Potential impacts of offshore oil and gas activities on deep-sea sponges and the habitats they form.

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Abstract

Sponges form an important component of benthic ecosystems from shallow littoral to hadal depths. In the deep ocean, beyond the continental shelf, sponges can form high- density fields, constituting important habitats supporting rich benthic communities. Yet these habitats remain relatively unexplored. The oil and gas industry has played an important role in advancing our knowledge of deep-sea environments. Since its inception in the 1960s, offshore oil and gas industry has moved into deeper waters. However, the impacts of these activities on deep-sea sponges and other ecosystems are only starting to become the subject of active research. Throughout the development, operation and closure of an oil or gas field many activities take place, ranging from the seismic exploration of sub seafloor geological features to the installation of infrastructure at the seabed to the drilling process itself. These routine activities and accidental releases of hydrocarbons during spills can significantly impact the local marine environment. Each phase of a field development or an accidental oil spill will therefore have different impacts on sponges at community, individual and cellular levels. Legacy issues regarding the future decommissioning of infrastructure and the abandonment of wells are also important environmental management considerations. This chapter reviews our understanding of impacts from hydrocarbon exploration and exploitation activities on deep-sea sponges and the habitats they form. These impacts include those (1) at community level, decreasing the diversity and density of benthic communities associated with deep-sea sponges owing to physical disturbance of the seabed; (2) at individual level, interrupting filtration owing to exposure to increased sedimentation; and (3) at cellular level, decreasing cellular membrane stability owing to exposure to drill muds. However, many potential effects not yet tested in deep-sea sponges but observed in shallow-water sponges or other model organisms should also be taken into account. Furthermore, to the best of our knowledge, no studies have shown impact of oil or dispersed oil on deep-sea sponges. To highlight these significant knowledge gaps, a summary table of potential and known impacts of hydrocarbon extraction and production activities combined with a simple "traffic light" scheme is also provided.

1. <u>Introduction</u>

Presently, offshore oil and gas production accounts for one third of worldwide hydrocarbon production (Bennear, 2015). Since the end of the 1960s and the beginning of offshore oil and gas exploration, the oil and gas industry has developed technologies that enable exploitation of deep-sea environments (Managi et al., 2005) and is, today, operating in deeper and complex marine settings (Muehlenbachs et al., 2013). Hydrocarbon exploration and production is taking place in areas where vulnerable benthic species such as deep-sea sponges are present. For example, in the Faroe-Shetland Channel, oil production activities are taking place within a Nature Conservation Marine Protected Area designated to protect the local deep-sea sponge grounds (Henry and Roberts, 2014).

Exploration for hydrocarbon and other resources in deep waters offshore has helped discover new deep-sea environments. For example, collaborative efforts between academia and industry partners have been very successful in increasing our understanding of deep-sea benthic ecosystems, e.g., the SER- PENT project (Scientific and Environmental ROV Partnership using Existing iNdustrial Technology) (Gates et al., 2016), and discovering previously unknown habitats such as the Darwin Mounds in the NE Atlantic (Huvenne et al., 2016). However, industrial operations in deeper settings are strongly correlated with recorded numbers of technical incidents such as blowouts, injuries or spills (Muehlenbachs et al., 2013) as well as operational discharges and disturbances leading to the chemical contamination of water and seafloor habitats as well as local-scale physical impacts from among others drilling, anchoring and pipelines (OSPAR Commission, 2009a). This was most starkly demonstrated by the 2010 Deepwater Horizon oil spill in the Gulf of Mexico, caused by a well blowout at 1500 m depth (Beyer et al., 2016 and references therein). Subsea well blowouts and pipeline leaks at depth have become more of a concern, while the number of tanker-related oil incidents at surface has decreased over time (Jernelöv, 2010). In addition, day-to-day operations can also have environmental impacts in the deep sea (Cordes et al., 2016). From the presence of man-made infrastructures on the seabed to the release of produced waters or the resedimentation of particles close to the drilling locations, the ecological footprints of the offshore oil and gas production activities are multiple (Kark et al., 2015). As it is known that recovery rates vary in the deep-sea depending on the region and biological communities already living there, understanding the impact of oil and gas industry-related activities on deep-sea benthic ecosystems is complex (Henry et al., 2017).

While pressures from anthropogenic activities such as the exploitation of oil and gas reserves on deep-sea ecosystems keep increasing, our understanding of deep-sea organisms and the scale of human impacts on ecosystem functioning remains limited (Ramirez-Llodra et al., 2011). Deep-sea ecosystems comprise a highly diverse set of physical and biological settings, many of which are hotspots of biodiversity including hydrothermal vents, abyssal plains, manganese nodule fields, cold-water coral reefs and sponge grounds (Ramirez-Llodra et al., 2011). Although many of these ecosystems may contribute significantly in global biogeochemical cycling (Ramirez-Llodra et al., 2011), the overall value of the ecosystem services provided by deep-sea ecosystems remains poorly quantified (Thurber et al., 2014).

Sponges (Phylum Porifera) play vital roles in sustaining global deep-sea biodiversity and ecosystem functioning. The diversity of sponges in the deep sea (Fig. 1A and B), the rarity of some poriferan taxa (members of the class Calcarea) and the ecological uniqueness of some poriferan groups such as carnivorous sponges of the family Cladorhizidae (Fig. 1C) and the stalked glass sponges of the family Hyalonematidae all add to the biological richness of life in the deep ocean (Hogg et al., 2010). Habitats formed by dense aggregations of one or several sponge taxa (sponge “grounds”, Fig. 1D) can extend over very large areas up to hundreds of km^2 and provide three-dimensionally complex stable habitats that support distinct biological communities (Maldonado et al., 2016). Maldonado et al. (2016) provide an extensive review of sponge grounds including deep-sea sponge grounds such as the hexactinellid sponge reefs in the North-East Pacific Ocean off, astrophorid sponge aggregations in the North Atlantic, lithistid sponge grounds or Antarctic sponge grounds more than 400 species rich. Sponges themselves host an array of organisms ranging from bryozoans or polychaetes to crustaceans (Kazanidis et al., 2016; Wulff, 2006), and sponge grounds act as nursery grounds and support many benthic species including commercially-important fish species such as rockfish, hake and blue ling (Du Preez and Tunnicliffe, 2011; Freese and Wing, 2003; Maldonado et al., 2016) (Fig. 1E–H). Therefore, sponge grounds meet several criteria of Vulnerable Marine Ecosystems (VMEs) as recognised by the UN Food and Agriculture Organisation (FAO). Deep-sea sponge grounds also meet the criteria of Ecologically or Biologically Significant Areas (EBSAs) as defined by the UN Convention on Biological Diversity (Table 1) (Hogg et al., 2010).

Despite their ability to enhance benthic biodiversity, the biology and ecology of deep-sea sponges has only started to be uncovered. What has been revealed most recently is that sponges play essential roles in the biogeochemical cycling of organic matter in the deep oceans (Cathalot et al., 2015). This is principally owing to sponges being very efficient at filtering large volumes of water as they rely on Particulate Organic Matter (POM) as well as Dissolved Organic Matter (DOM) for food (Rix et al., 2016). Up to 40% of the carbon and nitrogen assimilated by sponges are released back into the water column in the form of sponge detritus (Rix et al., 2016). Sponges, including deep-sea species, thus recycle DOM to POM which is then available for other benthic organisms and contributes to bentho-pelagic coupling in oligotrophic environments (Maldonado, 2016; Rix et al., 2016). Sponges host highly diverse microbial communities of bacteria, archaea and eukaryotes, often compared for their complexity to the microbial assemblages of the mammalian gut (Hentschel et al., 2012; Webster and Taylor, 2012). Deep-sea sponges participate in nitrogen cycling through these microbial symbionts capable of nitrification, denitrification and anammox reactions (Hoffmann et al., 2009; Li et al., 2014). The concept of a “sponge loop” has therefore emerged in the literature whereby sponges support oligotrophic food webs by recycling organic carbon and nitrogen (De Goeij et al., 2013; Maldonado, 2016). Furthermore, sponge skeleton elements (spicules) are composed of silica assimilated from the environment and sponges can play large roles in the cycling of silica. Glass sponge reefs composed of hexactinellid sponges such as *Aphrocallistes vastus*, which are composed of up to 80% of biogenic silica, concentrate huge amounts of Si in some areas of the seabed (Chu et al., 2011).

It is also becoming more evident that deep-sea sponges create other eco- system services: these "provisioning" services including the production of bioactive secondary metabolites related to sponge microbial associations that are of great interest to the biotechnology sector. Conservation of these ancient animals (individual sponges have been aged over 400 to over 2000 years old) and their habitats must therefore scale up with the rates and extent of emerging anthropogenic activity, and thus the impacts that deep-water oil and gas activities could have on these benthic organisms need to be considered in management plans (Fallon et al., 2010; McMurray et al., 2008).

The purpose of this review is to provide the first fully comprehensive review of the impacts of offshore oil and gas activities on deep-sea sponges and the habitats they create. Although studies on the resilience of deep-sea sponges to some oil and gas production activities are starting to emerge, many knowledge gaps persist. Relevant findings from shallow-water sponges or other benthic organisms have therefore also been used here to high- light possible impacts on deep-sea sponges and the habitats they form. Impacts can occur at all stages of offshore oil and gas activities from exploration, development and production through to decommissioning and legacy effects. Furthermore, effects of these activities can be detected across ecological scales from community, individual and cellular levels. This review therefore adopts this multiple-scale framework to assess impacts at the level of sponge habitats, at the individual sponge level and at the cellular and molecular level.

2. Effects on sponge habitats and communities

2.1. Impacts of Routine Activities on Deep-Sea Sponge Grounds and Associated Communities

2.1.1. Subsea infrastructure (Wells, Pipelines, Manifold and Platforms)

During the phases of exploration and development, offshore oil and gas activities require the drilling of wells and the installations of heavy infrastructure such as manifolds and pipelines that directly disturbs the seabed (Fig. 2). Physical disruption and smothering by sediments is one of the main impacts linked to the early stages of oil field development arising from installing pipe- lines, cables, bottom rigs, templates, skids and platforms including platform legs and anchoring (OSPAR Commission, 2010). Physical disruption and increased sedimentation (Fig. 1I and J) during these phases can locally diminish benthic communities by more than 90% in terms of megafaunal density within sponge grounds (Jones et al., 2006). Long-term effects on deep-sea sponge grounds from such physical disturbance are still detectable up to 10 years postdrilling and this slow, partial recovery, inversely related to the distance to the well and the time after drilling, could result from the long-lived nature, slow growth rates and low reproduction rates of most deep-sea organisms (Jones et al., 2012). Very limited recovery of megafauna was observed in areas where drill cuttings were not eroded 10 years post- drilling (Jones et al., 2012).

Physical disruption and increased sedimentation are also associated with the installation of pipelines, which export produced hydrocarbons onshore. Power transmission cable installations significantly impact local benthic communities inflicting a 100% mortality rates to glass sponges below the cables and a 15% mortality rate within 1.5 m of the cables all along its foot- path (Dunham et al., 2015) with potentially similar effects expected from pipeline deployments (OSPAR Commission, 2010).

2.1.2. Discharges of Drill Cuttings and Drill Muds

In the early stages of drilling, drill cuttings and muds, comprising residual rock fragments from the well and drilling fluid chemicals, are released directly into the environment at depth (Ellis et al., 2012). For the remainder of the drilling process, treated cuttings are typically discharged at the surface, from where they sink to the seafloor under the rig. Unless dispersed by active near-bed currents, drill cuttings can accumulate on the seabed and over time may release contaminants, especially if disturbed (OSPAR Commission, 2010). The usually customised drill muds can be classified into three types: oil-based, synthetic and water-based fluids all of which may contain toxic chemicals, including polyaromatic hydrocarbons and heavy metals. Only two studies have shown the impact of drilling mud and cuttings on mega-faunal communities with abundant sponges, both in the North-East Atlantic (Gates and Jones, 2012; Jones et al., 2012). Both studies indicate major reductions in sponge densities and reduced diversity close (100–200 m) to drilling activity that persist for several years (Fig. 3). The gravity of the impact of drill muds and cuttings has been better studied on other benthic communities where the impacts have been shown to depend largely on abiotic conditions such as depth and currents as well as the concentration of chemicals associated with the muds (Ellis et al., 2012; Henry et al., 2017). For synthetic and water-based muds, a decrease in community diversity and abundance has been measured up to 1000 m away from the release location (Ellis et al., 2012). Functional changes in benthic communities associated with a loss of suspension-feeding species and an increase in deposit feeders have also been detected at release sites (Ellis et al., 2012; Trannum et al., 2010). The spatial impact footprint is largest during the first 1–2 years after drilling and reduces in extent and contaminant concentration afterwards due to leaching into the water column (OSPAR Commission, 2016). Today the production and release of oil-based drill muds have been widely reduced in the North-East Atlantic by the oil and gas industry (OSPAR Recommendations R2001/1, 2006/5 and 2010/18), but the use of oil-based drill muds in the past has been shown to have a local but strong and lasting impact on benthic communities (Henry et al., 2017; OSPAR Commission, 2010). Potential impacts of past releases of oil-based drill muds on sponge grounds and associated benthic communities therefore still need to be understood.

2.1.3. Decommissioning

As offshore infrastructures age, decommissioning options for the physical removal of oil and gas infrastructure including pipelines, platforms, drill cuttings and the capping of wells need to be considered (Fig. 2). Worldwide, there are over 7500 oil and gas structures offshore and about 85% of them will need to be decommissioned by 2025 (Fowler et al., 2014). In the North-East Atlantic, the dumping, and leaving wholly or partly in place, of disused offshore installations has been prohibited within certain sea areas, under OSPAR Decision 98/3 on the Disposal of Disused Offshore Installations since 1998. Based on a predefined assessment demonstrating that there are significant reasons why an alternative disposal is preferable to reuse or recycling or final disposal on land, the competent authority of the relevant Contracting Party may authorise companies to leave some parts of the installations in place after consultation with the other Contracting Parties. Such derogations concern very heavy concrete and steel installations which might provide a suitable settlement ground also for deep-water sponges. Until 2009, 122 offshore installations have been brought ashore for disposal and only 5 permits have been issued for structures to be left in place (OSPAR Commission, 2009a). However, with more and more installations approaching their end of life, the industry has started to lobby for a modification of the Decision itself instead of using the derogation options provided by OSPAR Decision 98/3. The argument is that the physical impact on the seabed as well as the economic costs of such operations is substantial.

Environmental impacts caused by a complete removal of offshore infra- structure that could negatively affect deep-sea sponge grounds and associated communities may include: contamination of the water column by hydrocarbons and other chemicals, direct damage to the seabed and smothering by increased sedimentation (Fowler et al., 2014). Decommissioning of oil and gas industry infrastructure has not yet taken place within known deep-sea sponge grounds and so potential impacts of decommissioning at community level is for the moment unknown. Under UK regulation, decommissioning impacts on the environment must be considered in the Environmental Impact Assessment (EIA) produced in the beginning of any new oil and gas field development (Department of Energy and Climate Change, 2011).

2.2. Accidental Spills and Releases

The Deepwater Horizon oil spill was one of the largest and deepest offshore oil spills to date, with approximately 3.19 million barrels of oil released into the water at a depth of 1500 m (Beyer et al., 2016 and reference therein). It was also the first time dispersants were used to such an extent at depth to mitigate the formation of a surface oil slick that would have impacted upon sensitive coastal ecosystems (White et al., 2014). Almost 3 million litres of dispersant CorexitTM 95000 was released near the well head (White et al., 2014). A large amount of the oil released into the water column formed several subsurface oil plumes (Diercks et al., 2010). The most significant subsurface plume extended for 35 km at approximately 1100 m depth (Camilli et al., 2010). The Deepwater Horizon incident thus created a new kind of oil spill where deep-water ecosystems and habitats were exposed to high concentrations of dispersed crude oil and dispersants (Peterson et al., 2012).

Impact of accidental oil releases is better understood in shallow-water than in deep ecosystems. In shallow-water coastal environments, oil spills have shown both lethal (high mortality rate) and sublethal effects (carcinogenic and cytotoxic impacts) on benthic species leading to changes in community diversity, age structure and trophic interactions (Suchanek, 1993). Impact of oil spills on deep-sea benthic ecosystems is far less understood. After the Deepwater Horizon incident, significant decreases in macro- and meiofaunal diversity were detected after the blowout up to 17 km away from the well (Montagna et al., 2013). Other studies have shown high mortality rate of deep-water corals, colonial and pelagic tunicates, sea pens as well as glass sponges within a 2-km radius of the well, but no further result on deep-sea sponges is given (Valentine and Benfield, 2013; White et al., 2012).

Long-term impacts of oil spills in shallow-water ecosystems often take the form of community structure anomalies (absence of organisms of a specific age class) owing to the longevity and slow growth rate of some species (Kingston, 2002). Long-term impacts of deep-sea oil spill such as the Deep- water Horizon oil spill remain unknown. Deep-sea sponges display relatively slow and strongly seasonal growth rates varying from a few millimetres to a couple of centimetres per year (Dayton et al., 2013; Dunham et al., 2015; Fallon et al., 2010), suggesting that deep-sea spills in the vicinity of deep-sea sponge grounds could have a strong long-term community effect on these habitats.

3. <u>Physiological and Ecotoxicological Effects on Individual Sponges</u>

3.1. Main Impacts of Routine Offshore Oil and Gas Activities on Deep-Sea Sponges

3.1.1. Seismic Surveying During Hydrocarbon Exploration and Appraisal Phases

During the initial phases of exploration and appraisal, seismic surveys are conducted to assess subseafloor structures and determine drilling location (Department of Trade and Industry, 2001). Impact of seismic surveys on marine invertebrates and larval development and survival has been investigated in several studies (Aguilar de Soto et al., 2013; Nedelec et al., 2014). Developmental delays and malformations in scallops have been identified as potential effects of seismic surveys on benthic organisms (Aguilar de Soto et al., 2013). In gastropods, seismic pulses decrease larval development and increased mortality by over 20% (Nedelec et al., 2014). However, no studies have yet investigated the effect of seismic surveys on sponges or their larval stages.

3.1.2. Sedimentation from Seabed Disturbance

The phases of offshore exploration and development are characterised by drilling and the installation of heavy infrastructure, which are associated with resuspension of sediments that can affect local benthic organisms including deep-sea sponges (OSPAR Commission, 2010) (Fig. 2). Bell et al. (2015) summarised the often species-specific effects of sedimentation on marine sponges, focussing mainly on shallow-water species. Increased sedimentation impacts sponge filtration and feeding (Bannister et al., 2012; Reiswig, 1971), respiration (Bannister et al., 2012; Lohrer et al., 2006), reproduction (Roberts et al., 2006) and growth (Roberts et al., 2006; Wilkinson and Vacelet, 1979). Additionally, evidence of tissues sloughing in shallow-water sponge *Halichondria panicea* was found after exposure to increased sedimentation (Barthel and Wolfrath, 1989). Studies on deep- water sponges have confirmed some of the findings made on shallow-water sponges. Heavy sedimentation on deep-water sponge Geodia barretti led to a 50%–86% reduced respiration rate depending on sediment concentration tested but was associated with a fast recovery after exposure to sediments (Kutti et al., 2015; Tjensvoll et al., 2013). Furthermore, sedimentation caused a rapid arrest in feeding behaviour and chamber clogging in the two deep-sea glass sponges *Rhabdocalyptus dawsoni* and *Aphrocallistes vastus*. However, some aspects in the response of the two glass sponge species differed: feeding was resumed earlier in A. vastus and sediment level required to halt feeding was lower for *R. dawsoni* (Tompkins-Macdonald and Leys, 2008). This shows that increase in sedimentation has an overall negative impact on deep-sea sponges, with some species more resilient than others.

3.1.3. Release of Contaminants in the Environment During Routine Operations

Routine operations during the production phase of an oil field development include the discharge to the sea of produced water that contains small amounts of hydrocarbons such as polyaromatic hydrocarbons (PAHs), dissolved metals and naturally occurring radioactive elements such as radium-226 and radium-228 (Fig. 2) (Neff et al., 2011).

The overall volume of oil released into the North-East Atlantic through produced water discharges has been reduced following industry effort, through decisions such as the OSPAR recommendation 2001/1 (OSPAR Commission, 2010). However, produced water still remains the main source of hydrocarbons in the environment from oil and gas industry-linked activities (Neff et al., 2011). Upon release, produced water is believed to be diluted very rapidly into the ambient seawater (Neff et al., 2011). Therefore, although some PAHs are persistent compounds in the environment and can be toxic at higher concentration as discussed in the next section (for accidental releases of hydrocarbons), produced water is expected to have a very low impact on marine organisms (Neff et al., 2011). However, PAHs from produced water could have sublethal effects on deep-sea sponges. Benthic suspension feeders such as mussels have been shown to accumulate PAHs when exposed to produced water (Sundt et al., 2011). Moreover, low con- centration of PAHs can be bioaccumulated in sponges at higher levels than mussels (Batista et al., 2013; Gentric et al., 2016; Mahaut et al., 2013; Negri et al., 2006). Changes in fatty acid content in sponges exposed to PAHs have also been observed. It has therefore been suggested to use sponges as environmental bioindicators for PAHs concentration monitoring (Batista et al., 2013).

Dissolved metals can also be present in produced water including barium, iron, manganese, mercury and zinc. Shallow-water sponges are known to bioaccumulate zinc (Gentric et al., 2016). It is consequently possible that deep-sea sponges could also bioaccumulate metals in their tissue from produced water exposition, but no study has been conducted so far on this subject. Notably, zinc naturally present in the environment has been shown to be incorporated into sponge spicules (Hendry and Andersen, 2013). However, no studies looking at the impact of metal concentration from anthropogenic sources in sponge spicules have been conducted so far.

3.1.4. Decommissioning

Removal of ageing offshore infrastructures during decommissioning could lead to an increase in sedimentation and a release of hydrocarbons and other chemicals into the marine environment (Fig. 2) (Fowler et al., 2014). Yet targeted disturbance experiments of the drill cuttings accumulated on the seafloor demonstrate no major effect on the spatial distribution of cuttings contamination or the biological communities present in the seabed located greater than 100 m from the original location of the installation (OSPAR Commission, 2009b). It has to be born in mind, however, that the removal of large anchors or installations on the seafloor will likely cause resuspension of a much larger extent. Intensive water column and sediment monitoring will be required to assess the effects of the removal of individual or multiple installations.

As previously stated, no infrastructure decommissioning project has yet taken place within deep-sea sponge grounds and so potential impacts of decommissioning at individual level are for the moment unknown. It can only be hypothesised that impacts on deep-sea sponges associated with high sedimentation rate and hydrocarbon pollution described during the exploration, development and production phases could also occur during the decommissioning phase.

3.2. Impacts of Accidental Hydrocarbon Release and Dispersant Use on Deep-Sea Sponges

During accidental spills, large amounts of hydrocarbons are released directly into the marine environment. During oil spills, PAHs are of particular concern when considering ecotoxicological impacts on organisms present in the vicinity of the spill location (Blackburn et al., 2014 and references therein). In shallow-water sponges, high concentrations of PAHs have been shown to disturb sponge larval settlement and development (Cebrian and Uriz, 2007; Negri et al., 2016). Effects of dispersants and dispersed oil on larval stages of various other marine organisms have been investigated, but results of higher toxicity associated with the use of dispersant seem to depend on the organisms considered and the duration of exposition (Epstein et al., 2000; Singer et al., 1998; Stefansson et al., 2016). In tropical corals, exposure to dispersed crude oil resulted in increased mortality in larvae of the coral *Stylophora pistillata* and a stronger decrease in larvae settlement rate compared to exposure to crude oil alone (Epstein et al., 2000). Furthermore, exposure to dispersed oil and dispersants alone has led to a strong health decline (defined by percentage of live polyps and tissue coverage) in three deep-water coral species from the Gulf of Mexico (DeLeo et al., 2016). To the authors' knowledge no studies have yet tested the effects of dispersed oil or dispersants on marine sponges and sponge larvae.

Long-term impacts of a deep-sea oil spill could be derived from sediment-associated hydrocarbons. It is estimated that 35% of the oil released into the marine environment during the Braer oil spill off the Shetland Islands in the North-East Atlantic subsequently ended up in subtidal sediments (Davies et al., 1997). PAHs and hydrocarbon breakdown are slowed down in sediments owing to overall anoxic conditions within the sediments (Atlas and Hazen, 2011 and references therein). However, benthic organisms can be exposed to sediment-associated PAHs or hydrocarbon via sediment resuspension. Bivalves are able to accumulate PAHs from the sediment during resuspension episodes (Nandini Menon and Menon, 1999). It has been suggested that deep-sea sponges can derive part of their nutrition from resuspended matter (Hogg et al., 2010) and therefore could be impacted by PAH-contaminated sediments. Furthermore, Culbertson et al. (2008) showed that short-term and long-term exposure to 38-year-old residual petroleum associated with sediments led to a decrease in growth rate, lower health condition and decreased filtration rate in mussels. Dispersants have also been shown to persist in deep-sea sediments as dispersants were quantified in sediments collected within deep-sea coral communities 6 months after the Deepwater Horizon spill (White et al., 2014). This suggests that oil spill can have long-term impacts on deep-sea benthic organisms when hydrocarbon and dispersants enter the sediments, which is of concern for deep-sea sponges.

4. Effects On Deep-Sea Sponges At Cellular And Molecular Levels

4.1. Impacts of Offshore Oil and Gas Production Activities on Deep-Sea Sponges at Cellular Level

During the production phase of offshore oil field development, the release of drill muds has been shown to impact deep-sea sponges at a cellular level (Edge et al., 2016). Baryte, one of the major solid components of these drill muds, has been shown to decrease lysosomal membrane stability in the deep- sea sponge *G. barretti* (Edge et al., 2016).

Hydrocarbon contamination including PAH pollution is also a main concern when considering cellular impacts of offshore oil and gas activities on sponges. Water-accommodated oil fraction (solution of soluble hydrocarbons in seawater) activates the Mitogen-Activated Protein Kinase (MAPK) and apoptosis pathways in the sponge *Suberites domuncula* (Châtel et al., 2011). The MAPK pathway plays an important role in cellular response to environmental and oxidative stress (Regoli and Giuliani, 2014). Increased DNA damage was also detected in *S. domuncula* (Châtel et al., 2011), confirming previous work conducted by Zahn et al. (1981, 1983) showing exposure to PAH-induced DNA damage in the shallow-water sponge *Tethya lyncurium*.

The cytochrome P450-dependent monooxygenase system has also been shown to be involved in the detoxification of PAH benzo-a-pyrene, in two marine sponge species (Sol e and Livingstone, 2005). Lower yields of cytochrome P450 protein were detected in sponges compared with other Phyla (Cnidaria, Mollusca, Annelida, Arthropoda, Echinodermata and Chordata), but this could result from overall lower metabolic rates (Sol e and Livingstone, 2005). Under PAH-contaminated conditions produced in the laboratory, PAH molecules interact with the aryl hydrocarbon receptor and induce the cytochrome P450 pathway (Regoli and Giuliani, 2014). The cytochrome P450 pathway is known to play an important role in oxidative stress responses (Sol e and Livingstone, 2005), which are induced in many organisms after exposure to PAHs (Nebert et al., 2000; Puga et al., 2002; Regoli and Giuliani, 2014). Oxidative stress is a consequence of an imbalance in the antioxidant system in an organism. Normal aerobic metab- olism produces reactive oxygen species (ROS), which are neutralised by the antioxidant system. Exposure to xenobiotic compounds can increase the formation of ROS and decrease the antioxidant system’s functioning. Formation of ROS, in turn, downregulates the cytochrome P450, which limits the organism’s capacity to deal with contaminants such as PAHs (Regoli and Giuliani, 2014). The role of the aryl hydrocarbon receptor in organisms impacted by oil spills was recently confirmed in a transcriptomic study showing an induction of a large amount of stress response genes such as the aryl hydrocarbon receptor and the glutathione-S-transferase in oysters deployed during the Deepwater Horizon oil spill (Jenny et al., 2016). However, to the authors’ knowledge, no studies have reported the activa- tion of the aryl hydrocarbon receptor and cytochrome P450 pathway in deep-sea sponges.

Dispersants themselves have been shown to trigger cellular stress responses in different organisms. In the commonly used model organism Caenorhabditis elegans (Nematoda), exposure to dispersant CorexitTM 9500A caused the abnormal expression of 12 genes, involved in a wide range of biological processes ranging from egg laying to neurological functions and oxidative stress (Zhang et al., 2013). However, in the tropical coral *Montastraea franksi,* CorexitTM 9527 exposure led to increased expression of genes coding for P-glycoprotein, heat shock protein 70 and heat shock protein 90 and, to a lesser extent, proteins involved in other cellular stress responses (Venn et al., 2009). Furthermore, exposure to dispersants alone as well as dispersants and crude oil leads to an increase in cell membrane damages in diatoms, which was not observable in diatoms exposed to oil alone (Hook and Osborn, 2012). No studies so far have investigated the impact of dispersants on marine sponges.

4.2. Impacts of Offshore Oil and Gas Production Activities on Deep-Sea Sponge-Associated Microorganisms

Sponges host highly diverse microbial communities often compared for its complexity to the bacterial community of the mammalian gut (Hentschel et al., 2012). Although bacteria generally dominate deep-sea sponge micro- bial communities, eukaryotic and archaeal symbionts have also been described. Mainly found in the mesohyl of the sponges these microbes are metabolically very active and are believed to play important roles in the nitrogen and carbon metabolism (Li et al., 2014). Deep-sea sponges are a rich source of secondary metabolites of great interest as new therapeutic compounds, and it is often the associated microbial communities that synthesise these compounds. Sponges' secondary metabolites show proper- ties that include antifouling, antifungal, antibacterial or antiviral properties and are believed to play a major role in sponge defence against diseases or against other benthic organisms competing for the same substrata (Sipkema et al., 2005).

The impact of environmental pollution and specifically exposure to hydrocarbons or other offshore oil and gas extraction activities on the sponge-associated microbial communities are currently unknown. Studies have investigated the stability of the shallow-water sponge-associated microbial community when exposed to thermal stress, changes in seawater pH or to high metal concentrations (Fan et al., 2013; Fang et al., 2013; Selvin et al., 2009; Tian et al., 2014; Webster and Hill, 2001; Webster et al., 2008). However, only a few of these studies found, under stressed conditions, a shift in the associated microbial community composition (Fan et al., 2013; Tian et al., 2014; Webster and Hill, 2001; Webster et al., 2008). A change in associated microbes was also correlated with a decline in overall sponge host health status characterised by an increase in sponge tissue necrosis and increased expression of genes linked to cellular oxidative stress (Fan et al., 2013; Tian et al., 2014; Webster and Hill, 2001; Webster et al., 2008). An oil-degrading surfactant biosynthesis gene has been isolated from bacteria associated with the shallow-water sponge *Acanthella sp.* (Anburajan et al., 2015). However, the capacity of the bacteria to synthesise the surfactant when associated with the marine sponge and when exposed to crude oil was not investigated (Anburajan et al., 2015). In the Gulf of Mexico, the deep-sea sponge *Myxilla methanophila* growing on tubeworms near cold seeps was described to be associated with putative oil-degrading bacteria after deep sequencing of its associated microbial community (Arellano et al., 2013). In this case, it was hypothesised that the sponge had acquired the symbiont from its environment naturally rich in hydrocarbons (Arellano et al., 2013). Whether the oil-degrading bacteria played a role in hydrocar- bon detoxification or in sponge nutrition was not investigated (Arellano et al., 2013). The capacity of deep-sea marine sponges to acquire oil- degrading bacteria after an oil spill event has not yet been investigated.

5. Conclusions

Oil and gas activities are today taking place in deeper settings and will impact deep-sea ecosystems. Oil and gas production activities impact deep- sea sponges and the habitats they form at all stages of field development and at community, individual and cellular levels as summarised in Table 2. At com- munity level, physical disturbance and discharge of drill muds have been shown to decrease diversity and density of organisms associated with deep-sea sponge grounds. At individual level, physical disturbance and increased sedimentation inhibit the filtration systems of deep-sea sponges, while the discharge of produced water and drill cuttings could lead to bioaccumulation of hydrocarbons and metals (as shown in shallow-water sponges). At cellular and molecular levels, discharge of drill muds and produced water could trigger cellular stress responses as has been shown for shallow-water sponges exposed to PAH and metal-contaminated seawater. Accidental releases of hydrocarbons and the use of dispersants during oil spill could result in benthic diversity decrease, individual sponge mortality and larval settlement disruption as well as trigger oxidative stress. However, most of the possible impacts described in this review have not yet been studied in deep-sea sponges.

Offshore oil and gas activities are managed by national legislations within the exclusive economic zones and under United Nations legislations in the high seas. In most countries, oil companies are required to complete EIAs before starting any new operation (Budd, 1999). EIAs have become a major component of oil and gas industry regulation as their aim is to identify and manage adverse environmental impacts before they occur by: (1) screening for possible impacts, (2) completing baseline surveys, (3) producing Environmental Statements and (4) leading the decision-making process. The major benefits of EIAs are that the environment is considered in an early stage of the project and that scientific data are acquired during the EIA pro- cess (Budd, 1999). However, despite its widespread use in offshore activity regulation, EIAs' project-specific approach means that cumulative environ- mental impacts owing to the development of several oil fields in the same area cannot be taken into account (Barker and Jones, 2013) and by their nature EIAs have to rely on existing scientific understanding of ecosystems function. Despite promising advances in recent years the latter remains poorly developed in deep-water settings including those that support deep-sea sponge grounds. Strategic Environmental Assessments are there- fore now starting to be adopted by the oil and gas industry (Fidler and Noble, 2012). National jurisdictions apply only to waters within the 200 nm EEZ of coastal states. However, deep-sea sponge grounds occur beyond the EEZ of coastal states. The United Nations Convention on the Law of the Sea (UNCLOS) signed in 1972 first enabled the deep-sea floor and high seas to be exploited for biological and geological resources and technological improvements over time have made the deep sea acces- sible (Ramirez-Llodra et al., 2011). In 2008 Ecologically or Biologically Sig- nificant Areas (EBSAs) were defined by the United Nations Convention on Biological Diversity to help international organisations protect key marine environments. Following this, eight EBSAs were proposed in September 2011 in the NE Atlantic to protect cold-water corals and sponge grounds (Weaver and Johnson, 2012) but have not been subsequently developed. Since 2009, deep-sea sponge grounds are considered by the UN Food and Agriculture Organisation as Vulnerable Marine Ecosystems, as defined by the General Assembly resolution 61/105, calling states to restrict destruc- tive fishing practices. Although VME designations are used to control the adverse effect of fishing on marine species, it brings organisms with specific conservation needs to light and is therefore also useful in the context of off- shore oil and gas industry activities. In addition to EBSA and VME designations, the development of Marine Protected Areas (MPAs) and design of connected networks have gained momentum during the early 2000 under the OSPAR convention (Howell, 2010; O'Leary et al., 2012). Indeed, deep-sea sponges entered the OSPAR Threatened and/or Declining Spe- cies and Habitat list in 2008. Criteria for the designation of MPAs were determined by the World Conservation Union (IUCN) in 1994 and include ecological, scientific and economic importance (Howell, 2010).

Lack of scientific data on the effects of deep-sea hydrocarbon exploita- tion activities on deep-sea benthic organisms such as sponges is limiting the efficiency of national and international management and monitoring regu- lations. Collaborative initiatives between academic and industry partners provide a constructive way to close the current knowledge gaps. The access to and sharing of environmental data between industry and academia should also be encouraged. Furthermore, the increasing use of new technologies and methodologies such as Autonomous Underwater Vehicles and predic- tive habitat modelling to survey and map large areas of the seabed will offer new opportunities to increase our understanding of deep-sea benthic environments. As oil and gas production activities already occur within deep-sea sponge grounds, further collaboration between industry and research partners to better monitor the effect of oil and gas activities on deep-sea sponge and deep-sea sponge grounds is urgently needed.

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Figure 1: Example of deep-sea sponges and of the habitats they form. (A, B) Example of deep-sea sponge morphotypes from the Faroe-Shetland Channel. (C) Carnivorous sponges of the family Cladhorizidae constitute a deep-sea ecological oddity. (D) Present in high abundance, deep-sea sponges can form sponge grounds as seen here at 1890m depth from Orphan Knoll, NW Atlantic. (E to H) Deep-sea sponges and sponge grounds provide habitats for various benthic organisms (I and J) Sponges are impacted by offshore oil and gas activities amongst other through increased sedimentation. Photo credits: (D) Fisheries & Oceans, Canada (DFO). (G to I) SERPENT Project, National Oceanography Centre, Southampton UK.

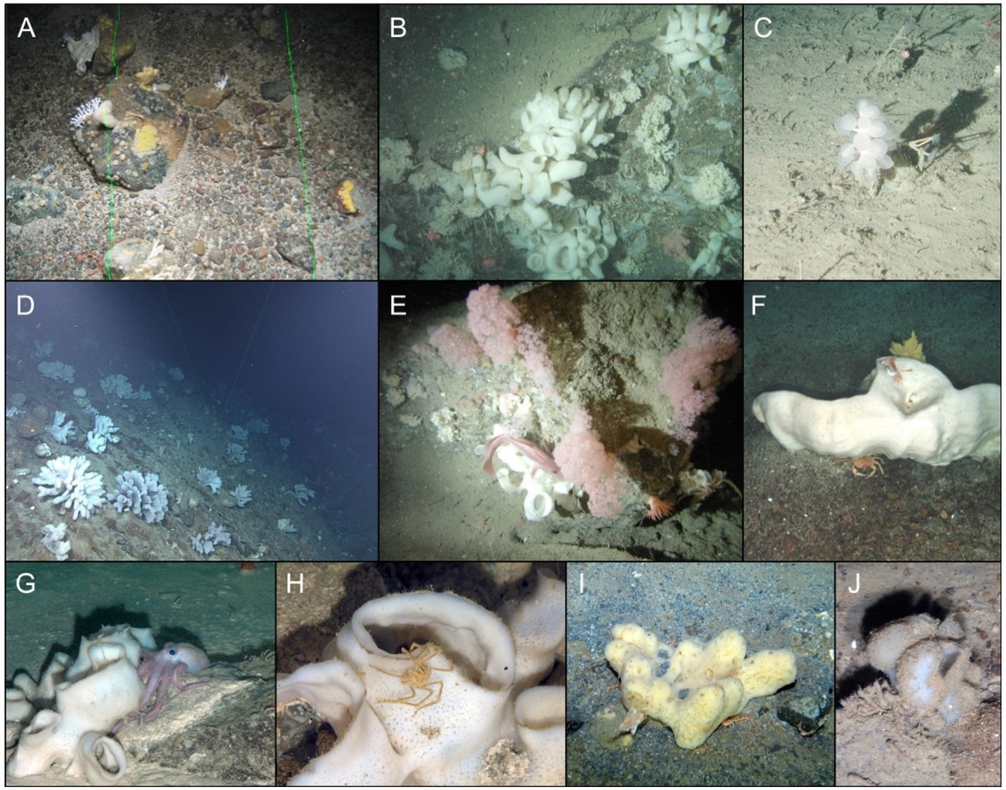

Figure 2: Flow chart of oil fields development process divided into 4 phases and main activities associated with each phase.

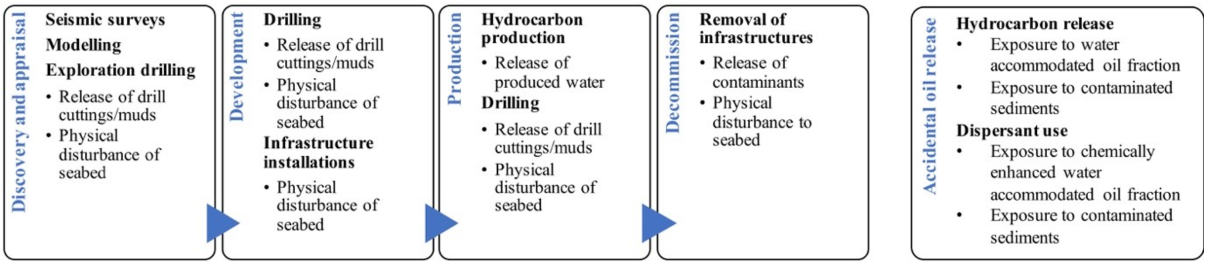

Figure 3: Field data on the initial impact and recovery from oil drilling disturbance in deep-sea sponges in the Faroe-Shetland Channel (FSC), at the Laggan site (Jones *et al.* 2012), and Norwegian Sea (NS), at the Morvin site (Gates and Jones 2012).

The density of all megafaunal sponges is shown with distance from drilling activity at different time points (colours) after drilling (units years [yr] and days [d]). Pre indicates densities prior to drilling activity.

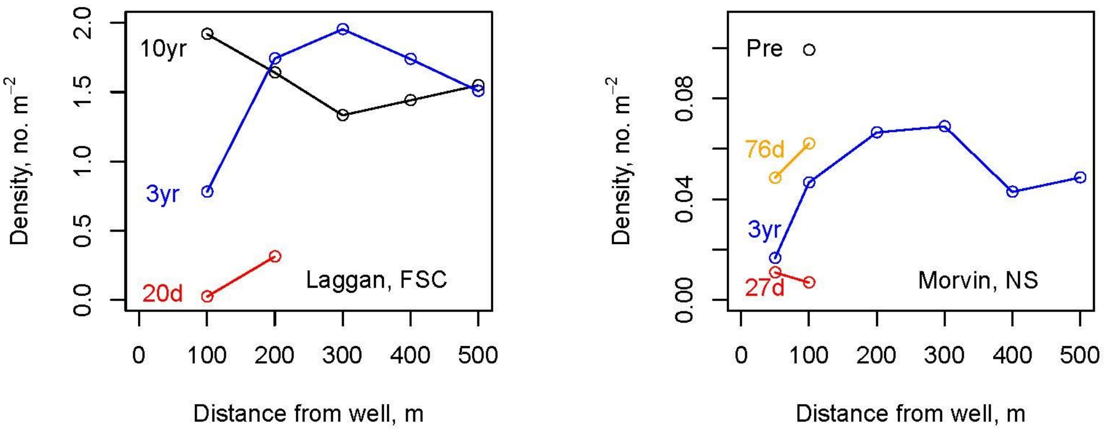

Table 1: VME and EBSA criteria and their applicability to sponge grounds as respectively defined by the UN FAO and the UN CBD.

Designation	Criteria	Characteristics of deep-sea sponges and/or sponge grounds fulfilling criteria
VME	Uniqueness or rarity	Deep-sea sponge grounds are not rare but occur in **specific and limited areas** where favourable abiotic conditions are present
	Functional significance of habitats	Deep-sea sponges increase **physical heterogeneity** of benthic ecosystems
	Fragility	Deep-sea sponges are **extremely vulnerable to physical damage** by trawling or other anthropogenic activities
	Life history traits making recovery difficult	Deep-sea sponges are considered as **slow-growing, long lived** organisms and their reproduction cycles are largely unknown
	Structural complexity	Deep-sea sponge grounds give **three-dimensionality** to seabed increasing the number of available microhabitats
EBSA	Uniqueness or rarity	Deep-sea sponge grounds are not rare but occur in **specific and limited areas** where favourable abiotic conditions are present
	Special importance for like history stages of species	Deep-sea sponge grounds constitute **nursery grounds** for fish and invertebrate species
	Importance for threatened, endangered or declining species and/or habitats	Deep-sea sponge grounds constitute nursery grounds for **threaten species** such economically important fishes
	Vulnerability, fragility, sensitivity or slow recovery	Deep-sea sponges are considered as **slow-growing, long lived** organisms, making them both vulnerable to anthropogenic activities and slow to recover
	Biological productivity	Deep-sea sponges play important roles in the **biogeochemical cycling** and the habitat they create support diverse benthic ecosystems
	Biological diversity	Deep-sea sponge grounds provide a **habitat** to diverse benthic vertebrate and invertebrate species
	Naturalness	Anthropogenic activities such as oil and gas exploitation and mining are **impacting deep-sea sponge grounds**

Table 2: Overview of major impacts of offshore oil and gas activities on deep-sea sponges and deep-sea sponge grounds at community, individual, cellular and molecular levels and throughout oil field development. Impacts described in deep-sea sponge species are highlighted in green. Impacts described in shallow-water sponge species but not yet confirmed for deeper species are highlighted in orange. Impacts described in other benthic organisms but not yet investigated in any sponge species are highlighted in red to emphasize current knowledge gaps.

		Exploration and appraisal	**Field Development**	**Production**	**Decommissioning**	**Deep-sea oil spill**
Community level	*Main concern*	*Physical disturbance of seabed and increase sedimentation*		*Discharge of drill muds and cuttings*	*Removal of structure*	*Exposure to high hydrocarbons and dispersant concentrations*
	Impacts				Benthic habitat destruction.	Changes in benthic community abundance, age structure and trophic interactions.
		Diminished benthic community.		Benthic community diversity/abundance decrease.		
Individual Level	*Main concern*	*Seismic survey and increase sedimentation*	*Increase sedimentation*	*Discharge of produced water*	*Release of chemical contaminants*	*Exposure to high hydrocarbons and dispersant concentrations*
	Impacts	Larval development delay and malformations.				Health decline, hydrocarbon bioaccumulation.
		Changed respiration rate and reproduction capacities. Decreased growth rate.		Bioaccumulation of PAH and heavy metals.		Larval settlement disturbance. Hydrocarbon bioaccumulation.
		Paused filtration.				
Cellular & Molecular levels	*Main concern*	*Discharge of drill muds and exposure to chemicals via release of produced water*				*Exposure to high hydrocarbons and dispersant concentrations*
	Impacts	Decrease immune system function.				Decreased immune system function.
		Activation of MAPKs and cytochrome P450 pathways. Oxidative stress.				Activation of MAPKs and cytochrome P450 pathways. Oxydative stress.
		Decrease of lysosomal membrane stability.				