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## Asphalt mounds and associated biota on the Angolan margin



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## ABSTRACT

Release of hydrocarbons from sediments is important in increasing habitat heterogeneity on deep ocean margins. Heterogeneity arises from variation in abiotic and biotic conditions, including changes in substratum, geochemistry, fluid flow, biological communities and ecological interactions. The seepage of heavy hydrocarbons to the seafloor is less well studied than most other cold seep systems and may lead to the formation of asphalt mounds. These have been described from several regions, particularly the Gulf of Mexico. Here, we describe the structure, potential formation and biology of a large asphalt mound province in Block 31SE Angola. A total of 2254 distinct mound features was identified by side-scan sonar, covering a total area of 3.7 km<sup>2</sup> of seafloor. The asphalt mounds took a number of forms from small (< 0.5 m diameter; 13% observations) mounds to large extensive (< 50 m diameter) structures. Some of the observed mounds were associated with authigenic carbonate and active seepage (living chemosynthetic fauna present in addition to the asphalt). The asphalt mounds are seabed accumulations of heavy hydrocarbons formed from subsurface migration and fractionation of reservoir hydrocarbons primarily through a network of faults. In Angola these processes are controlled by subsurface movement of salt structures. The asphalt mounds were typically densely covered with epifauna (74.5% of mounds imaged had visible epifauna) although individual mounds varied considerably in epifaunal coverage. Of the 49 non-chemosynthetic megafaunal taxa observed, 19 taxa were only found on hard substrata (including asphalt mounds), 2 fish species inhabited the asphalt mounds preferentially and 27 taxa were apparently normal soft-sediment fauna. Antipatharians (3.6 ± 2.3% s.e.) and poriferans (2.6 ± 1.9% s.e.) accounted for the highest mean percentage of the observed cover, with actinarians (0.9 ± 0.4% s.e.) and alcyonaceans (0.4 ± 0.2% s.e.) covering smaller proportions of the area. Asphalt mounds represent a common and important habitat on several margin systems globally and should be recognised in future environmental assessment and management of these areas.

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## 1. Introduction

Subsurface flows of hydrocarbons play an important role in increasing habitat heterogeneity in the deep sea (Cordes et al., 2009; Cordes et al., 2010; Cordes et al., 2008; Sibuet and Vangriesheim, 2009). Seafloor expressions of hydrocarbon seepage take a great number of forms depending on fluid flow, the constituents of the release and the substratum (Cordes et al., 2009; Pinheiro et al., 2003; Sibuet and Olu, 1998; Sibuet and Vangriesheim, 2009). Cold seeps, typically of lighter hydrocarbons such as methane, may support high biomass communities of microbes, chemosynthetic fauna, including siboglinid tubeworms, bathymodiolid mussels and vesicomid clams, and heterotrophic

fauna (Cordes et al., 2010). Microbial alteration of hydrocarbons and anaerobic methane oxidation in areas of active hydrocarbon seepage can lead to the formation of extensive areas of hard substratum in the form of authigenic carbonates (Formolo et al., 2004; Wallman et al., 1997). Habitat heterogeneity associated with carbonates, other substrata such as gas hydrates (Sibuet and Vangriesheim, 2009), and structure-forming organisms, in turn supports numerous protozoan and invertebrate species (Sibuet and Olu, 1998) that respond to changes in structural complexity, habitat geochemistry, nutrient sources, and interspecific interactions in different ways and at different scales (Cordes et al., 2010). The widespread occurrence of seeps and hard substrata produced by seabed fluid flow along the continental margins provides mechanisms for the broad-scale distribution of species, for example by facilitating genetic exchange across the Atlantic equatorial belt from the Gulf of Mexico to the seeps of the West Nigerian margin (Cordes et al., 2007). The increased habitat complexity and

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connectivity created by cold seeps on deep continental margins exerts a major influence on the abundance and diversity of species at both local and regional scales (Buhl-Mortensen et al., 2010; Cordes et al., 2009; Levin and Dayton, 2009).

Although the natural seepage of oil is less common than that of lighter hydrocarbons, it nevertheless accounts for nearly half of all oil input to the ocean (Kvenvolden and Cooper, 2003). Oil seeps also occur in a range of environments from the continental shelves (Allen et al., 1970; Vernon and Slater, 1963) to continental slopes (Kennicutt et al., 1988a; Kennicutt et al., 1988b) and deep basins (Didyk and Simoneit, 1989; MacDonald et al., 2004). Satellite imagery from the northwest Gulf of Mexico suggests 1900 km<sup>2</sup> of persistent natural oil slicks at the sea surface in that region alone (Hu et al., 2009), with many other seep regions dispersed globally. Oil seeps also typically release large quantities of methane (Kvenvolden and Rogers, 2005), which may support chemosynthetic communities (Valentine et al., 2010).

Despite the importance of oil seeps as sources of hydrocarbons to the ocean and atmosphere, and the large number of seeps that are likely to exist globally, only a small number of seafloor features (for example, mounds, tar flows, calderas) associated with active seepage of oil have previously been described, and preservation in the geologic record seems rare (Valentine et al., 2010). The seepage of heavy hydrocarbons can lead to the formation of asphalt mounds, large structures of solidified asphalt on the seafloor distinct from irregular mats and pools of viscous tar described from coastal (Hornafius et al., 1999) and continental slope (MacDonald et al., 2003) oil seeps (MacDonald et al., 2004). Asphalt mounds have been identified in deep water in the Gulf of Mexico and the Santa Barbara Basin. Asphalt mounds at the Campeche Knolls (MacDonald et al., 2004), in the Gulf of Mexico, are the most thoroughly investigated. These comprise extensive surface deposits of lava-like solidified asphalt emanating from points along the southern rim of a broad, craterlike graben near the crest of a salt dome (MacDonald et al., 2004). The released petroleum forms characteristic subcircular to linear flow structures at the seafloor up to 20 m wide with surfaces that are 'ropy' or 'rough', similar to magmatic lava flows. After extrusion, the asphalts are then subject to sequential alterations. The viscosity of the heavy petroleum increases and the volume reduces owing to the loss of volatiles. This solidification and subsequent shrinkage leads to the formation of visible cracks in the asphalt surface, followed by fragmentation of the entire deposit (Brüning et al., 2010). Asphalt mounds have also been found in the Gulf of Mexico at two commercial hydrocarbon appraisal and development areas, Puma (Weiland et al., 2008) and Shenzi (Williamson et al., 2008), both near the Sigsbee Escarpment in the Green Canyon Blocks over 600 km to the NNE of the Campeche Knolls. Furthermore, a single photograph was obtained at another asphalt mound in the Gulf of Mexico (Pequegnat and Jeffrey, 1979). All the asphalt mounds identified in the Gulf of Mexico are associated with shallow buried salt structures (MacDonald et al., 2004; Weiland et al., 2008; Williamson et al., 2008). In the Pacific, asphalt mounds were first identified in shallow waters in Santa Barbara County, California, by SCUBA divers (Vernon and Slater, 1963). Further offshore in the Santa Barbara Basin, high-resolution multibeam data (Keller et al., 2007) have revealed extinct asphalt volcanoes of apparently similar form to the asphalt structures described from the Gulf of Mexico (Valentine et al., 2010).

The biological communities associated with asphalt mounds are often extensive and diverse. Asphalt mounds usually seem to attract a non-chemosynthetic epifaunal assemblage living on the solidified asphalt or nearby authigenic carbonate with asphalt inclusions. In some cases there is also a chemosynthetic community, likely driven by microbial oxidation of hydrocarbons. Microbial films and mats have been found at the Chapopote site

in the Campeche Knolls (MacDonald et al., 2004), at Puma (Weiland et al., 2008), and at an asphalt mound site with active methane venting in the Santa Barbara Basin (Valentine et al., 2010). Vestimentiferan tubeworms (cf. *Lamellibrachia* sp.) were common in close proximity to asphalt flows at Chapopote (MacDonald et al., 2004) and at Puma (Weiland et al., 2008), which they colonized by extending the posterior ends of their tubes into sediments beneath the flow edges or into fissures. Large bivalve shells, including the chemosynthetic family Vesicomidae (cf. *Calyptogena* sp.), were widespread on the sea floor surrounding the asphalt flows and among asphalt pillows and cobbles at Chapopote. Shells and living specimens of chemosynthetic mussels (cf. *Bathymodiolus* sp. and *Solemya* sp.) were found at Chapopote (MacDonald et al., 2004) and associated with a large mound composed of authigenic carbonate at Puma (Weiland et al., 2008). Heterotrophic fauna at Chapopote included galatheid crabs (*Munidopsis* sp.) and shrimp, as well as non-endemic deep-sea fish and invertebrates (*Benthydites* sp., *Psychropotes* sp., and *Pterasterias* sp.). Crinoids and soft corals were attached to asphalt pillows found farthest downslope from the rim (MacDonald et al., 2004). The Puma and Shenzi asphalt mounds were inhabited by a range of epifaunal suspension feeders, such as gorgonians, that did not appear to rely on chemosynthetic production for nutrition (Weiland et al., 2008; Williamson et al., 2008). The Santa Barbara Basin asphalt mounds appear to harbour a community of non-chemosynthetic epifauna, such as anemones, crinoids and cup corals, and provide habitat for mobile species, such as squat lobsters (Galatheaidea) and fish, which are similar to the communities of other rocky reef environments throughout much of the Southern California Bight (Valentine et al., 2010). In general, asphalt mounds appear to be an important habitat in the deep sea, providing a source of hard substratum that attracts an apparently large variety of epifauna. In addition, it appears that areas of asphalt extrusion are often associated with chemosynthetic communities living on asphalt mounds or authigenic carbonates. Asphalt mounds are likely to be considerably more widespread than the current limited evidence suggest, particularly in the vicinity of shallow salt structures, and may be important to consider in regional assessments of deep-water biodiversity.

Here, we describe an extensive and hitherto unknown area of asphalt mounds on the continental slope of Angola, West Africa, the first to be reported from the South Atlantic and the eastern Atlantic continental margin. We describe the structure of the mounds and associated carbonate features, and discuss their possible mode of formation, based on extremely high-resolution acoustic data and seafloor images. In addition, we explore the role of these systems in increasing habitat heterogeneity and biodiversity on the west African margin, focussing specifically on the megafaunal communities associated with the mounds and adjacent benthic habitats. Finally, we demonstrate the variation across these unusual hydrocarbon-driven deep-sea habitats caused by different fluid flow conditions.

## 2. Materials and methods

### 2.1. Study site

Angolan licence block 31 covers a 5349 km<sup>2</sup> area of seafloor on the eastern edge of the southern Congo fan (Droz et al., 2003; Savoye et al., 2009). To the north of the block is the Congo submarine canyon, which connects with the Congo River (Savoye et al., 2009). An estimated  $55 \times 10^6$  t year<sup>-1</sup> of sediment from the Congo River, typically laden with particulate and dissolved organic matter, is deposited on the seabed from surface-derived flux and lateral transport in turbidity flows (Vangriesheim et al., 2009).

Sediment from the Congo River plume has been found up to 800 km from the coast (van Bennekom and Berger, 1984). Most of these sediments are diverted through the Congo Canyon, where sedimentation rates are around  $36 \text{ cm ka}^{-1}$  (Savoie et al., 2009). In the area of Block 31 the sediments are mostly hemi-pelagic in origin and sedimentation rates are lower at  $20 \text{ cm ka}^{-1}$  (Hill et al., 2010b). The surface waters of Block 31 are at the boundary between the tropical waters of the South Equatorial Counter Current to the north and the Benguela current, off Namibia, to the south. This convergence results in upwelling (van Bennekom and Berger, 1984) with high primary productivity in surface waters, estimated to be over  $200 \text{ gCm}^{-2} \text{ yr}^{-1}$  (Behrenfeld and Falkowski, 1997). The near-seabed water in the area of Block 31 appears to have typical temperatures ( $\sim 5^\circ\text{C}$ ) and salinities (34.9 PSU), as well as high dissolved oxygen concentrations ( $230 \mu\text{mol kg}^{-1}$ ) (Vangriesheim et al., 2009). Current speeds in Block 31 are low ( $0.04 \text{ m/s}$ ) (Hill et al., 2010b).

The geology of the Block 31 area is complex and driven by salt tectonics (Thomas et al., 2011; Evans, 2010; Hill et al., 2010a; Hill et al., 2010b). The entirety of Block 31 is underlain by mobile salt of Aptian age (lower Cretaceous, approximately 130–120 Ma). Mobilisation of the salt was initiated soon after deposition, likely during the early Cretaceous period (approximately 120–100 Ma) and continues to the present (Marton et al., 2000). Down-dip (basinward) movement of the suprasalt sedimentary section occurs by gravitational sliding and gravitational spreading over the weaker, mobile salt. Gravitational sliding has resulted in deformation of the sediments by extensional and contractional structures in the updip (landward) and downdip (basinward) regions of the salt province, respectively. Deformation of the salt takes the form of individual salt diapirs (majority of study area; easternmost side) and complex amalgamated salt bodies in the form of salt canopies (western side of study area). Depth to the top of the salt detachment is variable across the region, but is mostly within the range of 5–7 km, below seabed. Above the salt a complex fault system exists (Gay et al., 2004). In the study area investigated here this principally comprises domino faults (Mandl, 1987) above the shallow salt canopy (western side of study area, timing uncertain); polygonal faults in Pliocene mini-basins (between salt structures) and radial faults around the passive salt diapirs (eastern side of study area). Radial faults and polygonal faults are continuous with each other (Gay et al., 2004), reflecting a change in the stress regime near the diapir margins. Block 31 has an irregular morphology, as the sea floor is highly deformed by salt diapirism (Evans, 2010; Hill et al., 2010a; Hill et al., 2010b) and compressional structures, including salt domes and reverse faults (Savoie et al., 2009). Sediment fluid flow features are also present, such as pock marks (Olu-Le Roy et al., 2007; Savoie et al., 2009; Unterseh, 2013) and cold seeps (Cambon-Bonavita et al., 2009; Olu et al., 2009; Sibuet and Vangriesheim, 2009; Unterseh, 2013; Waren and Bouchet, 2009). The extensive hydrocarbon seepage at the seafloor at Block 31 is also indicated by satellite synthetic-aperture radar observations of persistent surface oil slicks (NPA Satellite Mapping Global Offshore Seepage Database).

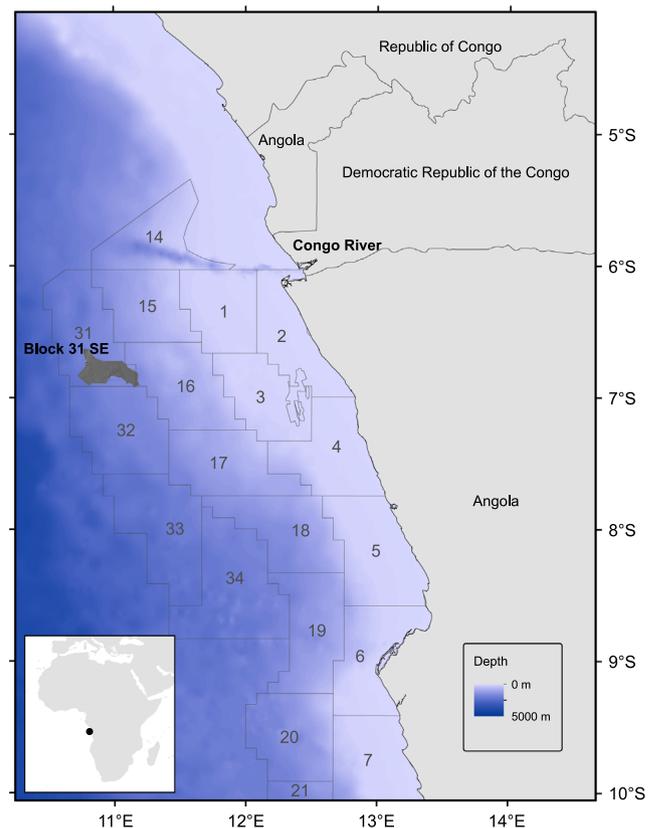
The benthic biology of the deep waters off Angola has received increasing attention (Arbizu and Schminke, 2005; Bianchi, 1992; Kroncke and Turkay, 2003; Sibuet et al., 1989; Van Gaever et al., 2009; Vinogradova et al., 1990) and has been the focus for a number of large international programmes with biological components including DIVA (Arbizu and Schminke, 2005), ZaiAngo (Savoie et al., 2009) and BioZaire (Galéron et al., 2009; Vangriesheim et al., 2009). These studies have mostly focussed on chemosynthetic systems in the deep bathyal (Sibuet and Olu-LeRoy, 2002; Sibuet and Vangriesheim, 2009) or deep-water coral reefs at the shelf-edge (Le Guilloux et al., 2009). Less scientific attention has been directed towards the bathyal depths of the

margin, although this area has been the subject of many unpublished environmental assessments by the oil industry.

## 2.2. Data collection

Data were collected on five surveys of the south-eastern section of Angola Block 31 (Block 31 SE; Fig. 1) using R/V *Northern Resolution*. The first two surveys in December 2007 to March 2008 (most of the area) and August 2008 (southwest area known as ‘South Dione’) obtained ultra-high-resolution seismic data and used a C&C Technologies Inc. *C-Surveyor II*<sup>TM</sup> autonomous underwater vehicle (AUV) to obtain simultaneous multibeam bathymetry, side-scan sonar and sub-bottom profiler data. An environmental survey on the M. V. *Sea Trident* captured several photographs and videos of the asphalt mounds using a towed camera platform (Seatrionics Digital Video Data Telemetry System (DTS) 6000) in April 2008. This was followed up by two remotely operated vehicle (ROV) surveys (Supplementary Fig. 1) specifically to investigate the asphalt mounds, carried out from M. V. *Russell Tide* using the *Oceaneering Millennium 76* ROV in November 2008 and June 2009 (10.6 and 17.4 km total track length on seabed respectively).

The acoustic survey area of Block 31 SE ( $6^\circ 45' \text{ S } 11^\circ 00' \text{ E}$ ; Fig. 1) covers around  $825 \text{ km}^2$  of seabed at a depth of 1350–2150 m (Supplementary Fig. 2). The 6700 km long combined AUV survey covered the area at very high resolution in a grid pattern with 150 m spacing between east-west tracklines and 1 km between north-south tracklines. The AUV was operated at an altitude of 40 m above the seafloor while surveying. AUV positions are



**Fig. 1.** Map showing the location of survey area in Angolan Licence Block 31 SE. The location of the outflow of the Congo River is labelled. The other Angolan licence blocks are shown in light grey. Depth is shown in different shades of blue. The position relative to the African continent is shown as a black dot on the inset map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

calculated using a Kalman filter algorithm, which uses input data from a Simrad HiPAP System (High Precision Acoustic Positioning), inertial navigation and Doppler velocity speed logs to provide a position solution. The AUV positions were recorded continuously at 125-m intervals. The post-processed positions for the AUV data are accurate to within  $\pm 5$  m. Multibeam bathymetry data were collected using a 200 kHz Simrad EM2000 swath bathymetric system. Side-scan sonar data were collected using an Edgetech side scan sonar system set to the 120 kHz frequency band and a range of 211 m per channel. The side-scan sonar transmits a sound pulse about 3 times per second resulting in an along track ping distance of about 60 mm when the AUV travels at  $2 \text{ m s}^{-1}$ . This system produces 111 beams or soundings across a swath of approximately 200 m width. Sub-bottom profiles were collected using an Edgetech Chirp subbottom profiler with transmission pulses generated in frequencies modulated between 1.5 and 4.5 kHz with a pulse rate of 33 milliseconds. All data were recorded in the Camacupa TM12SE coordinate reference system.

Identification of mound features from side-scan backscatter data was carried out manually in ArcGIS by experienced geoscientists. The identification was conservative, with high-backscatter (hard) features close to the resolution of the data (0.5 m pixel size) ignored. Thus, smaller-sized asphalt features may exist but not be mapped.

ROV images were obtained from around the study area for ground-truthing of asphalt presence and for biological analysis. Video and still images were obtained using a standard-definition video camera (576 lines; Phase Alternating Line (PAL)) and a Nikon E995 digital stills camera ( $2048 \times 1536$  pixels) in a pressure housing mounted on the ROV, which was equipped with parallel green lasers for scaling (500 mm apart). The ROV also had an ultra-short baseline navigational transponder attached, so its geographic location could be determined ( $\pm 20$  m). The ROV surveys targeted features of interest identified in the acoustic data, and as such, they were not unbiased quantitative samples. The ROV visited 9 areas with asphalt mounds (Figure S1) and obtained images along 4 transects in 2008 (covering  $\sim 10,500$  m) and 15 transects in 2009 (covering  $\sim 17,400$  m).

Percentage cover of biota visible on asphalt mounds was measured from seafloor photographs using ImageJ software (National Institute of Health). Parallel laser dots visible on each image were used for scaling. Percentage cover and area estimates were made by drawing around each organism or mound manually and calculating the area enclosed by the polygon. All organisms attached to each mound were measured in their entirety, so in some cases, with a large animal living on a small asphalt mound, percentage coverage was greater than 100%. All mounds visible in high-quality photographs were analysed. Mounds were delineated by the level of surface sediments, in some cases multiple mounds appeared (from their morphology) to be joined together under the sediment surface.

### 3. Results

#### 3.1. Geology

Bathymetric data from the study area show the seafloor expression of two large (up to 5 km diameter) domes (Fig. 2). Seismic profiles reveal that these domes are uplifted strata forced up by rising passive salt diapirs. Sub-bottom profiles across the diapirs show hard structures, confirmed by geotechnical sampling to be a mixture of hard authigenic carbonate, claystone and asphalt, reaching close to the sediment surface (Fig. 3). Faults in the stratified shallow soft sediments are visible in several sections (e.g. Fig. 3D). Polygonal faults are visible in seismic amplitude

extraction maps through these depth intervals. In at least one location a fault in the shallow section appears to correspond with locations of surface expressions of asphalts, although asphalt mounds are more commonly observed in areas with no obvious shallow faulting in the sub-bottom profile data (Fig. 3). Seismic data reveal more extensive fault networks underlying the shallow sediments.

#### 3.2. Distribution of asphalt on the seafloor

Extensive asphalt mounds were revealed at the seafloor in the side-scan sonar interpretation in the Block 31 SE area, with 2254 distinct mound features identified, covering a total area of  $3.719 \text{ km}^2$  of seafloor. The 2008 and 2009 ROV investigations were targeted to areas where mounds were predicted from side-scan sonar interpretation. Although not all of these areas with predicted mounds were investigated, every site the ROV visited had asphalt mounds present. Within specific areas investigated by the ROV, generally more asphalt features were identified in images than predicted from the side-scan sonar data. This may be because some of the features observed by ROV were smaller than the pixel size for the side-scan sonar data (i.e. 0.5 m diameter). The asphalt mounds measured from ROV photographs ( $n=106$ ) had a mean area per mound of  $0.22 \text{ m}^2 \pm 0.04 \text{ m}^2$  standard error. The smallest mound measured from photographs had an area of  $0.0002 \text{ m}^2$  and the largest covered most of the area of the photograph (mound area  $2.07 \text{ m}^2$ ). Larger mounds were observed in video but could not be quantified.

#### 3.3. Asphalt mounds

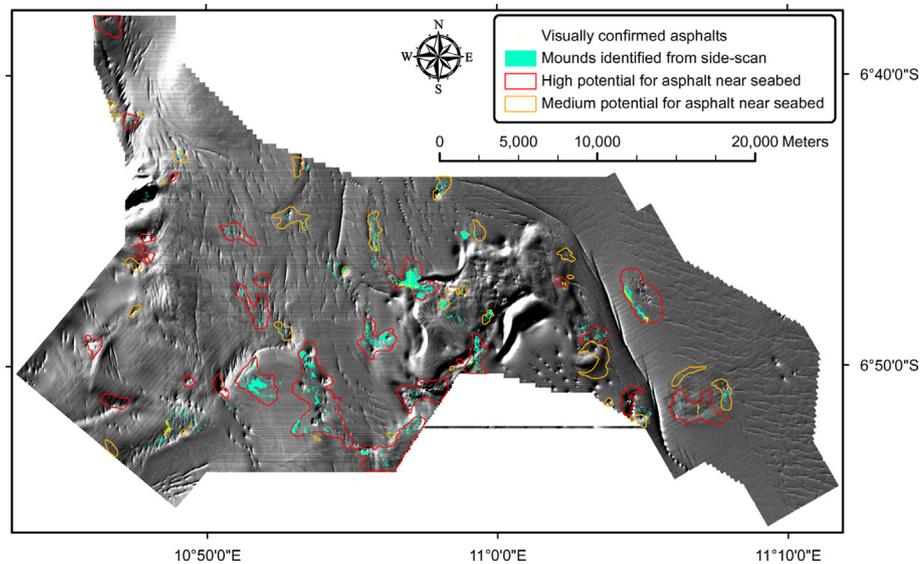
The asphalt mounds took a number of forms (Fig. 4) from small ( $< 0.5$  m diameter) discrete mounds to large extensive ( $< 50$  m diameter) structures. In single photographs of the seafloor (representing  $1\text{--}3 \text{ m}^2$  seafloor;  $n=435$ ) there was a range of asphalt coverage including: a single small mound (2.5% observations), multiple discrete small mounds (4.1% observations), coalesced small mounds (6.4% observations) and large mounds ( $> 0.5$  m diameter; 86.9% observations). The larger mounds occasionally formed distinct linear features (Fig. 4). Most mounds observed in the images had relatively little sediment on their surface; the covering was generally less than 5 mm thick. Carbonates were associated with the asphalt mounds in 3.2% of photographs. Active seepage, characterised by living chemosynthetic fauna, was observed in 6.2% of the photographs. Samples of carbonates taken at sites with chemosynthetic fauna showed asphalt on the surface, in interstices and as inclusions in the authigenic carbonates.

Careful ROV excavations of a discrete small asphalt mound showed a structure with a rounded base (Fig. 4) with no obvious subsurface asphalt attachment, suggesting that it was extruded elsewhere. Deck-based observations of retrieved samples suggest asphalt mounds range from a near-liquid consistency to hardened solid structures.

#### 3.4. Biology

The asphalt mounds were typically densely covered with epifauna (74.5% of mounds imaged at suitable resolution for faunal observations [ $n=106$  photographs] had visible epifauna). Antipatharians ( $3.6 \pm 2.3\%$  s.e.) and poriferans ( $2.6 \pm 1.9\%$  s.e.) accounted for the highest mean percentage of the observed cover, with actinarians ( $0.9 \pm 0.4\%$  s.e.) and alcyonaceans ( $0.4 \pm 0.2\%$  s.e.) covering smaller proportions of the area.

Individual asphalt mounds varied considerably in coverage of attached epifauna (from 0% to 236%). The area of each asphalt mound was positively correlated with the percentage cover of



**Fig. 2.** Artificially illuminated bathymetry (hill-shaded) of the survey area showing asphalt mounds identified from visual images (yellow) and side-scan sonar data (blue). Areas are also shown where there is an estimated high (red) and medium (orange) potential of asphalt on the seafloor from interpreted AUV sub-bottom profile and ultra-high-resolution seismic data. There are two features interpreted as surface expressions of salt diapirs (radius approx. 2000 m) centred  $11^{\circ}6'52.421''\text{E } 6^{\circ}50'58.156''\text{S}$  and  $11^{\circ}5'0.361''\text{E } 6^{\circ}47'36.295''\text{S}$  and several features associated with uplift of older sediments above salt features (see Fig. 8). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

epifaunal organisms (Spearman's rank correlation  $\rho=0.31$   $p<0.01$ ) and the number of species of epifaunal organisms ( $\rho=0.47$   $p<0.001$ ). Although the majority (58%) of the smallest mounds ( $<100$  mm in diameter) were devoid of megafauna, some had large epifaunal organisms, such as gorgonians and anemones, growing on them.

A total of 49 megafaunal taxa was distinguished in the survey area, not including those found at active seep sites. Of the apparently non-chemosynthetic fauna, 19 taxa were only found on hard substrata (Fig. 5), 2 fish species inhabited the asphalt mounds preferentially and 27 taxa were apparently normal soft-sediment fauna (Table 1; Fig. 6). It is not possible to ascertain if any species preferentially or exclusively live on asphalt mounds as opposed to other hard substrata. A total of 11 fish taxa, 14 echinoderms, 2 molluscs, 4 arthropods (one species, *Munidopsis* sp., was only found associated with one piece of wood (Fig. 6)) and was omitted from further analysis), 12 cnidarians and 6 sponges were found (Table 1). No scleractinian corals were observed. Owing to limited sample sizes, it is expected that these observations are an underestimate of true species richness.

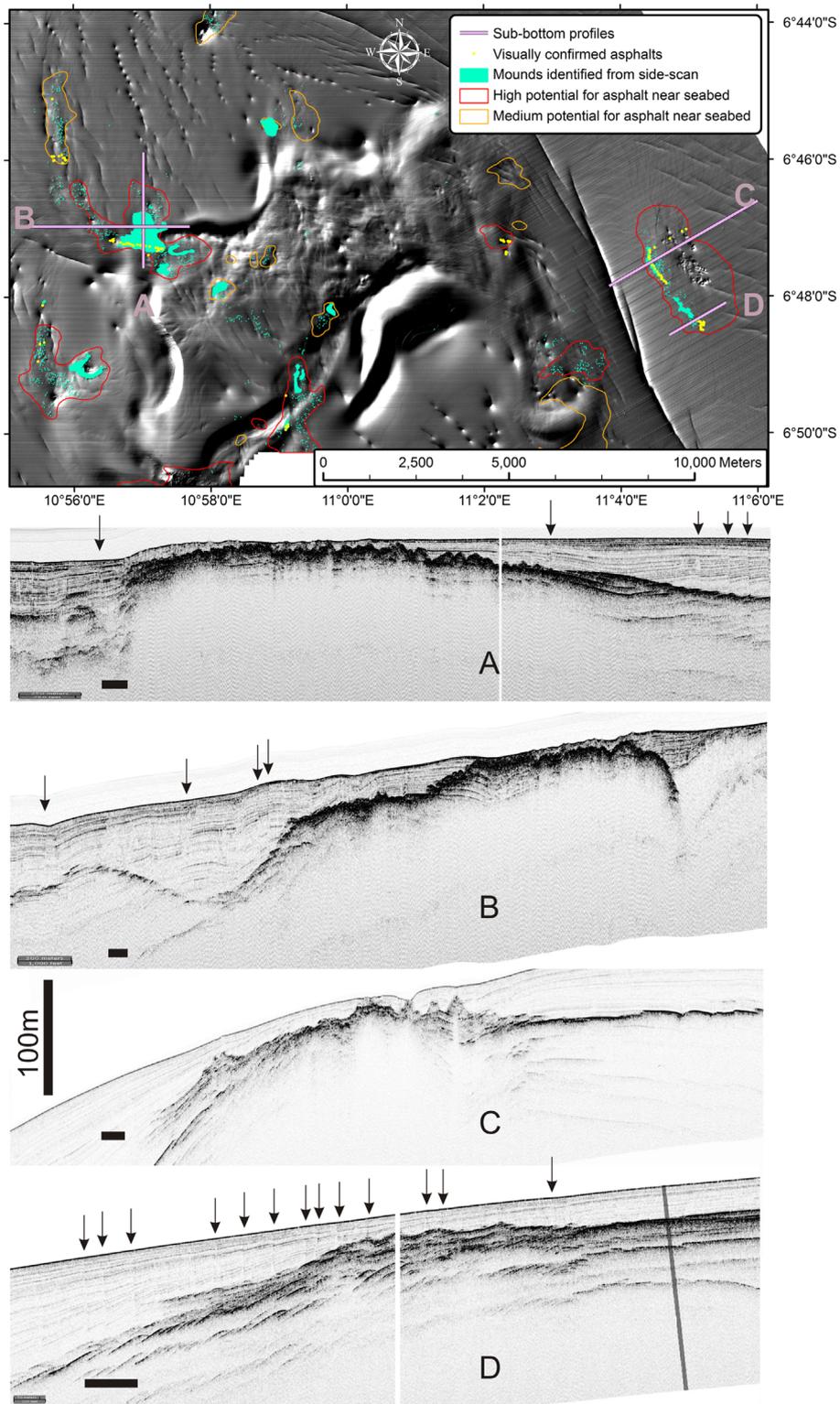
Close-up photographs revealed that the surface of the asphalt mounds with attached megafaunal organisms ranged from being apparently bare to having a relatively dense macrofauna growing on and living within interstices between the asphalt mounds. The macrofauna mostly comprised polychaetes, ophiuroids, and small arborescent structures, possibly cnidarians, foraminiferans or bryozoans. Occasional small gastropods and encrusting sponges or bryozoans were also seen. Some mounds were covered in thin ( $<5$  mm) patches of sediment, of similar colour and texture to seabed surface sediments. There was no obvious indication of the age of the mounds from the appearance of the surface of the asphalt.

Evidence of active seabed seepage was seen in one area to the east of Block 31 SE (centred  $11^{\circ}5'3.316''\text{E } 6^{\circ}47'17.03''\text{S}$ ; close to the centre of line C in Fig. 3) with 6 discrete seepage sites identified within 1-km radius of the central point (Fig. 7;  $\sim 1500$  m water depth). These areas had several dense patches of living fauna known to have chemoautotrophic symbionts, including *Bathymodiolus* sp. mussels and white vesicomid bivalves (both observed in patches up to  $1\text{ m}^2$ ). In some cases, these patches also had small ( $<70$  mm long) siboglinid tube worms (Fig. 7) that appeared to be

alive and occurred occasionally near to the bivalves in small ( $<0.25\text{ m}^2$ ) dense thickets. The active seepage sites also had a holothurian species associated with them that was not observed elsewhere. Unfortunately, the resolution of the video of the seep sites was relatively low, but small samples obtained verify the presence of siboglinids and chemosynthetic bivalves. Two gastropod species were also identified from samples, *Provanna reticulata* and *P. chevalieri*.

#### 4. Discussion

Asphalt structures appear to be a common feature in the Block 31SE area off Angola. This study is the first description of these features in the South Atlantic and on the eastern Atlantic continental margin. The Angolan asphalt mounds are formed as reservoir hydrocarbons migrate vertically around the margins of salt diapirs (Fig. 8). The buoyant hydrocarbons migrate through these overlying sediments to the seabed, a process probably facilitated by the extensive fault systems associated with the diapirs (Fig. 8). As the hydrocarbons migrate upwards through the sediments they presumably fractionate with lighter fractions migrating more quickly. In some areas in Block 31 SE seeps of light hydrocarbons, probably methane, occur at the sediment surface. These are easily visible because of their association with outcrops of authigenic carbonates (Fig. 4F) and chemosynthetic organisms. The heavier fractions (oils) become heavier during migration as lighter hydrocarbons are removed by both physical processes and bacterial and archaeal degradation, ultimately resulting in accumulation of viscous asphalt in the shallow subsurface and at the seabed. Carbonates found associated with asphalts could indicate microbial anaerobic oxidation of lighter hydrocarbons (Roberts et al., 2010). Occasional linear asphalt outcrops (Fig. 4B) correlate with faults seen in AUV sub-bottom profiles (Fig. 3) supporting the hypothesis that these faults may act as a pathway for asphalt. However, many asphalt mounds were found in locations with no obvious faults in the shallow section. It is likely that relatively warm, buoyant asphalts can rise from a subsurface source and migrate vertically through the shallow sediments, as has been observed in the Gulf of Mexico (Williamson et al., 2008). These asphalt nodules, or those breaking away from a larger seabed source, may then be extruded from the

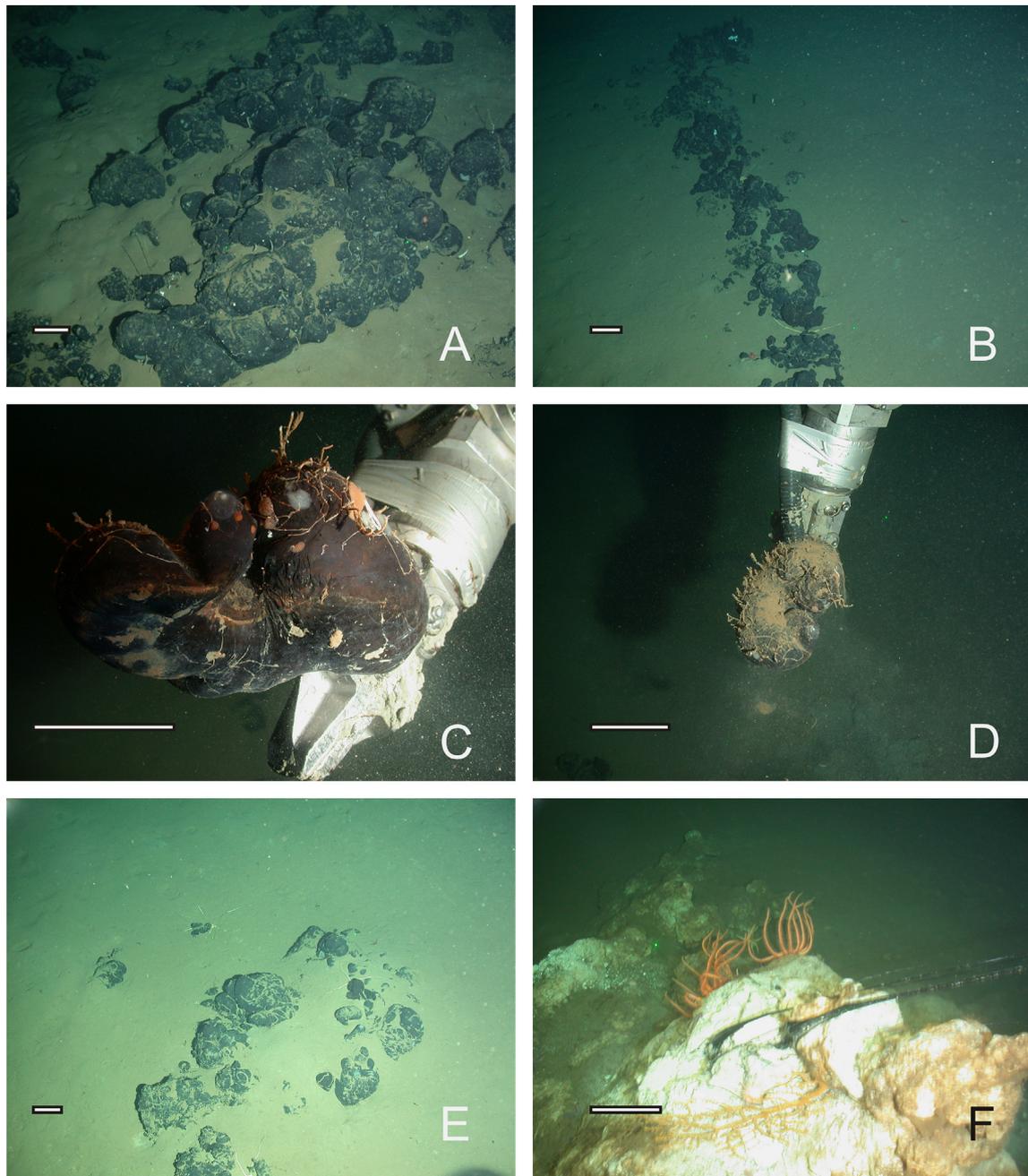


**Fig. 3.** Sub-bottom profile sections through two key mound areas. The upper part of the figure shows the hillshaded topography of part of the survey area. The section lines are marked, identified with letters. The position of the letter relative to the line indicates the left hand side of the profiles. The horizontal black scale bars represent 100 m. All profiles are scaled so that the single vertical scale bar represents 100 m in all profiles. Arrows indicate identified faults.

seabed into the water column, float away in the current and then cool, dropping onto the seabed at some distance from their source (ballooning). Careful excavation of a small discrete asphalt nodule found a few metres from its probable source showed that it had no visible root and a very even, rounded base that would be consistent with it having settled on the seabed from above rather than having been extruded from below (Fig. 4). Although not conclusive, this

strengthens the view that asphalt nodules can occur at some distance from their subsurface source. However, based on a review of ROV video and stills data, these “free nodules” do not tend to travel far and are generally found within a few tens of metres of their source.

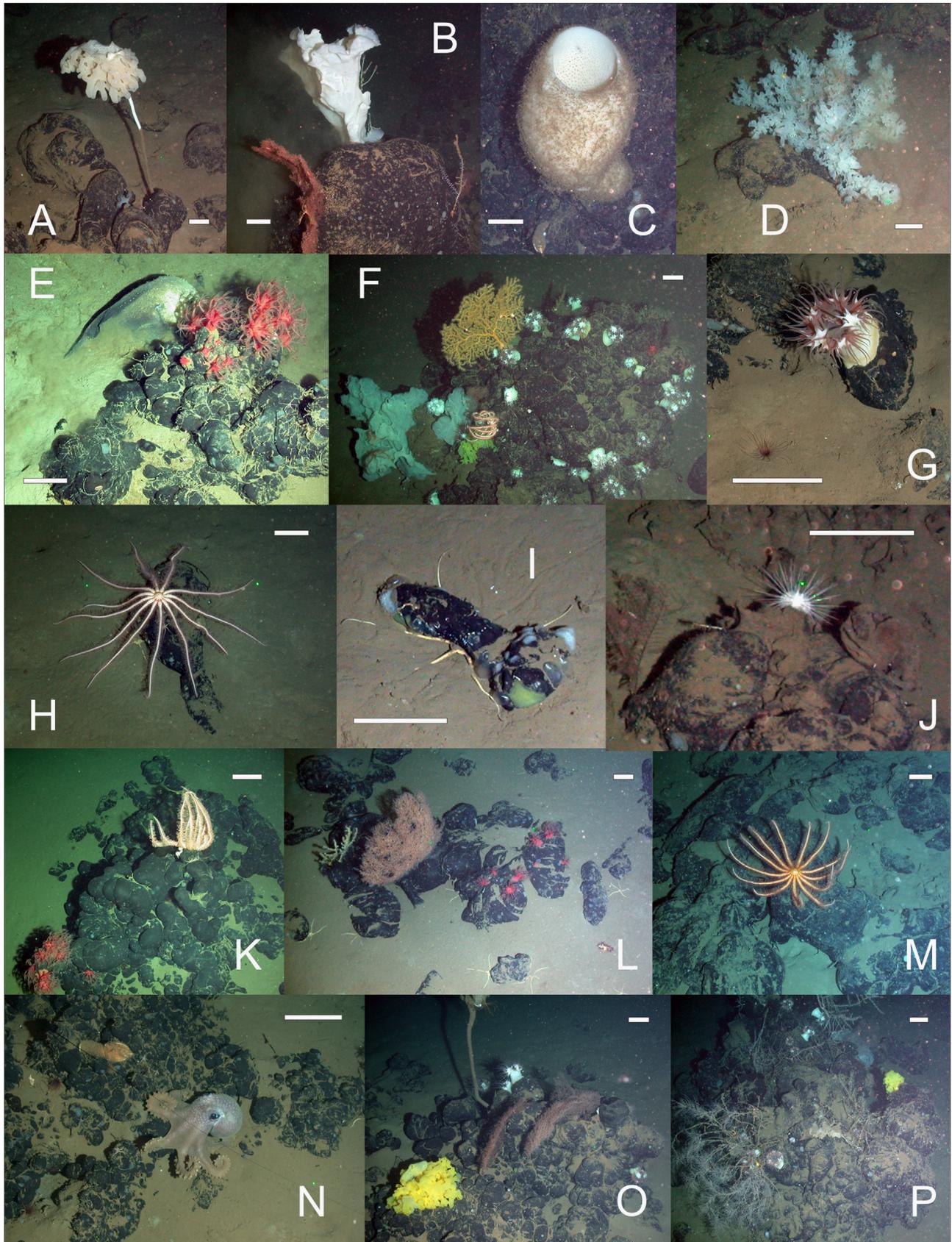
The asphalt mounds described here are similar to some of the smaller asphalt features described in other areas of the world. Most of the described asphalt mounds, such as those in the



**Fig. 4.** Photographs of asphalt mounds showing various forms of mound from single large mounds (A), linear features (B), detail of excavated mound (C, D), multiple small mounds (E) and carbonates with asphalt extrusions (F). White bar represents 100 mm.

Campeche Knolls (MacDonald et al., 2004) and the Santa Barbara Basin (Keller et al., 2007; Valentine et al., 2010), are considerably larger volcano-like structures, with more voluminous flows of subsurface fluid than those in Angola. However, similar smaller habitats to those observed here may also occur in both these other regions (and elsewhere). The asphalt mounds at the Puma site in the Gulf of Mexico (Weiland et al., 2008) are most comparable to those in the Angolan Block 31SE area, with discrete small mounds visible (Fig. 9D and F in Weiland et al. (2008)), although fluid flow appears to be more voluminous at the Puma site. The mounds at the Shenzi site (Williamson et al., 2008) are less extensive than those observed here and are covered in soft sediments, suggesting a potentially older age (Fig. 4B in Williamson et al. (2008)). There are some parallels between the fauna associated with the Angolan asphalt mounds and those observed elsewhere at the periphery of

asphalt provinces, such as similar aggregations of crinoids and soft corals found at the furthest downslope asphalt pillows at the Campeche Knolls (MacDonald et al., 2004), or in areas of smaller asphalt structures, like those at Puma and Shenzi (Weiland et al., 2008; Williamson et al., 2008). As in Block 31 SE, heterotrophic deposit feeders were found in sediments around the asphalt structures in the Gulf of Mexico, although they would be expected to inhabit all soft sediment areas. The depth of the chemosynthetic communities observed in Block 31 SE corresponded with that of a transition zone in the seep communities of the Gulf of Mexico (Cordes et al., 2007), but these are difficult to compare with the active seeps off Angola as limited data exist. The chemosynthetic communities observed off Angola may reflect an exchange of seep fauna across the Atlantic equatorial belt from the Gulf of Mexico, as already proposed in the case of seeps on the West Nigerian



**Fig. 5.** Megafauna found living on asphalt mounds. White bar represents 100 mm. (A) *Saccocalyx pedunculata*, (B) sponge possibly *Hexactinella* sp., *Stauropathes* sp. 2 and small possible primnoid gorgonian, (C) Rossellid sponge, (D) *Farrea* sp., (E) *Anthomastus* sp. and *Psychrolutes macrocephalus*, (F) yellow *Paramuricea* sp., sponges, c.f. *Actinernus michaelsarsi*, *Anthomastus* sp. and other megafauna (G) c.f. *Actinernus michaelsarsi* on asphalt, (H) brisingid, (I) ophiuroid under asphalt, (J) unknown echinoid, (K) brisingid, *Anthomastus* sp. and ophiuroids, (L) unknown yellow cnidarian, *Stauropathes* sp. 1, *Anthomastus* sp. and ophiuroids, (M) brisingid asteroid, (N) probable new *Graneledone* sp. octopus and pedunculid barnacle, note strand of asphalt extending over octopus, (O) *Stauropathes* sp. 1, yellow sponge and stalked sponge, (P) antipatharians, anemones and sponges.

**Table 1**  
Taxa observed in asphalt and soft sediment habitats of Block 31 SE. If taxa were observed on both asphalts and soft sediments they are included in both columns.

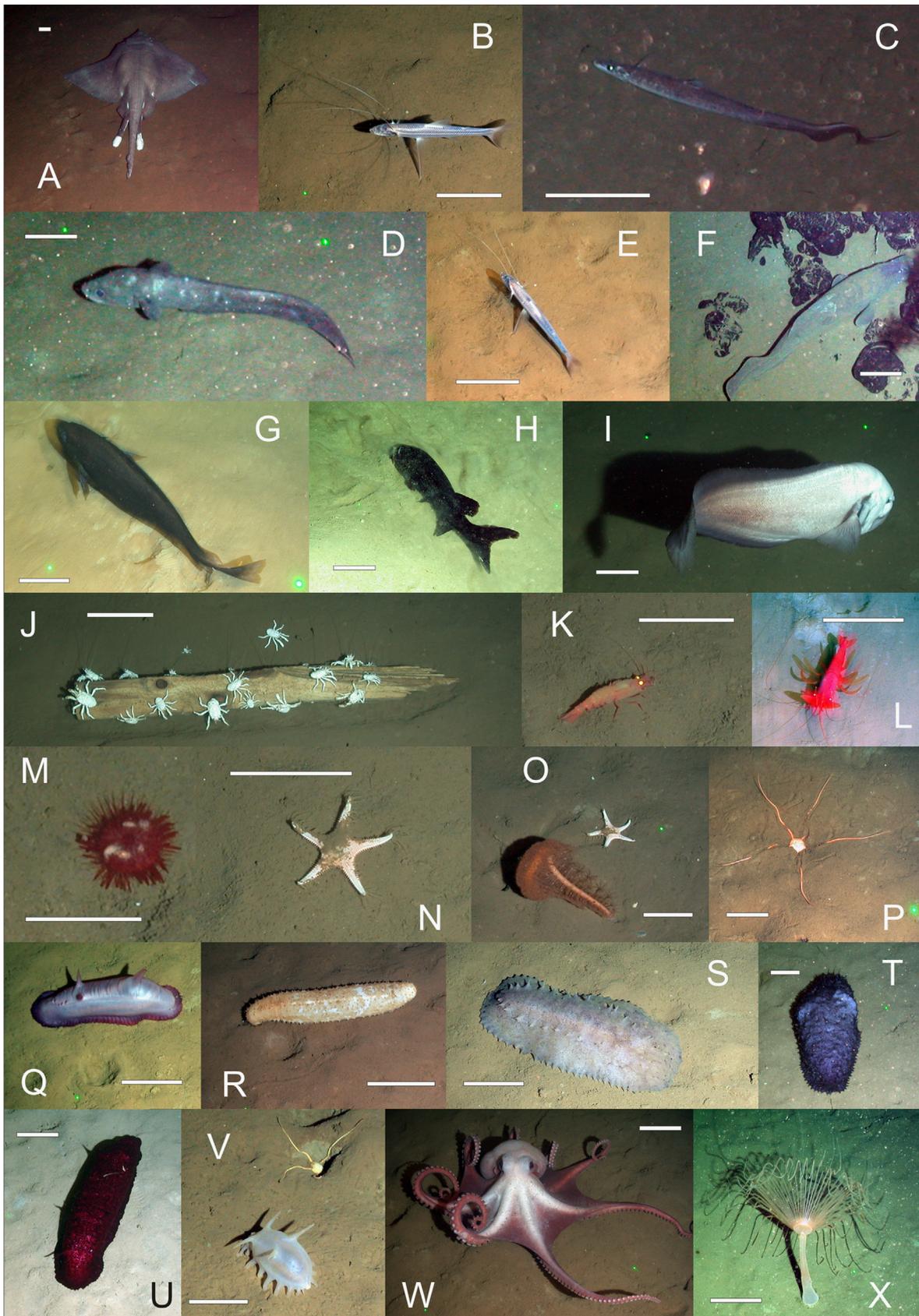
Phylum	Asphalt	Figure	Soft sediment	Figure	
Chordata			<i>Bathypterois</i> , either <i>B. phenax</i> or <i>B. atricolor</i>	6B,E	
			<i>Synaphobranchus kaupii</i>		
			<i>Aldrovandia oleosa</i>	6C	
			<i>Xyelacyba myersi</i>	6I	
			<i>Xenodermichthys copei</i>	6G	
			<i>Bathytroctes</i> sp.	6H	
			<i>Coryphaenoides</i> sp.	6D	
			<i>Coryphaenoides</i> sp. 2		
		<i>Psychrolutes macrocephalus</i>	5E	<i>Psychrolutes macrocephalus</i>	5E
		<i>Lycodes</i> sp.	6F	<i>Lycodes</i> sp.	6F
Echinodermata			<i>Bathyrāja richardsoni</i>	6A	
	Diadematiid	5J			
	<i>Brisinga</i> spp.	5H,K,M			
	Comatulid crinoid				
	<i>Stauropathes</i> sp. associated ophiuroid	5L			
			<i>Benthodytes</i> sp.	6U	
			<i>Psychropotes depressa</i>	6Q	
			<i>Peniagone diaphana</i>		
			<i>Scotoplanes globosa</i>	6V	
			<i>Benthothuria funebris</i>	6T	
		<i>Mesothuria</i> sp.	6R		
		<i>Pelopatides</i> sp.	6S		
		<i>Phormosoma placenta?</i>	6M		
		Ophiuroid	6V		
		<i>Plutonaster</i> sp.	6N		
Mollusca	<i>Graneledone</i> sp. nov.	5N			
Arthropoda			<i>Benthoctopus</i> sp.	6W	
	Pedunculid barnacle	5N			
Cnidaria			<i>Plesiopenaeus armatus</i>	6L	
			<i>Glyphocrangon</i> sp.	6K	
	<i>Actinermus michaelisarsari</i>	5F,G,O			
	Antipatharian	5P			
	Isidid or Primnoid	5B			
	<i>Stauropathes</i> sp.	5L			
	<i>Stauropathes</i> sp. 2	5B			
	<i>Paramuricea</i> sp.	5F			
	<i>Anthomastus</i> sp.	5E,K,L			
			<i>Corymorpha</i> sp.	6X	
		<i>Edwardsia</i> sp.			
		Cerianthid			
		Pennatulid	6O		
		Spiralling whip-like Antipatharian?			
Porifera	White sponge 1				
	<i>Hexactinella?</i> sp.	5B			
	Rossellidae	5C			
	White <i>Farrea</i> sp.	5D			
	Yellow sponge ( <i>Farrea</i> sp.?)	5O			
	<i>Saccocalyx pedunculata</i>	5A			

margin (Cordes et al., 2007) and supported by southward bottom water flow patterns off Angola (van Bennekom and Berger, 1984).

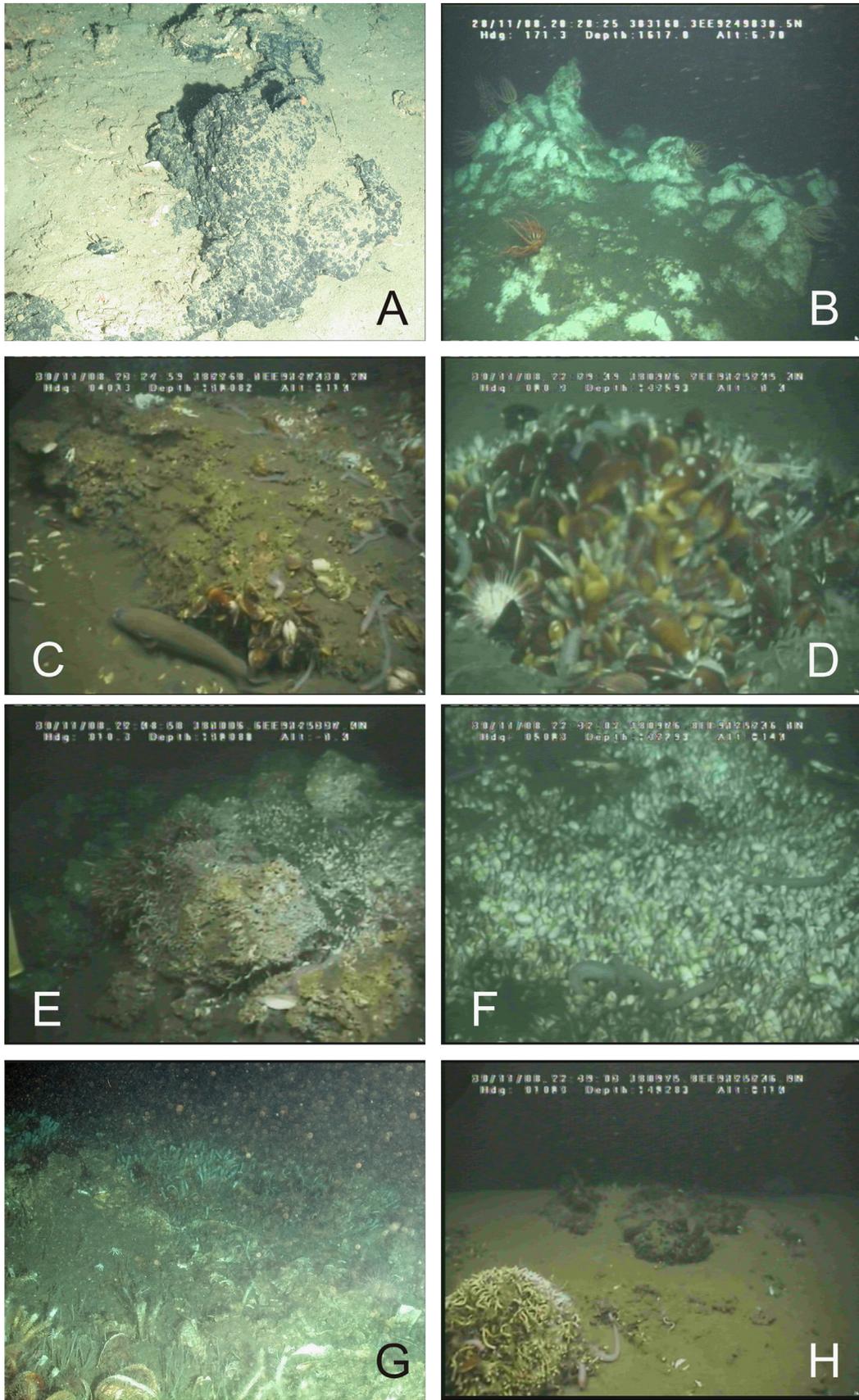
The fluid flow structures observed here undoubtedly increase habitat heterogeneity on the Angolan margin. The asphalt mounds vary in size, extent, composition and biology at scales ranging from metres to tens of kilometres. The features resulting from hydrocarbon escape vary along a continuum from asphalt mounds, comprising heavy hydrocarbons, to more typical cold seep systems, likely supported by release of methane. The fauna observed also vary across this gradient, presumably controlled by the amount and type of fluid flow. The fauna range from 'normal' hard-substratum heterotrophic epifauna inhabiting the asphalt mounds (Colman et al., 2005; Jones et al., 2013) to chemosynthetic fauna. The extensive biogenic habitats observed in some areas in Block 31 SE, such as the chemosynthetic communities and potentially large aggregations of heterotrophic megafauna, may also increase habitat heterogeneity, as observed at other seep (Cordes et al., 2010) and margin (Buhl-Mortensen et al., 2010) systems. The asphalt mounds in this region of Angola do not seem to be supported by the same level of fluid flow as in the Gulf of Mexico

(MacDonald et al., 2004) or off California (Valentine et al., 2010); it is possible that they are the products of a different geological process. No data exist to suggest whether the asphalt mound fields harbour increased densities of fauna compared to soft sediment areas with no proximal asphaltic/chemosynthetic habitats. Seep sites elsewhere, which have been studied in much greater detail, appear to elevate local heterotrophic production (Cordes et al., 2009). It is also unclear whether, in the absence of fluid seepage, different epifaunal assemblages colonise different kinds of hard substrate, for example, authogenic carbonates and asphalt structures. In the Gulf of Mexico extensive and diverse epifaunal communities, such as cold-water coral reefs, live on relic authogenic carbonates structures with low or no fluid flow (Cordes et al., 2008), but these are likely more extensive and at a later successional stage than the limited number of asphalt structures so far investigated (MacDonald et al., 2004; Weiland et al., 2008).

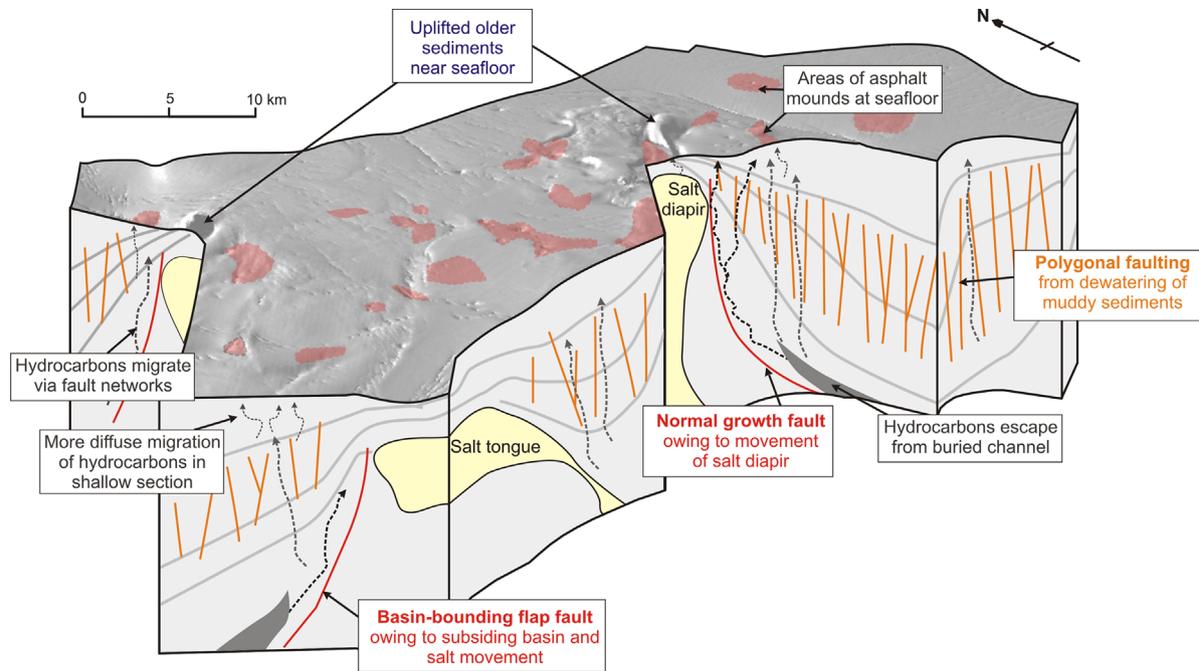
Asphalt mounds provide an important habitat for dense and diverse communities of epifaunal organisms. The megafaunal assemblages found on the asphalt mounds in Angola harbour around the same number of species and a higher biomass than the



**Fig. 6.** Megafauna found living near but not on asphalt mounds. White bar represents 100 mm. (A) *Bathyraja richardsoni*, (B and E) *Bathypterois*, either *B. phenax* or *B. atricolor*, (C) *Aldrovandia oleosa*, (D) *Coryphaenoides* sp., (F) *Lycodes* sp., (G) *Xenodermichthys socialis*, (H) probably *Bathytroctes* sp., (I) *Xyelacyba myersi*, (J) *Munidopsis* sp. found on sunken wood, (K) *Glyphocrangon* sp., (L) *Plesiopenaeus armatus*, (M) probably *Phormosoma placenta*, (N) astropectinid probably *Plutonaster* sp., (O) pennatulid, (P) ophiuroid, (Q) *Psychropotes depressa*, (R) probably *Mesothuria* sp., (S) *Pelopatides* sp., (T) *Benthothuria funebris*, (U) *Benthothytes* sp. likely to be *B. lingua* or potentially *B. sordida*, (V) *Scotoplanes globosa* and ophiuroid, (W) *Benthoctopus* sp., (X) Large athecate hydroid, *Corymorpha* sp.



**Fig. 7.** Examples of photographs with evidence of recent fluid flow. (A) Asphalt and authigenic carbonate mound, (B) large carbonate mound, (C) carbonate mound with small patch of living *Bathymodiolus* sp. mussels, (D) patch of living *Bathymodiolus* sp. and small pogonophoran tube worms, (E) carbonate mound with pogonophorans, (F) vesicomyid bivalves, (G) living *Bathymodiolus* sp. and small pogonophorans, (H) asphalt mounds near carbonate mound with pogonophorans. Scaling information not available.



**Fig. 8.** Simplified diagram of subsea fluid flow processes and features that result in asphalt mounds in Block 31SE. Please note the vertical dimension is not to scale and exaggerated compared with the horizontal scale. The top layer of the diagram is the three-dimensional bathymetry, with the greyscale representing hillshading. Red areas represent the areas of asphalt mounds on the seafloor (see Fig. 2). In the subsurface the yellow shapes represent salt structure, the light grey normal sediments and the dark grey hydrocarbon reservoirs. The orange lines represent polygonal faults, the red lines larger faults, they grey lines geological strata and the dotted lines represent hydrocarbon movement pathways. Important features are indicated with text boxes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

local soft-sediment assemblage. The preliminary observations in this study suggest that the smaller-sized fauna inhabiting the asphalt mounds may be also abundant and diverse. Many of the species found on the mounds are not found on the adjacent soft-sediment. The increased local habitat heterogeneity caused by fluid flow features, such as asphalt mounds, certainly increases beta diversity (Whittaker, 1960) at a range of scales. Asphalt mounds may also act as ‘stepping stone’ habitats (Olu et al., 2010) for general epilithic and chemosynthetic fauna (Cordes et al., 2007), likely increasing population connectivity (Shank, 2010) and ecosystem resilience in the area (Van Dover et al., 2012). As a result, asphalt mounds are important for the maintenance of biodiversity in the Angolan Block 31 area and should be considered in future environmental monitoring and management of this area of active hydrocarbon exploration and production.

## 5. Conclusions

Seepage of heavy hydrocarbons may lead to the formation of asphalt mounds in many ocean margins around the world. These asphalt structures occur in similar areas to hydrocarbon seeps above salt structures, but range from providing minor habitat within areas of active methane seepage, chemosynthesis and authigenic carbonate to discrete non-chemosynthetic habitats. This entire range of asphaltic habitats occurs in Block 31 Angola. These observations suggest that, at least for megafauna, asphalt mounds do not harbour an obligate fauna. Where no methane seepage occurs the asphalt mounds appear to provide hard substratum that is colonised by a normal epilithic assemblage. Unfortunately, the deep-water assemblages colonising hard substratum on the west African margin are rarely sampled and poorly known (Colman et al., 2005). The presence of asphalt mounds increases habitat heterogeneity providing substratum for epilithic megafauna, increasing local alpha and beta diversity,

and their presence may play an important role in maintenance of regional populations of epifauna.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2014.08.010>.

## References

- Allen, A.A., Schlueter, R.S., Mikolaj, P.G., 1970. Natural oil seepage at Coal Oil Point, Santa Barbara, California. *Science* 170 (3961), 974–977.
- Arbizu, P.M., Schminke, H.K., 2005. DIVA-1 expedition to the deep sea of the Angola Basin in 2000 and DIVA-1 workshop in 2003. *Org. Divers. Evol.* 5 (Suppl. 1), 1–2.
- Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* 42 (1), 1–20.
- Bianchi, G., 1992. Demersal assemblages of the continental-shelf and upper slope of Angola. *Mar. Ecol.-Prog. Ser.* 81 (2), 101–120.
- Brüning, M., Sahling, H., MacDonald, I.R., Ding, F., Bohrmann, G., 2010. Origin, distribution, and alteration of asphalts at Chapopote Knoll, Southern Gulf of Mexico. *Mar. Pet. Geol.* 27 (5), 1093–1106.
- Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, H., King, N.J., Raes, M., 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Mar. Ecol.* 31 (1), 21–50.

- Cambron-Bonavita, M.A., Nadalig, T., Roussel, E., Delage, E., Duperron, S., Caprais, J.C., Boetius, A., Sibuet, M., 2009. Diversity and distribution of methane-oxidizing microbial communities associated with different faunal assemblages in a giant pockmark of the Gabon continental margin. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.* 56 (23), 2248–2258.
- Colman, J.G., Gordon, D.M., Lane, A.P., Forde, M.J., Fitzpatrick, J.J., 2005. Carbonate mounds off Mauritania, north-west Africa: status of deep-water corals and implications for management of fishing and oil exploration activities. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-Water Corals and Ecosystems*. Springer-Verlag, Berlin, pp. 417–441.
- Cordes, E.E., Bergquist, D.C., Fisher, C.R., 2009. Macro-ecology of Gulf of Mexico cold seeps. *Annu. Rev. Mar. Sci.* 1, 143–168.
- Cordes, E.E., Carney, S.L., Hourdez, S., Carney, R.S., Brooks, J.M., Fisher, C.R., 2007. Cold seeps of the deep Gulf of Mexico: community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 54 (4), 637–653.
- Cordes, E.E., Cunha, M.R., Galeron, J., Mora, C., Olu-Le Roy, K., Sibuet, M., Van Gaever, S., Vanreusel, A., Levin, L.A., 2010. The influence of geological, geochemical, and biogenic habitat heterogeneity on seep biodiversity. *Mar. Ecol. - Evol. Perspect.* 31 (1), 51–65.
- Cordes, E.E., McGinley, M.P., Podowski, E.L., Becker, E.L., Lessard-Pilon, S., Viada, S.T., Fisher, C.R., 2008. Coral communities of the deep Gulf of Mexico. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 55 (6), 777–787.
- Didyk, B.M., Simoneit, B.R.T., 1989. Hydrothermal oil of Guaymas Basin and implications for petroleum formation mechanisms. *Nature* 342 (6245), 65–69.
- Droz, L., Marsset, T., Ondréas, H., Lopez, M., Savoye, B., Spy-Anderson, F.-L., 2003. Architecture of an active mud-rich turbidite system: the Zaire Fan (Congo–Angola margin southeast Atlantic). *AAPG Bull.* 87 (7), 1145–1168.
- Evans, T.G., 2010. A Systematic Approach to Offshore Engineering for Multiple-Project Developments in Geohazardous Areas. In: Gourvenec, S., White, D. (Eds.), *Frontiers in Offshore Geotechnics II*. CRC Press, London, pp. 3–32.
- Formolo, M.J., Lyons, T.W., Zhang, C., Kelley, C., Sassen, R., Horita, J., Cole, D.R., 2004. Quantifying carbon sources in the formation of authigenic carbonates at gas hydrate sites in the Gulf of Mexico. *Chem. Geol.* 205, 253–264.
- Galéron, J., Menot, L., Renaud, N., Crassous, P., Khripounoff, A., Treignier, C., Sibuet, M., 2009. Spatial and temporal patterns of benthic macrofaunal communities on the deep continental margin in the Gulf of Guinea. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 56 (23), 2299–2312.
- Gay, A., Lopez, M., Cochonat, P., Sermondadaz, G., 2004. Polygonal faults-furrows system related to early stages of compaction – upper Miocene to recent sediments of the Lower Congo Basin. *Basin Res.* 16 (1), 101–116.
- Hill, A.J., Evans, T.G., Mackenzie, B., Thompson, G., 2010a. Deepwater Angola Part II. In: Gourvenec, S., White, D. (Eds.), *Frontiers in Offshore Geotechnics II*. CRC Press, London, pp. 215–220.
- Hill, A.J., Southgate, J.G., Fish, P.R., Thomas, S., 2010b. Deepwater Angola Part I. In: Gourvenec, D., White, D. (Eds.), *Frontiers in Offshore Geotechnics II*. CRC Press, London, pp. 209–214.
- Hornafius, J.S., Quigley, D., Luyendyk, B.P., 1999. The world's most spectacular marine hydrocarbon seeps (Coal Oil Point, Santa Barbara Channel, California): Quantification of emissions. *J. Geophys. Res.* 104 (C9), 20703–20711.
- Hu, C., Li, X., Pichel, W.G., Muller-Karger, F.E., 2009. Detection of natural oil slicks in the NW Gulf of Mexico using MODIS imagery. *Geophys. Res. Lett.* 36 (1), L01604.
- Jones, D.O.B., Mrabure, C.O., Gates, A.R., 2013. Changes in deep-water epibenthic megafaunal assemblages in relation to seabed slope on the Nigerian margin. *Deep Sea Res. Part I: Oceanogr. Res. Pap.* 78, 49–57.
- Keller, E.A., Duffy, M., Kennett, J.P., Hill, T., 2007. Tectonic geomorphology and hydrocarbon induced topography of the Mid-Channel Anticline, Santa Barbara Basin, California. *Geomorphology* 89 (3–4), 274–286.
- Kennicutt, M.C., Brooks, J.M., Bidigare, R.R., Denoux, G.J., 1988a. Gulf of Mexico hydrocarbon seep communities – I. Regional distribution of hydrocarbon seepage and associated fauna. *Deep Sea Res. Part A: Oceanogr. Res. Pap.* 35 (9), 1639–1651.
- Kennicutt, M.C., Brooks, J.M., Denoux, G.J., 1988b. Leakage of deep, reservoired petroleum to the near surface on the gulf of Mexico Continental slope. *Mar. Chem.* 24 (1), 39–59.
- Kroncke, I., Turkay, M., 2003. Structural and functional aspects of the benthic communities in the deep Angola Basin. *Mar. Ecol. Prog. Ser.* 260, 43–53.
- Kvenvolden, K.A., Cooper, C.K., 2003. Natural seepage of crude oil into the marine environment. *Geo-Mar. Lett.* 23 (3), 140–146.
- Kvenvolden, K.A., Rogers, B.W., 2005. Gaia's breath – global methane exhalations. *Mar. Pet. Geol.* 22 (4), 579–590.
- Le Guilloux, E., Olu, K., Bourillet, J.F., Savoye, B., Iglésias, S.P., Sibuet, M., 2009. First observations of deep-sea coral reefs along the Angola margin. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 56 (23), 2394–2403.
- Levin, L.A., Dayton, P.K., 2009. Ecological theory and continental margins: where shallow meets deep. *Trends Ecol. Evol.* 24 (11), 606–617.
- MacDonald, I.R., Bohrmann, G., Escobar, E., Abegg, F., Blanchon, P., Blinova, V., Bruckmann, W., Drews, M., Eisenhauer, A., Han, X., Heeschen, K., Meier, F., Mortera, C., Naehr, T., Orcutt, B., Bernard, B., Brooks, J., de Farago, M., 2004. Asphalt volcanism and chemosynthetic life in the Campeche Knolls, Gulf of Mexico. *Science* 304 (5673), 999–1002.
- MacDonald, I.R., Sager, W.W., Peccini, M.B., 2003. Gas hydrate and chemosynthetic biota in mounded bathymetry at mid-slope hydrocarbon seeps: Northern Gulf of Mexico. *Mar. Geol.* 198 (1–2), 133–158.
- Mandl, G., 1987. Tectonic deformation by rotating parallel faults: the “bookshelf” mechanism. *Tectonophysics* 141 (4), 277–316.
- Marion, G.L., Tari, G.C., Lehmann, C.T., 2000. Evolution of the Angolan passive margin, West Africa, with emphasis on post-salt structural styles. In: Mohriak, W., Talwani, M. (Eds.), *Atlantic Rifts and Continental Margins*. American Geophysical Union, Washington, D. C., pp. 129–149.
- Olu-Le Roy, K., Caprais, J.C., Fiffis, A., Fabri, M.C., Galeron, J., Budzinsky, H., Le Menach, K., Khripounoff, A., Ondreas, H., Sibuet, M., 2007. Cold-seep assemblages on a giant pockmark off West Africa: spatial patterns and environmental control. *Mar. Ecol.-Evol. Perspect.* 28 (1), 115–130.
- Olu, K., Caprais, J.C., Galeron, J., Causse, R., von Cosel, R., Budzinski, H., Le Menach, K., Le Roux, C., Levache, D., Khripounoff, A., Sibuet, M., 2009. Influence of seep emission on the non-symbiont-bearing fauna and vagrant species at an active giant pockmark in the Gulf of Guinea (Congo-Angola margin). *Deep-Sea Res. Part II-Top. Stud. Oceanogr.* 56 (23), 2380–2393.
- Olu, K., Cordes, E.E., Fisher, C.R., Brooks, J.M., Sibuet, M., Desbruyeres, D., 2010. Biogeography and potential exchanges among the Atlantic Equatorial belt cold-seep faunas. *PLoS ONE* 5 (8), e11967.
- Pequegnat, W.E., Jeffrey, L.M., 1979. Petroleum in deep benthic ecosystems of the Gulf of Mexico and Caribbean Sea. *Contrib. Mar. Sci.* 22, 63–75.
- Pinheiro, L.M., Ivanov, M.K., Sautkin, A., Akhmanov, G., Magalhaes, V.H., Volkonskaya, A., Monteiro, J.H., Somoza, L., Gardner, J., Hamouni, N., Cunha, M.R., 2003. Mud volcanism in the Gulf of Cadiz: results from the TTR-10 cruise. *Mar. Geol.* 195, 131–151.
- Roberts, H.H., Feng, D., Joye, S.B., 2010. Cold-seep carbonates of the middle and lower continental slope, northern Gulf of Mexico. *Deep-Sea Res. Part II: Top. Stud. Oceanogr.* 57 (21–23), 2040–2054.
- Savoye, B., Babonneau, N., Dennielou, B., Bez, M., 2009. Geological overview of the Angola–Congo margin, the Congo deep-sea fan and its submarine valleys. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 56 (23), 2169–2182.
- Shank, T.M., 2010. Seamounts deep-ocean laboratories of faunal connectivity, evolution, and endemism. *Oceanography* 23 (1), 108–122.
- Sibuet, M., Lambert, C.E., Chesselet, R., Laubier, L., 1989. Density of the major size groups of benthic fauna and trophic input in deep basins of the Atlantic Ocean. *J. Mar. Res.* 47 (4), 851–867.
- Sibuet, M., Olu-LeRoy, K., 2002. Cold seep communities on continental margins: structure and quantitative distribution relative to geological and fluid venting patterns. In: Wefer, G., Hebbeln, D., Jorgensen, B.B., Van Weering, T. (Eds.), *Ocean Margin Systems*. Springer, Berlin, pp. 235–251.
- Sibuet, M., Olu, K., 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Res. Part II: Top. Stud. Oceanogr.* 45, 517–567.
- Sibuet, M., Vangriesheim, A., 2009. Deep-sea environment and biodiversity of the West African Equatorial margin. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 56 (23), 2156–2168.
- Thomas, S., Clare, M., Shreeve, J., Unterseh, S., 2011. Understanding Engineering Challenges Posed by Natural Hydrocarbon Infiltration and the Development of Authigenic Carbonate. *Proceedings of Offshore Technology Conference*, 2–5 May 2011, Houston, Texas, USA. Offshore Technology Conference.
- Unterseh, S., 2013. Early Recognition of Seabed and Sub-Seabed Natural Hydrocarbon Seeps in Deep Offshore Angola. *2013 Offshore Technology Conference*, May 06–09, 2013, Houston, TX, USA.
- Valentine, D.L., Reddy, C.M., Farwell, C., Hill, T.M., Pizarro, O., Yoerger, D.R., Camilli, R., Nelson, R.K., Peacock, E.E., Bagby, S.C., Clarke, B.A., Roman, C.N., Soloway, M., 2010. Asphalt volcanoes as a potential source of methane to late Pleistocene coastal waters. *Nat. Geosci.* 3 (5), 345–348.
- van Bennekom, A.J., Berger, G.W., 1984. Hydrography and silica budget of the Angola Basin. *Neth. J. Sea Res.* 17, 149–200.
- Van Dover, C.L., Smith, C.R., Ardron, J., Dunn, D., Gjerde, K., Levin, L., Smith, S., 2012. Designating networks of chemosynthetic ecosystem reserves in the deep sea. *Mar. Policy* 36 (2), 378–381.
- Van Gaever, S., Galéron, J., Sibuet, M., Vanreusel, A., 2009. Deep-sea habitat heterogeneity influence on meiofaunal communities in the Gulf of Guinea. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 56 (23), 2259–2269.
- Vangriesheim, A., Pierre, C., Aminot, A., Metz, N., Baurand, F., Caprais, J.-C., 2009. The influence of Congo River discharges in the surface and deep layers of the Gulf of Guinea. *Deep Sea Res. Part II: Top. Stud. Oceanogr.* 56 (23), 2183–2196.
- Vernon, J.W., Slater, R.A., 1963. Submarine tar mounds, Santa Barbara County, California. *AAPG Bull.* 47 (8), 1624–1627.
- Vinogradova, N.G., Galkin, S.W., Kamenskaja, O.E., Levenstein, R.Y., Romanov, V.N., 1990. The distribution of the deep sea bottom fauna in the transoceanic section in the south Atlantic Ocean along 31° 30'. *Trans. P. P. Shirshov Inst. Oceanol.* 126, 7–19.
- Wallman, K., Linke, P., Suess, E., Bohrmann, G., Sahling, H., Schlueter, M., Daahlmann, A., Lammers, S., Greinert, J., Von Mirbach, N., 1997. Quantifying fluid flow, solute mixing, and biogeochemical turnover at cold vents of the eastern Aleutian subduction zone. *Geochim. Cosmochim. Acta* 61, 5209–5219.
- Waren, A., Bouchet, P., 2009. New gastropods from deep-sea hydrocarbon seeps off West Africa. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.* 56 (23), 2326–2349.
- Weiland, R.J., Adams, G.P., McDonald, R.D., Rooney, T.C., Wills, L.M., 2008. Geological and Biological Relationships in the Puma Appraisal Area: from Salt Diapirism to Chemosynthetic Communities. *Offshore Technology Conference*, 5–8 May 2008, Houston, Texas, USA.
- Whittaker, R.H., 1960. *Vegetation of the Siskiyou Mountains, Oregon and California*. *Ecol. Monogr.* 30, 279–338.
- Williamson, S.C., Zois, N., Hewitt, A.T., 2008. Integrated site investigation of seafloor features and associated fauna, Shenzi Field, Deepwater Gulf of Mexico. *2008 Offshore Technology Conference*, 5–8 May 2008, Houston, Texas.