primary formulation used in the DWH disaster) are a mixture of nonionic surfactants (~30% Tween and Span surfactants), an anionic surfactant (~20% dioctyl sodium sulfosuccinate (DOSS)) and solvent carriers (~50% petroleum distillates)[39]. However, prior to the DWH disaster, dispersants had been applied only to surface oil spills[38] with their use determined by wind speed, wave height and oil age and composition. Dispersants were used on the sea surface during the DWH disaster, but they were also applied directly at the wellhead in the first deep-sea dispersant application. The fate of these added dispersants was a public and scientific concern; after all, $2.9 \times 10^6$ l dispersant were added to the deep sea with unknown consequences. Because dispersants are a complex mixture, specific components had to be analysed separately to ascertain the lability and persistence of the dispersants during and after the disaster.

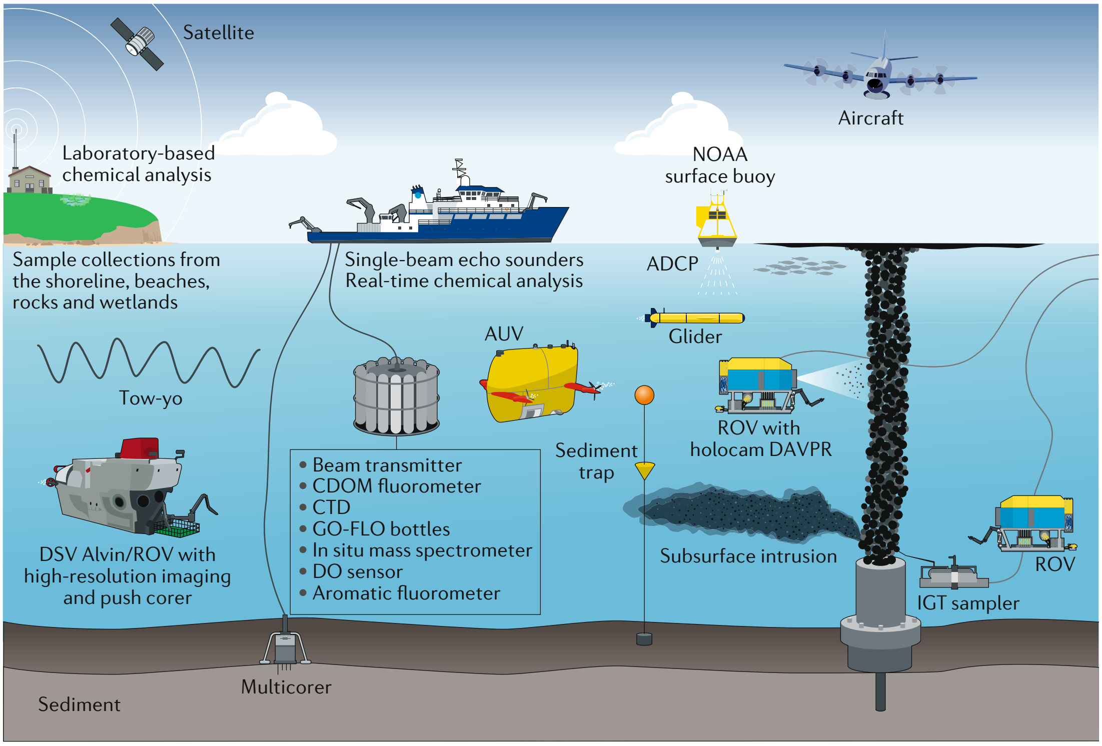

Fig. 2 | **Integration of technologies used in Deepwater Horizon oil spill response.** Numerous oceanographic tools were deployed to assess surface and deep expressions of oil, gas and dispersants between April and July 2010. These included autonomous vehicles, water and sediment sampling equipment, and aerial assets. ADCP, acoustic Doppler current profiler; AUV, autonomous underwater vehicle; CDOM, coloured dissolved organic matter; CTD, conductivity, temperature, depth; DAVPR, digital autonomous video plankton recorder; DO, dissolved oxygen; DSV, deep-submergence vehicle; IGT, isobaric gas-tight; NOAA, National Oceanic and Atmospheric Administration; ROV, remotely operated vehicle. Adapted from REF.[164], CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/).

After the disaster, DOSS was used to track the fate of the deep-sea dispersants because it comprised a large and relatively constant fraction of Corexit and other dispersant formulations and it was amenable to existing analytical protocols. Samples taken during and a few months after the disaster indicated that DOSS persisted in the subsurface intrusion and was not degraded[27], contrary to expectations based on laboratory experiments performed at surface conditions[40]. These data suggest that the chemical dispersants were not degraded appreciably in the deep sea in the aftermath of the DWH disaster. Subsequent laboratory work showed that DOSS was less labile than the solvent carriers in the dispersants under deep-sea conditions[40], and others have found minimal degradation of DOSS at low temperatures[41], further supporting this conclusion. Other surfactant components have been more challenging to detect and quantify due to their isomeric diversity and amphiphilic properties[42], but recent studies have shown that these components were present in the subsurface intrusion layers (typically below 15 µg/l)[43] and are degraded at deep-sea (4 °C) temperatures[44].

Once it appeared that deep-sea dispersants were retained in the subsurface intrusion, the primary question was whether dispersant application had indeed shifted the oil-droplet size distributions as intended. Unfortunately, empirical observations, laboratory data and modelling efforts offer conflicting conclusions as to the efficacy of the dispersants in this regard. Operational tests during the DWH disaster noted oil reduction at the sea surface during an 'on/off' test[45]. Modelling results are equivocal on whether dispersants entrained additional oil and gas into the subsurface intrusion layers, with one group of researchers arguing that they did[4] and another arguing that they did not[33,34]. The inconsistency of the modelling results may be due to the challenges of accurately parameterizing the complex physics of the outflow at the wellhead, including the impacts of initial droplet size distribution, churn flow[46], source pressure, orifice geometry, and dispersant applicator type. Nevertheless, dispersant addition in the deep sea potentially impacted sea surface oil expression, which would fulfill the first motivation of the response teams. Whether dispersants shifted the droplet size distribution or enhanced oil degradation in the subsurface intrusion layer remains a matter of debate.

## Oil, gas and dispersant biodegradation

During and after the DWH disaster, most microbiology research focused on the subsurface intrusion layer because of its novelty. Although some oil biodegradation was observed in the surface waters during the incident[47], Gulf of Mexico surface waters have low concentrations of nutrients that prevented bloom formation and comparatively few data were collected on the microbes responding to oil in surface waters.

Amphiphilic
A chemical compound that has both hydrophilic and hydrophobic properties.

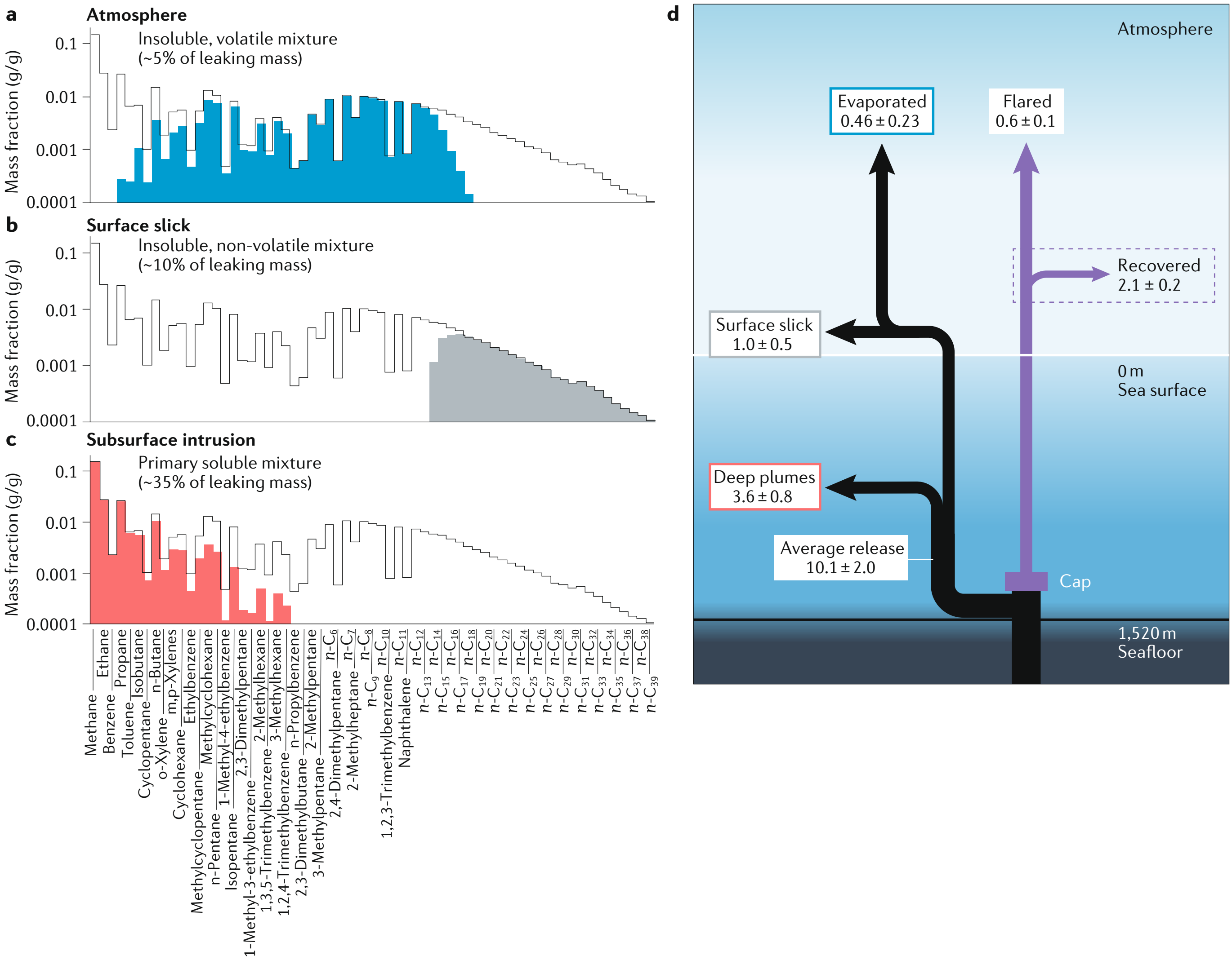

Fig. 3 | **Distribution of Deepwater Horizon hydrocarbons in three primary reservoirs in the Gulf of Mexico.** **a** | Hydrocarbons in the atmosphere. **b** | The ocean surface. **c** | The subsurface intrusion. **d** | During the spill, oil and gas were partitioned among these reservoirs, based on estimates for 10 June 2010, in millions of kilograms per day. A substantial portion of the oil dissolved into the deep ocean, which was unique from previous surface oil discharge accidents. Adapted with permission from REF.[5], PNAS.

The lack of data is in part because microbial degradation was responsible for minor losses of surface oil relative to the natural processes of evaporation and photochemical weathering[48] and the responder oil mitigation efforts of skimming and burning. The limited data indicated an increase in *Cycloclasticus* in the microbial community, with minor contributions from organisms including *Alteromonas*, *Colwellia*, and *Pseudoalteromonas* in the surface slick[49] (FIG. 4). Enrichments showed that *Cycloclasticus* and *Colwellia* were dominant phenanthrene-degraders, whereas *Alteromonas* dominated the naphthalene-degrading community[50,51]. Some of these organisms were observed in pre-DWH studies in surface Gulf waters[52,53].

Unlike in the surface waters, nutrients are present at higher concentrations at depth in the Gulf of Mexico, setting the stage for microbial blooms driven by the entrainment of hydrocarbon substrates defining the subsurface intrusion layers. Microbial degradation was the only option available for oil mitigation in this environment because perpetual darkness prevents photo-oxidation, and meaningful recovery of dilute oil from depth is technically infeasible. The sudden influx of oil, gas, and dispersants enriched a community of hydrocarbon-degrading organisms[11], the composition of which was influenced by the physical forms and chemical composition of the oil-gas-dispersant mixtures. As the hydrocarbon composition in droplets and dissolved phases changed[54], different microbes bloomed[55,56] following the succession pattern of Oceanspirillales, *Colwellia*, *Cycloclasticus*, *Methylophaga* and Methylococcaceae, Flavobacteriaceae and Rhodobacteriaceae[11,55,56] (FIG. 4). This succession was captured in groundbreaking detail through the first effective application of combined systems biology tools to an environmental event, which was previously prohibitively expensive and computationally unfeasible[57]. The use of metagenomics, metatranscriptomics, and other molecular biology tools on hundreds of samples offered

Photo-oxidation
A chemical modification reaction resulting from the absorption of light in the presence of oxygen.

Metagenomics
The study of the genes (DNA) present in a mixed community, which provides an assessment of metabolic potential in that community.

Metatranscriptomics
The study of the transcripts (RNA) present in a community, which provides a snapshot of the genes being expressed at the time of sampling.

Stable isotope probing (SIP). A technique to trace the microbial consumption of a substrate through the examination of the stable isotopic composition of the substrate and the resulting biomass of the consumer.

a view into the response of the hydrocarbon-degrading microbial community to released oil and gas over environmentally relevant spatial (metres to kilometres) and temporal (days to weeks) scales[57].

In addition to enabling the rapid assessment of the identities of the responding microorganisms, the biological data (including stable isotope probing (SIP)) provided insight into the microbial potential for degradation of hydrocarbons in the contaminated deep sea (reviewed in REF.[53]). Field-based microbial community composition assessments[11] combined with metagenomics[58] and transcriptome microarray data[11] noted a rapid enrichment of Oceanospirillales spp. (Gammaproteobacteria) within the subsurface intrusion. These organisms were the first to bloom (FIG. 4) and likely degraded highly labile *n*-alkanes and cycloalkanes[58], based on metabolic potential reconstructed from DNA sequences within field populations (metagenomes and single-cell amplified genomes)[58]. Similarly, SIP incubations and single cell-amplified genome data suggested that *Cycloclasticus* and *Colwellia* degraded the dissolved gases, propane and ethane[59,60], and *Marinobacter* and *Alcanivorax* degraded *n*-hexadecane[50,51]. *Cycloclasticus* populations likely also mineralized less labile hydrocarbons, such as the aromatic compounds benzene, toluene, ethylbenzene, and xylenes (BTEX)[59], based on the presence of genes encoding aromatic hydrocarbon degradation in SIP incubations with $^{13}$C-benzene. Lastly, *Cycloclasticus* collected from the deep sea contained the genetic potential for various divergent monooxygenases, which are enzymes that oxidize alkyl functional groups on hydrocarbons[60], and expressed those genes at high abundance in DWH-contaminated waters[61].

By late May and early June 2010, genes for methane oxidation were enriched in the subsurface intrusion, suggesting an increase in methane- and methyl-degrading bacteria, such as *Methylomonas*, *Methylococcus* and *Methylophaga*[2,56,61–63] (FIG. 4). Finally, in late August and September 2010, bacterial clades with members such as Flavobacteriaceae and Rhodobacteriaceae bloomed in the subsurface intrusion, with likely roles in degrading residual hydrocarbons and complex organic matter released by earlier microbial blooms[56]. The increase in transcript abundance was higher than the relative increase in bacterial cell numbers (factor of 2–3 cell number increase in subsurface intrusion samples versus unaffected samples)[11], suggesting a broad ability of indigenous deep-sea Gulf of Mexico bacteria to degrade hydrocarbons. In total, few bacteria were inhibited by the presence of oil and gas (~5% of taxa showed decreased

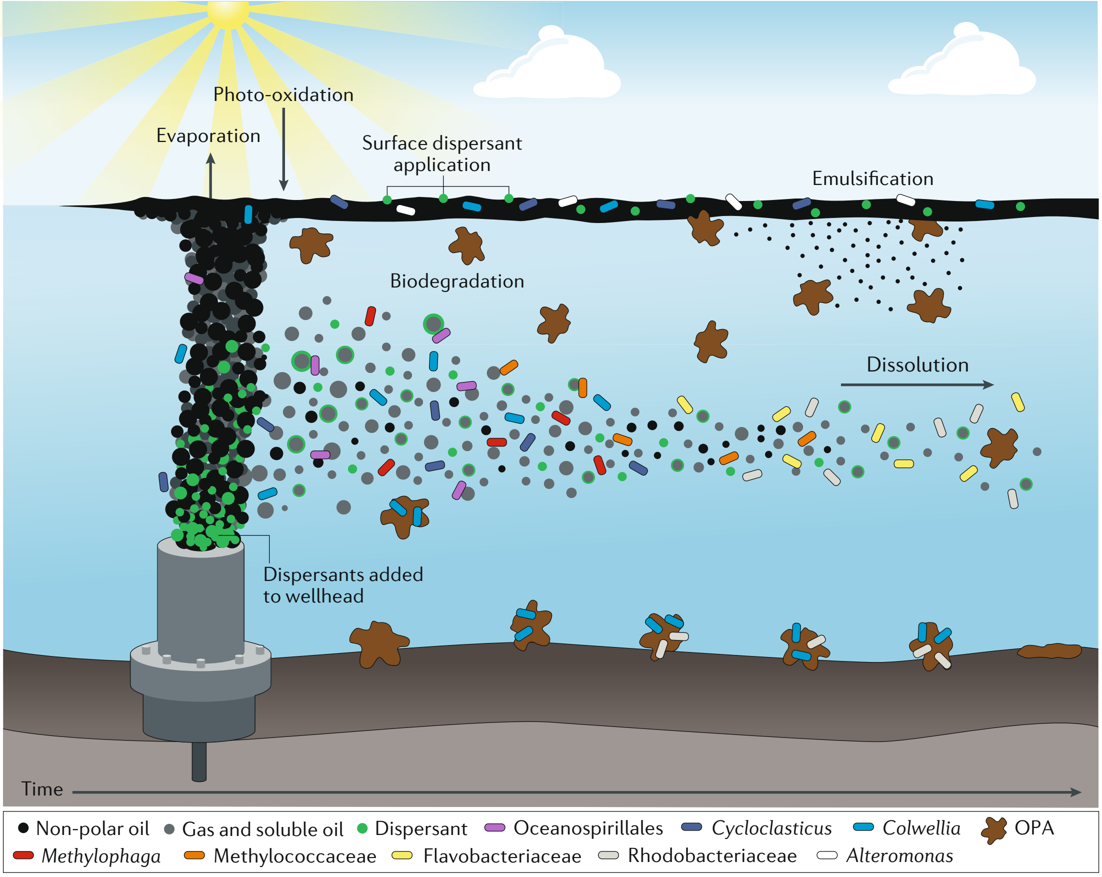

Fig. 4 | **Schematic of subsurface intrusion, microbial succession and flocculent material.** Microbes degraded oil and gas released during the Deepwater Horizon event, with various members of the microbial communities blooming at different times, following the succession pattern Oceanspirillales, *Colwellia*, *Cycloclasticus*, *Methylophaga* and Methylococcaceae, Flavobacteriaceae and Rhodobacteriaceae[11,55,56] in the deep sea. Dispersants were present in both the subsurface intrusion and the surface slicks, while flocculent material (oil–particle aggregate (OPA; also known as marine oil snow sedimentation and flocculent accumulation (MOSSFA)) was deposited on the sediment floor.

transcript expression in the intrusion layer relative to uncontaminated samples)[61] and many common non-hydrocarbon degrading deep-sea bacteria, such as SAR11, did not respond to the oil, gas or dispersants[64].

The metabolic map and succession of hydrocarbon-degrading communities described above was developed with gene-based analyses, including meta- and single-cell genomics, metatranscriptomics, and microarrays. These tools were applied to field samples, stable-isotope probing enrichments, and cultured isolates. Converting these data into rates of hydrocarbon degradation, however, is not straightforward. Instantaneous rate measurements were possible for selected DWH components, most notably methane[3,61,63], the largest component by mass[1], but most substrate degradation rates remain unknown[65]. Rate assays with chemical monitoring of substrates are challenging experiments, particularly when microbial consortia (rather than monocultures) work synergistically to degrade released oil and gas, and when the hydrocarbon substrates are present in complex mixtures, rather than in single additions. Selecting microbes[66] (or groups of microbes) and their substrates[67] (or groups of substrates) is fraught with potential artefacts; yet these experiments are critically needed to support predictive modelling of oil degradation under different environmental scenarios. Whereas indirect geochemical referencing provided long-term degradation rates for some compounds[68], a fundamental challenge for future oil spills will be to connect the intricacy of hydrocarbon-degrading metabolism, inferred from gene-based data, with the complexity of the petroleum substrate.

The addition of chemical dispersants like Corexit 9500 impacted the response of the microbial community to the DWH disaster, though the type and magnitude of the impact is unresolved[28], and the effects of the dispersants depend on the specific oil compounds and on the bacterial species present[69–72]. Current evidence indicates that the dispersant Corexit 9500 is effective at decreasing oil droplet size, leading to increased microbial degradation of hydrocarbons relative to untreated oil, especially at higher temperatures (such as 25 °C) and/or when oil concentrations are in the low to sub-ppm range[41,73–77]. Investigators established mesocosms with uncontaminated deep Gulf seawater to explore the microbial responses to oil, Corexit or both additions. *Colwellia* spp. were likely consumers of ethane and propane[59] but were also enriched within oil and dispersed oil treatments, and dominated flocs, in mesocosms[40]. Other mesocosms reported enrichment of *Colwellia* spp. within Corexit 9500 and dispersed oil treatments, but not in oil-only treatments, where *Marinobacter* spp. were enriched instead[67]. This evidence is consistent with results from dispersed oil enrichments yielding *Colwellia* spp. strain RC254, an isolate that could degrade DOSS and oil in pure culture[40,69]. However, the initial microbial community influenced enrichment outcomes. For example, mesocosms using surface Gulf of Mexico inocula containing mostly *Vibrio* spp. did not enrich *Colwellia* spp. with Corexit or dispersed oil[74]. Mesocosms in the same study using a deep Gulf of Mexico water column community inoculum for Corexit 9500-only enrichments saw a marked increase in *Colwellia* activity and an increase in *Winogradskyella* spp. abundance[74]. When similar experiments were repeated with other inocula and alternative oil sources, *Marinobacter* spp., *Alcanivorax* spp., *Cycloclasticus* spp. and *Alteromonas* spp.[73,78,79] were enriched in treatments with Corexit 9500 or dispersed oil. Regardless of the specific organisms enriched, many of these mesocosm experiments showed distinct and repeatable differences between microbial responses to oil and dispersed oil, suggesting phylogenetic or metabolic differences manifesting between the two substrate mixtures.

Some incubation-based studies showed enhanced oil degradation[41,74] with Corexit whereas others observed no enhancement[75,76] or suppressed[67] hydrocarbon biodegradation in the presence of Corexit (reviewed in REF.[80]). Where enhanced biodegradation occurred, degradation followed the typical pattern in which lower molecular weight hydrocarbons, and those in more labile forms like alkanes, were preferentially degraded relative to larger molecules or those with aromatic structures such as polycyclic aromatic hydrocarbons (PAHs)[68]. Thus, although Corexit 9500 can sometimes improve biodegradation at low oil concentrations and/or higher temperatures, it has a range of effects that include inhibition of biodegradation, at least in the limited number of laboratory studies. Such experiments are challenging to design and interpret due to the uncertainties associated with complex initial microbial communities, disparate oil sources, the physical form of the oil and dispersants, and the difficulty of mimicking partitioning and dilution that occur in the environment. Nevertheless, the release of oil and application of dispersants during the DWH disaster provided an opportunity to link basic microbial concepts with the real-world complexity of marine ecosystems, providing insight to the interplay of petroleum's physical and chemical behaviour with seed populations, metabolic specificity, nutrient availability and growth dynamics, and interaction with the non-microbial components of deep-sea ecosystems.

## Oil weathering at the sea surface

Oil is an exceedingly complex mixture, composed of millions of compounds containing primarily carbon and hydrogen, and sometimes oxygen, nitrogen and sulfur[1] (FIG. 5). Each of these molecules has different physical-chemical properties and reactivities towards light and biology, and on the ocean surface, they are subjected to environmental weathering processes, including evaporation, dissolution, biodegradation, and photo-oxidation[5] (FIG. 4). Weathering physically fractionates the initial oil composition between phases (such as oil residue, water, and air) and chemically alters the original oil molecules[1,81–84]. Evaporation from the sea surface removes low-boiling ('light') compounds, whereas dissolution removes remaining 1–3 ring aromatics with few alkyl groups[82,85] and highly polar species, such as naphthenic acids and alcohols[86]; however, the extent of one process over the other depends on the physical–chemical properties of each compound.

Prior to the DWH disaster, few studies (for example, REF.[87]) were able to comprehensively apportion the

Flocs
Masses of loosely-associated particles formed from the aggregation of minerals and organic particles suspended in water.

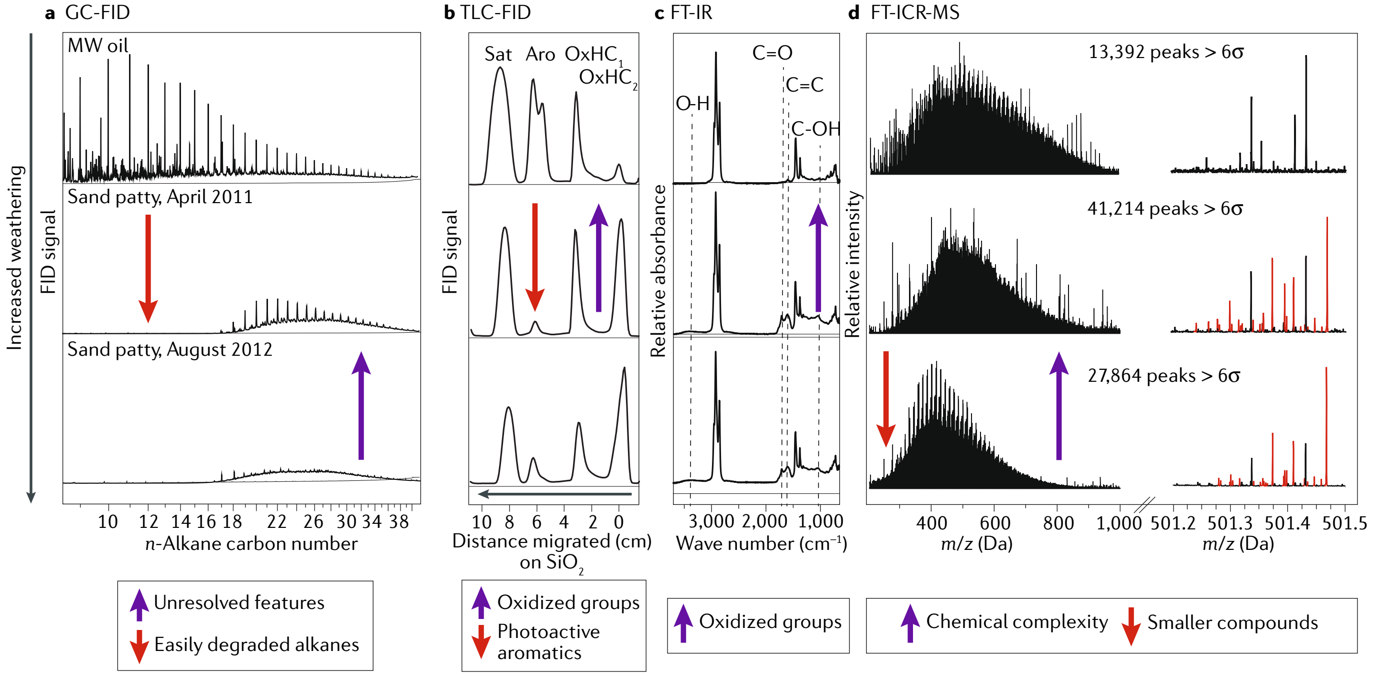

Fig. 5 | **Analysis of Deepwater Horizon oil and field sample chemical compositions.** Four different techniques capture the collective effects of abiotic and biotic weathering on oil (initial oil spectra along top row), which are manifested in changes of: gas chromatography flame-ionization detection (GC-FID) chromatograms (panel **a**), thin-layer chromatography flame-ionization detection (TLC-FID) chromatograms (panel **b**), Fourier transform infrared (FT-IR) absorbance (panel **c**) and broadband Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR-MS) spectra (panel **d**). Field samples include sand–oil patties collected from Gulf of Mexico beaches. Overall, weathering led to degradation of saturated and aromatic compounds leaving behind recalcitrant compounds in the unresolved complex mixtures, to an increase in oxidized hydrocarbon (OxHC) fractions relative to saturated and aromatic compounds and to increases in hydroxyl and carbonyl functional groups. The negative ion mode ESI FT-ICR-MS revealed a complexity increase in the number of peaks (from m/z 200–1000) and the appearance of oxygenated species (red peaks) in a mass-scale expanded 400 mDa segment, at 501 Da. Of note, similar molecular information is available for all other nominal masses in the mass spectrum. Panels **a**–**c** adapted with permission from REF.[101], ACS.

relative importance of various weathering processes due to under-sampling in time and space, and analytical barriers to assess compositional differences between oil types[88]. The oil released during the disaster was a light crude oil dominated by saturated hydrocarbons[1] (~74%) and, as a result, up to 60% of its mass was lost to evaporation within hours to days of surfacing[82]. Due to the subsurface oil release, though, dissolution played a larger role in the DWH disaster than in prior surface spills where evaporation was dominant[89]. The physical changes and mass losses resulting from evaporation and dissolution together increased the viscosity of the remaining oil and the relative proportion of surfactants present[90,91]. The enrichment of these naturally-occurring surfactants and the physical mixing of seawater into oil led to the formation of thick emulsions from the oil that reached the sea surface, which hampered oil recovery efforts and resisted most microbial degradation[47,92,93].

However, the observed emulsions (also referred to as mousses) did not form solely from the result of oil-derived surfactants or mass loss. They were also due to in situ photo-chemical changes, which modified some oil components to products with more oxygen and increased surfactant-like properties (that is, they were interfacially active and displayed both oil and water partial solubility)[94–97]. Specifically, photo-oxidative weathering[98–100], the dominant weathering process acting on DWH surface oil[48,81], increased the oxygen content of surface oil[81,84,101] and added ketone, hydroxyl, and carboxylic acid functionalized (singly and in combination) hydrocarbons that were either lost to the air[37] or remained on the sea surface[102] (FIG. 5). The weathering changed the surface oil's physical properties, and reduced the effectiveness of surface-applied dispersants to <45% at 2–4 days transit time on surface[92]. Further oxidation of interfacially-active molecules yielded water soluble species that move from the oil into seawater as photo-solubilized bioavailable carbon[103]. Indeed, as determined through ultrahigh resolution mass spectrometry (Fourier-transform ion cyclotron resonance mass spectrometry (FT-ICR MS)), elemental assignments for tens-of-thousands of molecules within each crude oil fraction (oil-soluble non-interfacially active, oil-soluble interfacially active, and water soluble) indicate that (decreasing) carbon and (increasing) oxygen number determined the progression of molecules from oil-soluble to water-soluble[104] (FIG. 5). Both the oil- and water-soluble photo-transformed species span aliphatic to highly aromatic structures[81,102], indicating that these products originate from both aliphatic and aromatic hydrocarbon precursors[105]. These results suggest that

**Saturated hydrocarbons**
Chemical compounds that are comprised of carbon and hydrogen (hydrocarbons) in which all carbon–carbon bonds are single bonds.

both direct and indirect photo-oxidation contribute to the generation of transformation products.

The use of novel analytical chemistry technologies developed in academic settings enabled detailed quantitative estimation of photochemical oxygenation[101,105] and exploration of photochemical mechanisms and rates[48,92,106] unattainable during previous oil disasters, such as the Exxon Valdez spill. In parallel, advanced characterization of the molecules within the emulsions provided new insights into remediation efforts aimed at these compound types[104]. Ultra-high resolution FT-ICR MS equipped with ionization sources, such as electrospray-ionization (ESI) or atmospheric pressure photoionization (APPI), allowed researchers to analyse oil (and oil weathering products) irrespective of boiling point. Thus, it provided access to important molecular information on the changes induced by weathering for oil, interfacially active species, and ultimately water soluble compounds that affect the fate, transport, toxicity, and viscosity of surface oil[81,84,103,107,108].

Similarly, comprehensive two-dimensional gas chromatography (GCxGC) increased the chemical resolution, assessment of chemical ordering, and capacity to model weathering processes achievable through GC analyses, giving new understanding into source oil composition, biodegradation, photochemical oxidation, water-column processes, and accurate measurements of biomarkers[105,109–112]. These research efforts advanced the collective understanding of weathering and its effect on the initial oil composition, which previously was characterized by conventional gas chromatography (GC)-based techniques. The GCxGC approach is now scientifically mature and is used to examine changes in the abundance of compounds and/or compound classes in the parent oil, which are then ascribed to various categories of physical and chemical weathering[85,88,89,110,111,113–118]. However, even with the expanded compositional information[105] through GCxGC, GC-based techniques are unable to detect many oxidative transformation products, notably those that are highly oxidized with boiling points outside of the GC range[119].

Although predicting the fate of discharged oil is extremely challenging on a molecular level and requires knowledge of the original oil composition, new technologies facilitated substantial advances during the DWH disaster. The complexity of oil requires a suite of analytical tools to comprehensively explore the weathering mechanisms and products. In addition to the GC-based and FT-ICR MS tools highlighted here, thin-layer chromatography flame-ionization detection (TLC-FID)[101] and Fourier transform infrared spectroscopy (FT-IR)[120] provided quantitative and informative estimates of functional group changes from weathering processes. Together, this suite of technologies provided a greater understanding of the reaction mechanisms and impacts of weathering processes such as photo-oxidation and the identity of its transformation products, as well as their impacts on physical properties, bioavailability and toxicity of the discharged oil. The expanded understanding, combined with application of complementary analytical platforms, will inform real-time responses in future oil spills.

## Broader environmental impacts

The magnitude and duration of the Deepwater Horizon event, as well as its occurrence at depth, led to impacts over a wide area that encompassed different types of ecosystems (FIG. 6). Coastal marshes and beaches received oil washed ashore from the oil well discharge approximately 80 km away, while deep-sea sediments[121] and corals[122] received fallout oil from the surface and intrusion layers in the form of oil-associated detritus and mineral aggregates. Pelagic fish and cetaceans swam through surface and deep-sea oil, and thus were exposed to the oil, gas and dispersant mixtures present in these areas[123–125]. Although the general impacts of oil on coastal organisms and environments were known prior to the DWH disaster[126], the duration, magnitude, and scope of the discharge posed challenges to assessing the overall impact and recovery, particularly in the deep sea where baseline studies are rare to nonexistent. In many cases, the ecosystems recovered as predicted from previous oil

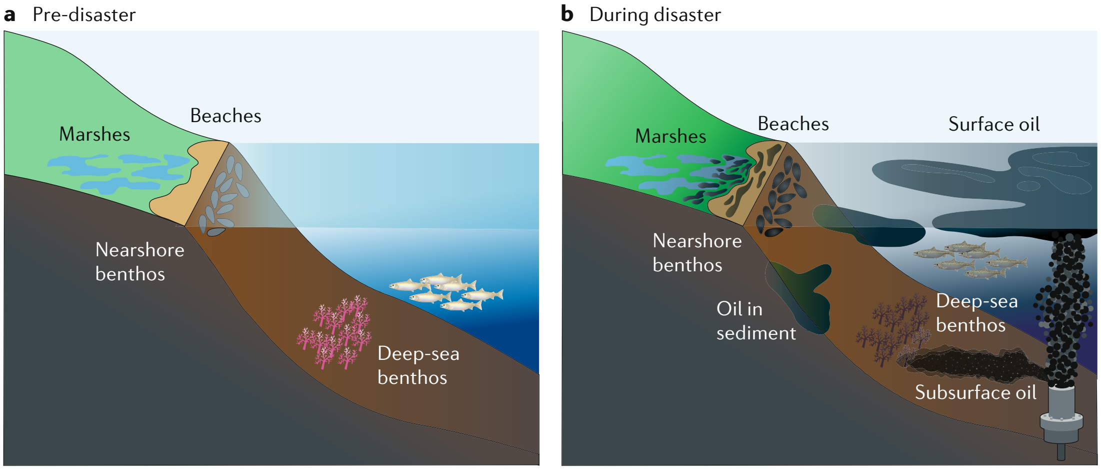

Fig. 6 | **Comparison of marine ecosystems.** Primary impacts on the marine environment before the Deepwater Horizon disaster (panel **a**) and after oiling during the disaster (panel **b**) included the subsurface intrusion, oiled sediments and corals, and oiled beaches and marshes.

**Denitrification**
A multistep microbial process that reduces nitrate to molecular nitrogen.

discharge studies, but in others, the oil discharge combined with other stressors to cause larger impacts than expected[122,127,128].

Oil contaminated over 2,000 km of Gulf Coast shoreline, half of which was located in Louisiana[8]. The oiling was patchy in both quantity and location, and impacted predominantly marsh ecosystems[129] and beaches[130]. For marshes, instances of heavy oiling (such as seen in Barataria Bay, LA, USA) led to substantial grass die-off at the marsh edge, and subsequent enhanced shoreline erosion[128] led to permanent damage to the marshes. In marshes that were less oiled, grass re-growth was evident after 2 years[129]. On oiled beaches, oil-contaminated sands hosted blooms of hydrocarbon-degrading bacteria (such *Alcanivorax*, a genus within the Oceanspirallales[131], and *Candidatus* Macondimonas diazotrophica)[132] within days of oiling, followed by a succession to bacteria (such as Rhodobacteriaceae) that likely degraded more recalcitrant oil compounds over the course of the disaster[131]. Despite the removal of large quantities of oiled materials during the response phase[133], oiled sand patties were found years after the disaster on beaches in the states of Florida, Alabama, Mississippi and Louisiana[101,134]. Many of these oil-sand patties are impervious to water and have few nutrients, thus they are not effectively degraded by bacteria[135]. However, other than being unsightly, no significant problems or concerns have been identified with these oil residues, although for unknown reasons, the pathogen *Vibrio vulnificus* was enriched on these 'tar balls' compared with in sand and seawater[136]. Continued monitoring of the oil content in marshes and beaches is necessary to understand long-term impacts and recovery of these ecosystems to pre-DWH conditions.

Compared with the relatively well-understood nearshore ecosystems, the impact of oil from DWH on the deep sea was unprecedented and unknown[137]. A unique aspect of the DWH disaster was the observation of significant flocculated material in sediments near the site of the blowout. This material was determined to be aggregates of phytoplankton detritus, mineral aggregates, and microbial extracellular polymeric substances (EPS), commonly referred to as "marine snow". During the DWH disaster, marine snow captured oil and then sank to the sea floor, transporting oil through the water column in a process dubbed Marine Oil Snow Sedimentation and Flocculent Accumulation (MOSSFA)[138–140]. Surface dispersant applications appear to enhance floc formation in experimental systems[40,67,141,142] due to interactions of EPS and dispersants that form quickly-sedimenting material[143]. MOSSFA-derived oil on the sea floor is estimated to account for 0.5–14% of the total oil released[14,15], and two regions of the sea floor with heavy marine oil snow suggest that the spatial extent of MOSSFA deposition is between 12,805 and 35,425 km$^2$ (REF. [144]). Sediment microbial communities responded to the influx of hydrocarbons to the sea floor, including the enrichment of *Colwellia* and uncultured gammaproteobacterial strains that were similar to strains observed in the subsurface intrusion layer[145]. In heavily oiled sediments, genes from anaerobic microbes such as *Desulfovibrionales, Desulfomonodales* and *Desulfobacterales* in the Deltaproteobacteria[146] and from anaerobic metabolism such as denitrification[145] were observed. Even after 4 years, significant oil residue was still present in sediments within 40 km of the DWH blowout, with biodegradation most inhibited in concentrated seafloor oil deposits[68].

Sedimented oil harmed deep-sea benthic organisms, causing decreases in sediment macro- and meiofauna diversity[121,147] and high mortality rates of benthic foraminifera[148,149]. Coral communities were also impacted, where octocorals were damaged or dead after being covered in flocculent material containing oil and dispersant from the disaster and response activities[137,150,151]. Recovery of the corals after two years was mixed, with the average overall visible impact to corals decreasing over time[152]. In some instances, the tissue on the impacted corals had died and the remaining skeletons were colonized by hydrozoa[152], indicative of coral deterioration. Colonization of corals by brittle stars, however, was a sign of recovery as brittle stars are hypothesized to deter hydroid larvae from settling on coral branches[153]. As recently as 2018, heavily oiled areas near the DWH blowout hosted lower biological diversity of deep-sea megafauna, although with higher numbers of arthropods (such as crabs and shrimp) in many sites[154], underscoring the long term impact of the DWH disaster on benthic communities.

## Outlook

The needs and opportunities following the Deepwater Horizon disaster led to a renaissance in oil spill science, with numerous breakthroughs on the transport and behaviour, fate, and short-term and long-term effects of acute releases of oil and gas in the marine environment. Scientists and engineers from fields outside oceanography were engaged; a generation of scientists was trained; new chemical and biological methods were developed, often with novel technology or modified from other scientific fields; highly detailed insights were gained on the rates, specificity, mechanisms, and products of abiotic and biotic processes; and case studies, lessons learned, and recommendations on mechanical and chemical response technologies were proposed and presented[28,155].

In the 10 years since the disaster, detailed monitoring and observations have yielded the most comprehensive oceanographic investigation of the northern Gulf of Mexico. The collective scientific effort identified what was unknown before the DWH (photo-oxidation of surface oil, MOSSFA, deep-sea dispersant use and fate) and prioritized new knowledge that was necessary to change the scientific or practical response to the spill. There is now a deeper understanding of the microbial degradation of petroleum hydrocarbons and whether nutrient stimulants can or should be applied to offset potential nutrient limitation during bioremediation (while being mindful to avoid full oxygen depletion, which would shut down efficient aerobic degradation)[57]. There have been several paradigm shifts in our understanding of oil weathering, most notably regarding the onset and rates of oil photo-oxidation[48], and the molecular specificity of its transformation products. In particular, we learned that oxygenated products from oil photo-oxidation are polyfunctional[102], impact the efficacy of surface applications of dispersants[92], and have very complex roles in emulsion formation[104]. With the ability to isolate and characterize these transformation products, new mitigation strategies can be developed.

How the results from the DWH disaster can be applied to future of oil spills must be considered, as drilling and recovery technologies are implemented and deep-sea oil drilling is expanded, wider and multi-seasonal shipping lanes in northern latitudes are opened, above and below ground pipelines near aquatic environments are installed, and oil recovery in remote locations is increased[156]. The response and continued studies of the DWH disaster benefited from the relatively accessible location for a deep-water well (80 km offshore) and nearly-optimal weather (favourable summer currents, mild winds and calm seas). Along the relatively populated Gulf Coast, responders and scientists used existing infrastructure for shipping, housing, and land and water access. A more remote location with limited infrastructure, such as in the high latitudes, would prohibit a commensurate response, and would effectively exclude academic scientists. A further complication would be the uncertain impact of temperature and different oil composition on the processes observed in the DWH disaster, such as microbial biodegradation, floc formation and weathering. For example, dispersants seem to be less effective at stimulating biodegradation at colder temperatures[41,74]. In addition, heavier crude oils in high-latitude reservoirs are more polar and contain more oxygen, nitrogen, and sulfur than those discharged during DWH; consequently they will be more viscous, harder to disperse and less bioavailable[157]. Lastly, some studies have implicated the polar components of oil in higher ecotoxicity to resident fish populations[158], with implications for local fisheries and tourism. All of these factors inhibit simple extension of DWH results to a high-latitude spill.

A critical area for additional research lies at the nexus of systems biology and analytical chemistry in the context of oil degradation. Metabolic databases are relatively complete for the degradation of simple hydrocarbons and aromatic compounds like BTEX but they are missing information on the metabolic pathways that degrade heteroatom-containing hydrocarbons[159]. In other words, we can detect degradation products but do not know which genes or microbes are responsible for producing them from the source oil. Moreover, as there could be substantial functional redundancy between different oil-degrading communities[61,79,160–162], identifying the members of the microbial community might not matter in assessing degradation potential if the functional genes are present and expressed similarly. Ideally, chemical or biological markers will be identified that allow assessment of the ‘state’ of an oil discharge event, supporting response strategies that increase oil degradation rates. Inexpensive portable long-read sequencing technology, like that from Oxford Nanopore, could provide near real-time microbial functional gene expression measurements, enabling adaptive responses and mitigation strategies tuned to microbial functionality[57]. As high-throughput approaches for reconstructing microbial genomes, monitoring chemical transformations, and combining biological and chemical characterizations mature, this problem is poised to be solved.

One of the biggest open questions after the DWH disaster concerns the use of dispersants and their complicated cost-benefit calculations. A primary goal of dispersant application during DWH was reduction in oil droplet size to enhance sequestration of oil in the deep sea[38]. The potential to enhance biodegradation was a secondary consideration and although dispersants potentially improve hydrocarbon degradation, they could also prevent or delay this desirable impact, depending on environmental and biological circumstances[28]. Interdisciplinary teams of chemists, biologists, ecologists and geochemists must work to ascertain the conditional tradeoffs in dispersant use, particularly in deep-sea environments where degradation potential is greater but oxygen is finite and megafauna such as pelagic fish and sessile corals have much longer generation times and slower recovery times. Importantly, tradeoffs with dispersant use are not binary, adding another layer of complexity to the decision process. For example, if the subsurface dispersant to oil ratio effectively modulates droplet size, it is possible to envision a scenario in which dispersant applications could be used dynamically to control the extent, rate and location of oil reaching the surface.

Between the Exxon Valdez and the DWH disaster, expertise in the academic community on oil spill response and oil degradation dwindled due to lack of funding and the effectiveness of the Oil Pollution Act of 1990 in assigning blame and assessing fines. Although the scientific community was able to re-tool quickly to respond to DWH, we are now at a similar crossroads with the ending of the GoMRI research program and the fading memory of the 2010 event. A substantial cohort of graduate students, postdoctoral researchers and early career scientists have been trained in oil chemistry and microbiology, but their future interests, job prospects in this field and funding portfolios for federal and private agencies are uncertain. The DWH disaster benefited from the expertise of scientists and responders who were involved in the Exxon Valdez and the Ixtoc spills (1979, in the Gulf of Mexico), but many of these key knowledge-holders are retiring. Even if they are replaced, there will be a loss in critical mass of talented individuals who can apply and interpret the new chemical and biological technologies. We are concerned about future funding for known knowledge gaps, particularly in the usage of dispersants. A consortium of academics, government scientists and industrial partners must continue to explore these chemicals and their short- and long-term impacts on marine environments. Whereas there have been great strides with academia developing and collaborating with government and industry, these relationships should be fostered and clear channels of communication between these different groups must be strengthened[163]. These relationships will allow for trust building and recognition that while the interests of academia are not always lockstep with the response community, overlapping interests can provide key opportunities for future funding and collaborative research[163].

As we look back on the past decade, a few signals rise from the collective noise and provide a framework for planning effective responses to future oil spills. First, scientific findings and recommendations should influence policy and regulators, with a strategic embrace of complex biological and chemical data as diagnostics of environmental processes. Second, the intricacies of interacting microbes and environmental factors make understanding the oceans before, during, and after oil spills extraordinarily challenging, requiring a plan for interacting and complementary analytical platforms across molecular biology and chemistry. We cannot retreat again to one or two analytical methods as they unintentionally blind us to the interdependent cascade of environmental processes, some of which are likely to be more important in the next spill than they were in the DWH disaster. Finally, response teams and research collaborations with common purpose are capable of working together to understand the impact of this disaster on affected ecosystems such as the Gulf of Mexico; in so doing, they are responding to a critical societal need.

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## Author contributions

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