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Organic carbon transfer and ecosystem functioning in the terminal lobes of the Congo deep-sea fan: outcomes of the Congolobe project

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1. Introduction: historical background, first observations and puzzling questions

The terminal lobe complex of the Congo deep-sea fan is a fascinating environment. It is located at 5000 meters depth and 750 km offshore Africa. It is currently connected with the Congo River by a canyon and deep-sea channel system starting in the estuary and still fed by turbidity currents (Babonneau et al., 2002; Savoye et al., 2000, 2009). It thus displays most of the characteristics of a subaquatic delta: large sedimentation rates, high concentration of organic carbon of terrestrial origin, active diagenesis. In addition, this peculiar zone of the deep ocean hosts unexpected biological assemblages resembling those of cold seeps: chemosynthetic vesicomyid bivalves, microbial mats and reduced sediments in metric size discrete habitats.

Previous observations in the Congo-Angola margin off the Congo River revealed that turbiditic activity is presently ongoing as shown by cable breaks (Heezen et al., 1964), direct observations of turbidity currents (Khripounoff et al., 2003; Vangriesheim et al., 2009) and sampling of turbiditic deposits from the last century (Savoye et al., 2009). Transport processes and recycling of biogenic particles (OC, BSi) across the margin are dominated by transfers through the canyon and deep-sea channel to the terminal lobe zone with very little lateral input mid-slope down to 4000 meters (Rabouille et al., 2009; Ragueneau et al., 2009). This material is essentially terrigenous which implies a direct origin from the river and low inputs of autochthonous marine production from the surface ocean (Baudin et al., 2010; Treignier et al., 2006).

The building of the present lobe complex started after the last avulsion of the turbiditic channel at an age estimated at about 4 ka BP (Picot, 2015). It covers an area of about 2500 km^2 with the last lobe showing an area of about 400 km^2 collecting the most recent deposits since the last 1000 y. However, the generally large sediment accumulation rates in the area (0.5 and 1.2 cm/y) suggest that the whole lobe complex still collects significant amounts of sediments (Rabouille et al., 2017). The previous and now abandoned lobe complex, which lies further north, was built between 6 and 4 ka (Picot 2015).

In the terminal lobe complex, two ROV video surveys conducted in 2000 (Savoye and Ondreas, 2000) detected the presence of patches of biological structures typically associated with cold seeps: white patches of filamentous bacterial mats looking like those occurring in low-oxygen, high-sulfide habitats (Nelson et al., 1989) and large bivalves visually attributed to the Vesicomyidae family, known from cold seeps to carry sulfide-oxidizing symbionts (Fiala-Médioni and Felbeck, 1990; Sibuet and Olu, 1998).

The existence of these dense ecosystems in the Congo lobe complex raised several questions concerning their functioning: is it based, as in cold seeps, on chemosynthesis with methane and sulphide oxidation? If so, is the source of reduced substances linked to the recycling of organic matter in recent sediment layers, or is it related to deeper sources in fossil channels of the Congo deep-sea fan? Are the inputs of terrestrial organic matter from the present Congo channel large enough and easily metabolizable to start and sustain the development of these peculiar ecosystems? Do they sustain high faunal densities? In the context of land-ocean carbon transfer, can we calculate mass balances for the buried and mineralized carbon originating from the Congo River?

This special issue summarizes the first biological and biogeochemical survey performed in 2011-2012 during the WACS (Olu, 2011) and CONGOLOBE (Rabouille, 2012) cruises on board the N.O. Pourquoi Pas? within the framework of the Congolobe programme (www.congolobe.fr). It also provides multidisciplinary answers to the above questions.

2. Objectives and initial conceptual framework of the Congolobe project

In this context, the Congolobe project aimed at establishing the functional relationship between the organic matter input from the Congo canyon, its recycling in the sediment, and the structure and functioning of the ecosystem based on chemosynthesis in the sedimentological context of the Congo deep-sea fan.

The initial conceptual framework summarizing the hypotheses for the chemosynthesis-based ecosystem functioning in the terminal lobe complex is represented in Figure 1.

It was hypothesized that large organic inputs from the Congo canyon are deposited in the terminal lobes where they were mixed with pelagic inputs from the marine production. The proportions of the two end-members were not known and represented one objective of the study in terms of quality and biodegradability of the organic substrates. Indeed, depending on its reactivity, organic matter degradation induces a series of microbial metabolisms which creates multiple geochemical and microbiological gradients in the sediment: oxidants are generally consumed in the following order: $O_2 \rightarrow NO_3^- \rightarrow Mn(IV) \rightarrow Fe(III) \rightarrow SO_4^{2-} \rightarrow CH_2O$, but alternative biogeochemical pathways can be present in the lobe complex, as repartition and availability of oxidants in these turbidites are generally unknown. The contribution of each pathway to early diagenesis was of prime interest in this study and was extensively studied as some of these pathways lead to the production of sulfide which is the key of symbiotic bivalves' colonization.

Indeed, sulfide plays a key role in the habitats where it fuels vesicomyid symbionts and allows their development (Fiala-Médioni and Felbeck, 1990). It can be produced by bacterial sulfate-reduction which is a major pathway for organic matter mineralization in organic-rich sediments (Jorgensen, 1982) and by Anaerobic Oxidation of Methane (AOM) performed by a microbiological consortium where specific *Archaea* use methane as a reduced compound (Boetius et al., 2000). Constraining the balance between these two processes and understanding the control on dissolved sulfide by iron were two important objectives of this study. Furthermore, the understanding of the formation of methane in deeper layers and its transport by diffusion or in microfaults throughout turbidites was another aim as methane plays a key role in the production of sulfide by AOM.

The colonization and maintenance of discrete habitats by dense bivalve populations is another striking feature of the lobe complex. The presence of chemosynthetic fauna was hypothesized to be linked to the existence of “hot spots” of organic matter recycling and to the “shallow” early diagenesis of the large organic inputs from the Congo River. Our project aimed at elucidating the functioning of these ecosystems and calculating mass balances for the input of organic matter in the lobe complex.

The detailed objectives of the multi-disciplinary study of the Congolobe project were to:

- Determine quantitatively and qualitatively the origin and fate of biogenic particles (carbon and silica) transferred to the terminal lobes. Using the data collected during the cruises, budgets of organic carbon and biogenic silica were calculated especially recycling and burial. This study focused particularly on the recycling of organic matter and the generation of reduced fluids which were linked to chemosynthesis over different time scales, from years to thousand years.

- Study biological community structure from microbial communities to megafauna, and ecosystem functioning in heterogeneous habitats of this lobe complex. The link with the direct input of organic matter from the Congo channel and with the reduced fluids generated by the recycling of formerly buried organic matter was investigated. The interactions between the living organisms’ size classes from microbes to macrofauna were also considered. Functional biodiversity of the peculiar sites observed in the lobe zone were compared to cold seep sites known from active “pockmarks” in this region. Phylogenetic links among vesicomyid bivalves from the lobes and from deep sea cold seeps were investigated (Teixeira et al. 2013). Finally, the direct impact of turbiditic material deposits on the benthic ecosystem outside of chemosynthesis-based habitats was investigated to assess the consequence of this exceptionally high input of organic matter in deep sea sediment.

These two main objectives were divided in several tasks that served as building blocks of the project:

- The understanding of sedimentological characteristics and history of the lobe complex

- The determination of terrestrial and marine organic matter inputs to the lobe zone using biomarkers and isotopic tracers

- The estimation of recycling and burial of organic matter and biogenic silica in the lobe zone and the establishment of mass balance for carbon and silica in the lobe area

- The assessment of the geographical distribution of megafauna and peculiar habitats, and their functioning with respect to chemosynthesis *versus* detrital organic matter

3. The multidisciplinary framework of Congolobe: articles’ description

- Geological context

The Congo lobe complex is a large (2 525 km²) but thin (maximum 70 m thick) sedimentary body that lies at an abyssal depth (5000 m) making its detailed structure and composition difficult to investigate with ship-based acoustic tools. The acquisition of ROV-based high-resolution bathymetry and video observations unveiled incredible and unsuspected morphologies that have provided new insights in the build-up processes of channel-mouth lobes of silicoclastic mud-rich turbidite systems.

The general morphology and structure show that the lobe complex consists in five lobes that partly overlap and have prograded onto the abyssal plain (Dennielou et al., 2017). The progradation, aggradation and, probably, the size of a specific lobe are controlled by the local slope that allows the turbidity currents to flow. When the top of a lobe becomes too flat, turbidity currents find their way on steeper slopes on the side of the lobe and this process triggers the development of a new lobe (Dennielou et al., 2017). In this respect, the most distal lobe receives more recent sediment than the upstream lobes (Rabouille et al., 2017). However, sediment accumulation rates are very high over the entire lobe complex, in the order of 0.3 to 12 $cm.yr^{-1}$ and show that turbidity currents flowing in the feeding channel are largely unconfined (maximum channel depth is 40 m) and can spill over the whole lobe complex (Rabouille et al., 2017).

The lobe complex is dominantly composed of turbiditic mud. A network of distributaries shows that channelization and turbidity current spillover represent the sedimentary processes that first control the development of the lobes. Sand is strictly confined in the feeding channel and distributaries and is estimated to represent ca. 13% of the lobe complex (Dennielou et al., 2017). One striking feature is the occurrence of mass wasting deposits nearly everywhere where cores were collected. Spectacular pervasive mass wasting morphologies are also visible on the high-resolution bathymetry. Sliding and blocks occur dominantly along the feeding channel and distributaries (Dennielou et al., 2017) but also on the lobes rim (Croguennec et al., 2017) showing that mass wasting processes are a second order, but intrinsic, control on the lobe build-up.

The extremely high accumulation rates also show that the lobe complex is young, probably about 4 ka (Picot et al., 2016), and has significantly grown during the last century (Rabouille et al., 2017). Moreover, transient state observed from pore water geochemistry (sulfate and methane) clearly shows that sediment sliding has occurred during the last century (Croguennec et al., 2017). Thus, these slidings were responsible for changes in the fluid flow within the sedimentary column, visible on the pore water profiles.

- The Congo terminal lobe complex: a large organic carbon burial center with hot spots of anoxic recycling

An intensive effort was carried out to quantify and characterize the organic matter using bulk geochemical techniques (elemental and isotopic analyses, Rock-Eval pyrolysis), molecular investigations (fatty acids, amino acids, hydrocarbon fractions, BIT index, molecular isotopy) as well as optical observations of the organic particles. These studies allowed to assess the sources and the state of preservation of the organic matter accumulated in the sediments of the lobe complex (background, bacterial mats, vesicomyid habitats) and to compare it with the bedload, the material recovered in particle traps and suspended sediments from the Congo River watershed (Spencer et al., 2012; Talbot et al., 2014).

The mud-rich sediments of the distal lobe contain high amounts of organic matter (~3.5 to 4.0 wt % OC), the origin of which is a mixture of terrestrial higher-plant debris, soil organic matter and deeply oxidized phytoplanktonic material (Baudin et al., 2017b; Stetten, 2015; Stetten et al., 2015). The terrestrial fraction is dominant according to bulk and molecular organic geochemical signature. The dominance of n-C_{29} over aliphatic hydrocarbons, the occurrence of specific terpenes (gammacerene, lupene, ursene or oleanene), the preeminence of very long chain fatty acids (≥ 24 atoms of C) and the depleted isotopic ratios of most of the fatty acids ($\delta^{13}C$) all support the dominance of continental derived C3 land plant organic matter in the sediment (Méjanelle et al., 2017; Stetten, 2015; Stetten et al., submitted). Optical analysis of the organic matter also supports this conclusion as delicate plant structures, cuticle fragments and plant cellular material are well preserved in the distal lobe complex (Schnyder et al., 2017).

The organic matter distribution seems homogeneous at different scales, from a single turbiditic event to the entire lobe, and changes in accumulation rates have a limited effect on the quantity and quality of the preserved organic matter, although the organic particles may be locally sorted by density or buoyancy under the influence of turbidity currents (Schnyder et al., 2017). Nevertheless, particle remobilization and oxygen diffusion in the first centimeter of the sediment could influence the degradation of organic matter, but this process remains limited (Baudin et al., 2017a; Stetten, 2015). The first degradation steps for terrestrial inputs in the suboxic sedimentary layers are reflected by high phytadiene concentrations, while an even mode of C_{12}-C_{18} saturated n-alkanes, presumably of bacterial or fossil origin, is progressively enriched as the degradation proceeds further (Méjanelle et al., 2017). By contrast, organic matter recycling is particularly intense in vesicomyid habitats and bacterial mats, where biological action enriches the sediment in fatty acids and amino acids (Pruski et al., 2017). The terrigenous organic matter, with an initial low reactivity, is bio-transformed and becomes more labile, favoring its use by benthic macrofauna (Pruski et al., 2017).

This intense recycling of organic matter and the changes in the geochemical composition of pore waters and sediments were investigated using a suite of *in situ* and *ex situ* techniques. Profilers and benthic chambers were used *in situ* to determine diffusive and total recycling fluxes of oxygen (Khripounoff et al., 2017; Olu et al., 2017; Pastor et al., 2017; Pozzato et al., 2017), while porewater composition was analysed using voltammetric microelectrodes and after extraction on board (Pastor et al., 2017; Taillefert et al., 2017). The whole suite of electron acceptors and their by-products were quantified both in background sediments, which constitutes most of the levees and channel sediments, and within the different types of specific habitats such as microbial mats, vesicomyid bivalves and reduced sediments (Pastor et al., 2017; Pozzato et al., 2017; Taillefert et al., 2017). The biogeochemical contrast is particularly striking between the background sediments and the habitats occurring in "hot spots" patches. Background sediments are characterized by increased penetration of oxygen (≈ 1 cm), the dominance of iron reduction (Beckler et al., 2016; Taillefert et al., 2017) and the absence of other anoxic diagenetic pathways. Diffusive oxygen fluxes are around 2-5 mmol m^{-2} d^{-1} which is more active than surrounding areas outside the Congo deep-sea fan indicating an increased mineralization activity due to the inputs of terrigenous organic matter compared to nearby abyssal plains (Pozzato et al., 2017; Wenzhoefer and Glud, 2002). Amorphous silica originating from the continent is recycled together with the mineralization of terrigenous organic debris (Raimonet et al., 2015).

In contrast, pore water biogeochemistry and potential metabolic pathways are highly different in the habitats. The oxygen penetration is limited to 1-2 mm, the oxygen flux rises to 8-40 mmol m^{-2} d^{-1} and, in most instances, anoxic diagenesis involving complete sulfate reduction, methanogenesis and anoxic oxidation of methane (AOM) is indicated by pore water composition (Pastor et al., 2017). The presence of dissolved sulfide allows the colonization of habitats of several meters in size by compact vesicomyid bivalves, often associated with white filamentous microbial mats looking like sulfur-oxidizing bacteria and reduced black sediments. Evidence from microbiology indicates the simultaneous presence of ANME (ANaerobic MEthanotrophs) and sulfate reducing bacteria suggesting that AOM is probably active in these sediments although the sulfate-methane transition zone is not obvious (Pastor et al., 2017). This observation could be linked to the deposition regime of the turbidites which involves high accumulation rates (0.5-20 cm y^{-1}) and discontinuous deposition (1 turbidite every 6-17 years). The edges of these habitats are well-defined and presumably linked to the precipitation of iron-sulfide minerals (Taillefert et al., 2017), indicating that the coupling of iron and sulfur cycles plays a major role in controlling the establishment and size of the habitats.

Mass balance indicates that burial largely outweighs remineralization processes. The averaged 3.5 to 4 wt% OC associated to high sedimentation rates in the Congo distal lobe complex implies a large burial rate of organic carbon. Finally, the Congo deep-sea fan represents an enormous sink of terrestrial organic matter when compared to other turbiditic systems over the world (Baudin et al., 2017a, 2017b). Recycling is limited by the short residence time in surface sediments and the refractory nature of the substrate in most of the sediment except in the 'hot spots' colonized by the fauna which reprocesses the initial organic matter deposition (Pruski et al., 2017).

- Congo fan turbidites sustain high faunal densities and cold seep-like ecosystems

Cold-seep like habitats have been observed, along about 70km in the five successive terminal lobes from the entrance of the lobe complex to the main depositional area, but not further downstream. Vesicomyid bivalve patches, microbial mats and reduced sediments were mapped using ROV still imagery and mosaic processing along transects over several kilometers, and their distribution were related to micro-topography (Sen et al., 2017). Vesicomyid clam patches were preferentially located along the channel flanks affected by sliding, and on levees formed by channel overspill. They avoid the channel center likely due to high current speed, but colonize it where it becomes wider and shallower in the main depositional area, coping with exceptionally high sedimentation rates (Rabouille et al., 2017). Locally, vesicomyids are closely related to slide scars or collapsed blocks of sediments, which likely facilitate sulfide exhumation (Sen et al., 2017). Vesicomyid and microbial mats show a patchy distribution, and a limited colonization of black sediment patches, reflecting a balance between favorable habitat provision and disturbance by turbiditic currents.

Stable isotope and fatty acid analyses of faunal tissues evidenced that the fauna colonizing sulfide-rich habitats mainly rely on microbial chemosynthesis, either through symbioses for vesicomyid clams, or by the feeding on several microbial populations (aerobic or anaerobic methane oxidizers, sulfate-reducers) by heterotrophic macrofauna (Pruski et al., 2017). The associated fauna shows a strong similarity with cold seeps habitats, with characteristic patterns of high density and low diversity (Olu et al., 2017). This macrofaunal community varies among habitats and sites and is dominated by several sulfide-tolerant polychaete families which are hypothesized to change over time with habitat geochemistry evolution and vesicomyid colonization, starting in microbial mats. Engineering effect on geochemical gradients and infauna is hypothesized to differ between the two vesicomyid species, *Christineconcha regab* and *Abyssogena southwardae*, related to their ability to burrow (Olu et al., 2017). Indeed, these species differ in the properties of their respiratory pigments allowing them to tolerate hypoxic or anoxic conditions (Decker et al., 2017).

Respiration rates were estimated in situ with ROV-manipulated benthic chambers above vesicomyid clusters, and on individual clams isolated from the sediment (Khripounoff et al., 2015; 2017). Both techniques revealed high oxygen uptakes (from 6.2 to 22.9 µmol.gdw^{-1}.h^{-1}) and large fluxes of dissolved inorganic carbon (DIC) and methane in the range of those measured for cold seep bivalves, showing high levels of anaerobic metabolism.

The large terrestrial organic matter inputs also sustain exceptional macrofaunal densities in the whole lobe sediments (on the levees, the channel flanks and in the depositional area, outside of chemosynthesis-based habitats). In the sediments of the terminal lobe complex, these densities were 7 to 8 higher than in the abandoned lobe complex, where they seem also high compared to similar depth abyssal sediment (Olu et al., 2017). Densities are consistent with total oxygen uptake, high and quite homogeneous over the entire lobe complex, lower in the abandoned lobe and in abyssal sediment at similar depth (Olu et al., 2017). Megafauna dominated by detritivores (large size agglutinated foraminiferans, holothurians) and filter/suspension-feeders (sponges) rely on these detritic, turbiditic, mainly terrestrial-originated inputs (Pruski et al., 2017; Sen et al., 2017;). This fauna is supported by the exceptional amounts of organic carbon, which provide enough biopolymeric carbon and proteinaceous nitrogen, despite poor digestibility of soil-derived organic matter (Pruski et al., 2017). Nevertheless, macrofaunal communities, dominated in non–reduced sediments by peracarid crustaceans but also by cossurid and spionid polychaetes were more closely related to those colonizing low-flow cold seeps than those of typical deep-sea sediment, likely related to the high organic content of the sediments (Olu et al., 2017).

4. The conceptual model revisited

The new findings published in the 15 articles of this special issue provided a new conceptual framework for the functioning of this complex area. The first striking feature is the existence of two different environments at a distance of a few kilometers (and sometimes a few meters). This is what we named “background” and “reduced habitats”. The reduced habitats are largely related to sedimentological features such as large deposition of recent and relatively fresh terrestrial organic matter and to sediment sliding on the flanks of the feeding channel (Croguennec et al., 2017; Dennielou et al., 2017). These processes promote the production/exhumation of reduced substrates either from previously buried sulfides or from intense diagenesis of recently deposited organic matter (Pastor et al., 2017; Taillefert et al., 2017). They are colonized by dense populations of chemosynthetic vesicomyid bivalves and microbial mats (Olu et al., 2017; Sen et al., 2017) which feed on sulfide produced by sulfate reduction or anaerobic oxidation of methane in proportion that remains unknown (Pastor et al., 2017). In these reduced habitats, the penetration of oxygen is limited (Pozzato et al., 2017), the metabolism is amplified as recorded by *in situ* incubation experiments (Khripounoff et al., 2017) and organic substrates generation (Pruski et al., 2017). The macrofauna is dominated by species tolerant to or taking advantage of sulfide with their symbionts and is very similar to cold seep assemblages (Decker et al., 2017; Olu et al., 2017), though the source of methane might be located in shallow sediments (Pastor et al., 2017).

On the contrary, most of the levees show very different biological assemblages dominated by large sized foraminifera (*Bathysiphon* sp.; Sen et al. 2017). The biogeochemistry of this zone show large content of terrigenous organic matter (Méjanelle et al., 2017; Schnyder et al., 2017) which is very similar in concentration and type to the reduced habitats (Baudin et al., 2017b) but larger oxygen penetration depth (Pozzato et al., 2017) and a noticeable absence of sulfide with large concentration of dissolved iron in pore waters (Beckler et al., 2016). These features indicate a shift from sulfide-dominated to iron-dominated diagenesis when moving from reduced habitats to the background exemplified by the levees (Taillefert et al., 2017).

Overall, the terminal lobe complex is a hot spot of organic carbon burial compared to the hosting abyssal plain (Baudin et al., 2017a) with specific burial of terrigenous organic carbon as large as 1000 g C m^{-2} y^{-1} in the most distal lobe and average values of around 100 g C m^{-2} y^{-1} over the 2525 km^2 of the active lobes of the deep-sea fan. This mega-burial is accompanied by equivalent quantities of biogenic silica originating from land (Raimonet et al., 2015). These values are 1000 to 10000 times larger than average burial in the deep Atlantic Ocean (Rabouille et al., 2017; Stetten et al., 2015). Recycling represents at most 25% of the deposited fluxes with lower values (5%) in the most distal lobes.

5. An attempt to understand temporal evolution of the ecosystems

The different types of reduced habitats (reduced sediment, microbial mats, vesicomyid clusters) that co-occur in the terminal lobe complex may correspond to a hypothetical sequence of successional stages. Observations based on macrofaunal community patterns (composition, diversity, vertical distribution), vesicomyid population characteristics (size, species) and geochemical composition and gradients can be interpreted as temporal evolution of these chemosynthesis-based habitats, with interplay between the biotic and abiotic components involving biogeochemical as well as biological controls (Olu et al., 2017; Taillefert et al., 2017). From these observations, it is hypothesized that reduced sediments and microbial mats are the first to develop along the sulfide-rich patches generated by exhumation or intensification of diagenetic processes. Vesicomyid clams that colonize microbial mats contribute to deepen the suboxic layer and displace the sulfide-rich layer deeper in the sediments by bioturbation, bio-irrigation and sulfide uptake. Bio-irrigation also allows sulfate replenishment leading to an increase of net sulfide production at depth (Pastor et al., 2017) and oxygen penetration which contributes to favorable conditions for associated macrofauna. In the first steps of colonization, the small size macrofauna may also modify the biotope, by grazing microbial mats, or by irrigation of the first sediment layers. Indeed, the depth of the sulfide-rich layer has been observed to vary with the vesicomyid shell length and between the vesicomyid species, assumed to differently bio-irrigate the sediment due to their burrowing abilities (Decker et al., 2017; Olu et al., 2017). When moving 10 km away from the main active channel, the sulfide-enriched layer occurs deeper in the sediment (Pastor et al., 2017; Taillefert et al., 2017), which is accompanied by the dominance of another vesicomyid bivalve of larger size, *A. southwardae*, assumed to burrow deeper and be adapted to efficient O_2 storage and transport (Decker et al. 2017). The sulfidic layer eventually disappears in the abandoned northern lobe (50km North) together with the cold-seep like habitats.

Although similarities with community succession at cold-seeps have been observed, the limited resources, without methane stock at depth such as in cold seeps is assumed to limit the development of chemosynthesis-based habitats to a very patchy distribution: only a limited number of black reduced sediment patches observed in the youngest lobe are colonized by microbial mats and vesicomyids, (Sen et al., 2017). The high rate of disturbance by turbidite deposition also limits the development of the habitats and is also hypothesized to increase the rate of faunal succession in very short-lived habitats. Indeed, with a turbidite frequency estimated every 6 to 17 years (Dennielou et al., 2017), a vesicomyid cluster should develop within 5 to 10 years, which is consistent with the highest estimated growth rates for cold seep vesicomyids (see discussion in Sen et al., 2017). Long-term interdisciplinary observation and sampling at inter-annual scale is clearly needed to test the proposed habitat succession model, to assess vesicomyid growth rates and species succession, to clarify the rate of macrofaunal community dynamics in relation with biogeochemical and sedimentological changes as they both are the final drivers of the ecosystem evolution.

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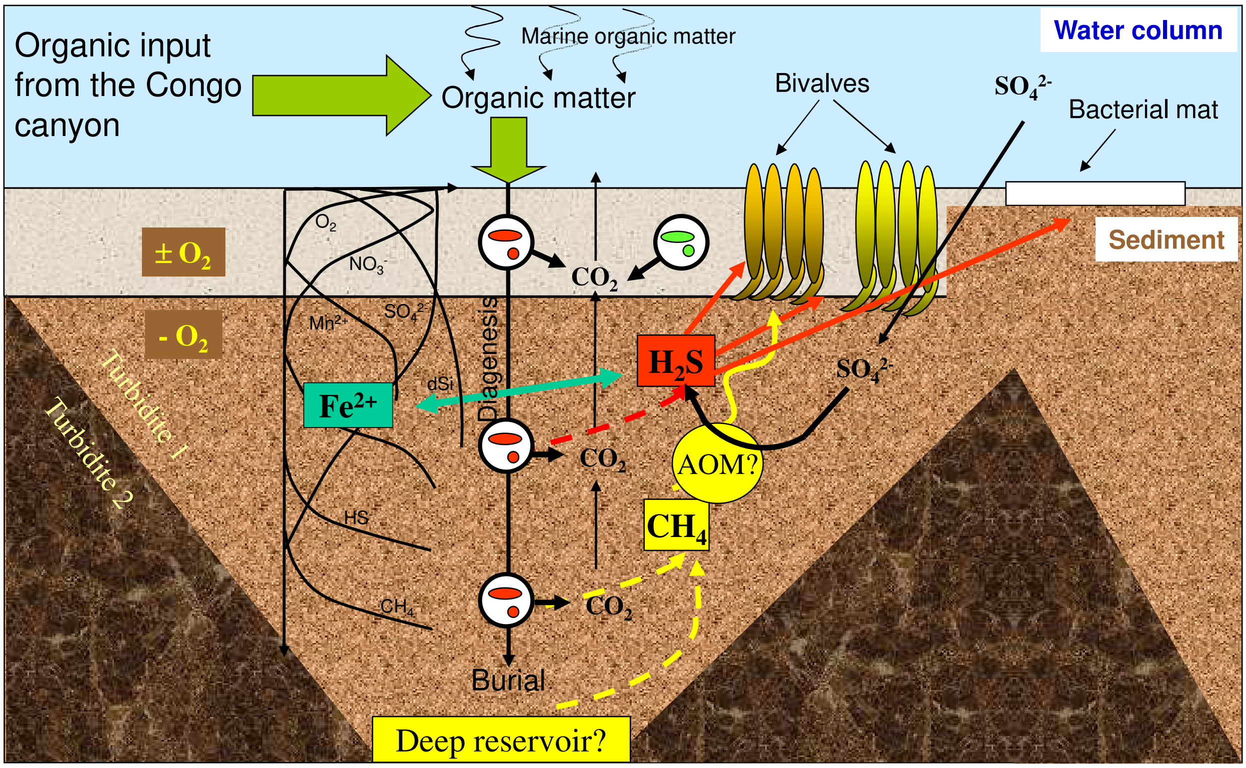
Figure caption:

Figure 1: Initial conceptual framework for our study of the Congo lobe ecosystems.

Figure 2: Final conceptual framework emphasizing the link between geological structures, biogeochemical processing of organic matter and fauna. White parts of the schematic lobe complex represent fine muds, while yellow dotted parts represent more sandy sediments.



Organic input from the Congo canyon
Marine organic matter
Organic matter
Water column
Bivalves
SO_4^{2-}
Bacterial mat
Sediment
$\pm O_2$
$- O_2$
O_2
NO_3^-
Mn^{2+}
SO_4^{2-}
dSi
HS^-
CH_4
Fe^{2+}
Diagenesis
CO_2
H_2S
SO_4^{2-}
AOM?
CH_4
CO_2
CO_2
Burial
Turbidite 1
Turbidite 2
Deep reservoir?

Figure 1

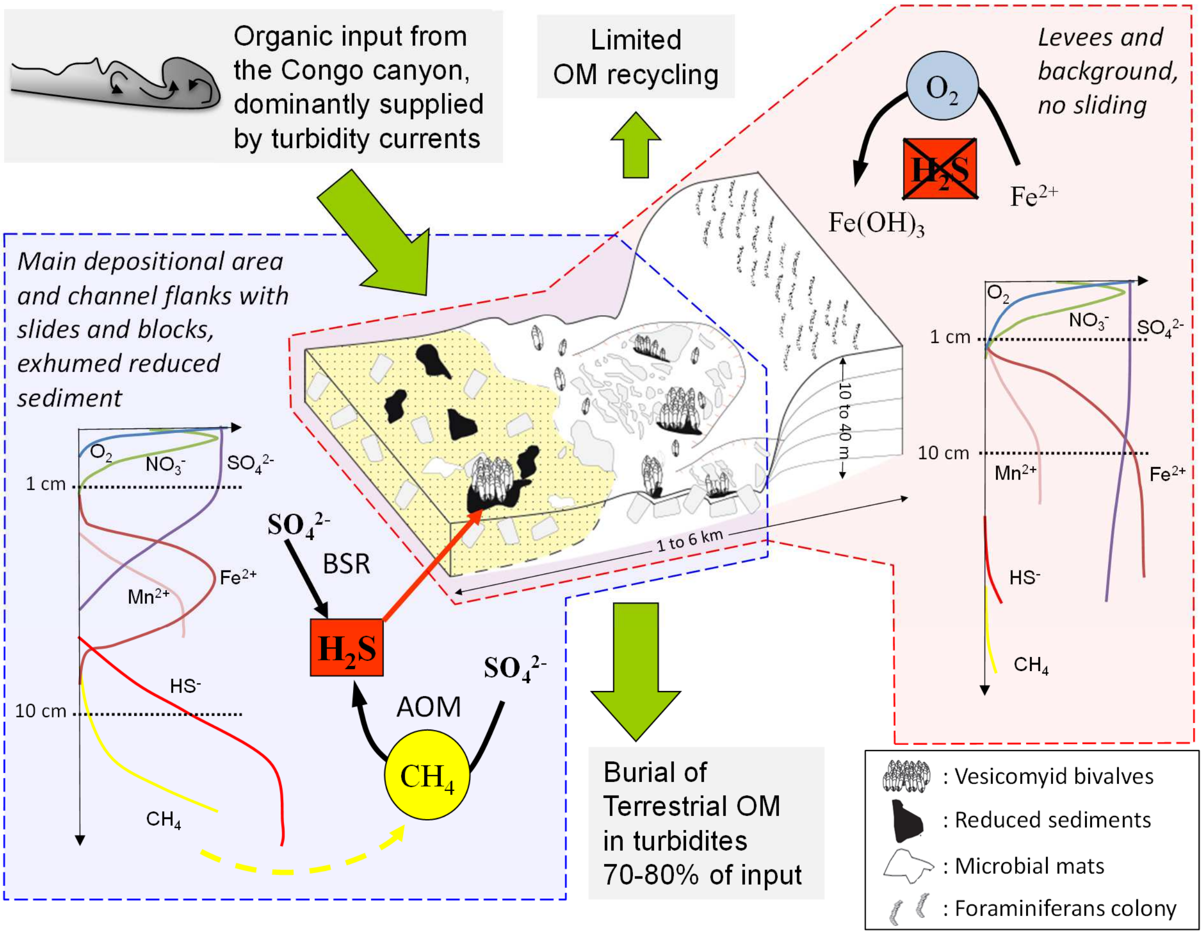

Organic input from the Congo canyon, dominantly supplied by turbidity currents
Limited OM recycling
Levees and background, no sliding
O_2
H_2S
$Fe(OH)_3$
Fe^{2+}
Main depositional area and channel flanks with slides and blocks, exhumed reduced sediment
O_2
NO_3^-
SO_4^{2-}
1 cm
10 cm
Mn^{2+}
Fe^{2+}
HS^-
CH_4
SO_4^{2-}
BSR
H_2S
AOM
CH_4
SO_4^{2-}
10 to 40 m
1 to 6 km
Burial of Terrestrial OM in turbidites 70-80% of input
: Vesicomyid bivalves
: Reduced sediments
: Microbial mats
: Foraminiferans colony

Figure 2