Organic matter transport and deposition in the Whittard Canyon and its possible effects on benthic megafauna

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ABSTRACT
The Whittard Canyon (NE Atlantic) is one of the largest canyon systems on the northern Bay of Biscay margin. It likely receives a high input of organic matter from the productive overlying surface waters, and part of this organic matter may eventually be transferred down the canyon into the Whittard Channel extending from the canyon mouth onto the Biscay Abyssal Plain. In this study we re-examine and integrate the current knowledge on the possible transfer of organic matter through this canyon and its effects on the megafauna communities. We show that the canyon-mediated transport of OM can provide favourable environmental conditions (current regime, food input) to sustain megafauna communities, but that at greater depths other mechanisms can also be important. The insights obtained here contribute to our wider understanding of submarine canyons in general.

1. INTRODUCTION
Submarine canyons are large geomorphological structures that incise continental shelves and steep slopes along continental margins. They can be highly dynamic sedimentary environments where sediments rich in organic matter (OM) are trapped or transported downslope across the shelf and slope to greater depths (e.g. Rowe et al., 1982; Hecker, 1990; Duineveld et al., 2001; Tyler et al., 2009; De Stigter et al., 2007; Garcia et al., 2010; Canals et al., 2013; Puig et al., 2012). This capacity enriches the canyon ecosystem and has profound consequences on the biota (Maurer et al., 1994; Vetter and Dayton, 1998; Ingels et al., 2009; De Leo et al., 2010; Amaro et al., 2010; Huvenne et al., 2011). When compared to adjacent areas of the continental slope, canyons are up to 30 times more effective in burial of organic carbon (e.g. Nazaré Canyon, Masson et al., 2010; Pusceddu et al., 2010). For instance, the presence of frenulate siboglinids and thyasirid bivalves (typical organisms from chemosynthetic environments) in canyon sediments is indicative of high organic loading (Cunha et al., 2011). Canyons also play an important role in feeding and reproduction of a broad range of benthic and demersal species (Vetter et al., 2010) as there is enhanced food availability in these areas. They provide important habitats for various life stages of benthic and demersal fishes and invertebrates along continental margins and they constitute important sources of larvae for surrounding habitats (Vetter and Dayton, 1998, 1999; Company et al., 2008). As a result, submarine canyons have often been termed hotspots of biomass, abundance, metabolic activity and carbon mineralisation when compared to the adjacent slope at comparable depths (Vetter, 1994; Tyler et al., 2009; Amaro et al., 2010; De Leo et al., 2010).
Submarine canyons are also one of the most heterogeneous habitats in the deep sea. They typically encompass a range of sub-habitats, reflecting their topographic and geomorphological diversity. This high degree of heterogeneity supports abundant and diverse burrowing, epibenthic mobile and sessile faunal communities of all size classes. Nevertheless, each canyon is a unique system with a large degree of heterogeneity (McClain et al., 2010).

The Celtic margin situated in the NE Atlantic is incised by a large number of submarine canyons (Fig. 1). The comparatively productive waters overlying this area supply the deep-sea sediments with high levels of OM and carbon (Lampitt et al., 1995; Longhurst et al., 1995; De Wilde et al., 1998; Joint et al., 2001). It seems likely that the canyons on the Celtic margin concentrate part of this export and are important focal areas for budgeting carbon fluxes.

The Whittard Canyon is one of the large canyons on the Celtic margin and has recently become the object of detailed investigations. As a large and dendritic canyon system, with multiple branches converging into a single deep-sea channel extending onto the Biscay Abyssal Plain, and situated below comparatively productive surface waters supporting a high export flux of OM, the Whittard Canyon seems the ideal focal area for concentrating OM fluxes on the continental margin. Whilst the Whittard Canyon has recently become the object of detailed investigations, information on its physical functioning and its ecosystem is still limited (Reid and Hamilton, 1990; Duineveld et al., 2001; Duros et al., 2011; Huvenne et al., 2011; Ingels et al., 2011). Following earlier observations indicating relatively rich benthic life in the Whittard Canyon (Duineveld et al., 2001), we seized the opportunity to provide an overview of the current knowledge in the Whittard Canyon, focusing our paper on the OM transfer through this canyon and its effects on the megafauna communities.

2. SITE DESCRIPTION

The Whittard Canyon is a large dendritic canyon system that lies in the continental slope off the Celtic margin between the Goban Spur and the Meriadzek Terrace (Fig. 1). The canyon system extends from the upper slope around the 200 m isobaths to down-slope into larger channels onto the abyssal plain. The upper part of the canyon is a complex system of smaller canyons and valleys distinctly V-shaped in cross section and narrow thalweg. The width of the canyon falls to 700 m, with the sidewalls attaining a height of 800 m. The main canyon branches form the middle and lower canyon, are more U-shaped in section and have a broader thalweg. Towards the abyssal plain the height of the side walls reduces to about 100 m (Reid and Hamilton, 1990). The westernmost branch of the Whittard Canyon is the longest, with an along- channel length of 160 km. At almost 4000 m depth, all branches come together at the foot of the continental slope. Beyond 4000 m the canyon continues as a single broad valley that gradually descends for another 150 km to the Biscay abyssal plain at 4300 m depth (Zaragosi et al., 2000).

On the abyssal plain the Whittard Canyon continues as a meandering channel. Together with the Shamrock Channel it constitutes the main tributary of the Celtic Fan, a deep-sea fan fringing the continental margin, fed by sediments originating from the shelf and adjacent land masses and tunneled through submarine canyons down the continental slope. The morphology of the Celtic Fan and its tributary channels is described in detail by Zaragosi et al. (2000), on the basis of multibeam and 3.5 kHz seismic data and sediment cores. The Whittard Channel starts at the base of the continental slope at about 4100 m depth, where it connects to the mouth of the dendritic Whittard Canyon system. From there it descends along a sinuous course in Sth to SE direction for about 100 km until the junction with the Shamrock Channel at about 4600 m. Further downstream the single channel splits up in a number of smaller and less distinct channels in the middle fan area. The Whittard Channel is 2.5-3 km wide, with 70-150 m of relief from the channel floor to the right levee crest. Levees bordering the channel are strongly asymmetrical; the right levee named Whittard Ridge is 60 km wide and covered with sediment waves, while the left one is less than 10 km wide. On the basis of analyses on cores collected from the fan, Zaragosi et al. (2000) concluded that frequent low-density turbidity currents were predominant during the last glacial lowstand and rise of sea-level, whilst during high sea-level conditions hemipelagic deposition prevailed, punctuated only occasionally by high-density turbidity currents and/or non-cohesive debris flows. Current meter observations by Reid and Hamilton (1990) suggest that the present-
day environment is characterized by weak bottom currents, too weak to resuspend and transport sediments from the seabed. Yet, Duineveld et al. (2001) found indications for biological enrichment in the Whittard Canyon extending to the lower canyon reaches, which they attributed to lateral transport of fresh OM down the canyon.

Figure 1. The Whittard Canyon (A) Location of the study area on the western European continental margin; (B) Multibeam bathymetric map of the lower Whittard Canyon and proximal part of the Whittard Channel. Bathymetry courtesy HMS Scott.

3. ORGANIC MATTER
3.1. Suspended particulate matter (sPOM)

There have been very few studies examining concentrations and composition of suspended particulate organic matter (sPOM) in the Whittard Canyon. Near bottom (<10 m above bottom) sPOM collected using stand-alone pumps in Huvenne et al. (2011) were 2 to 3 times higher in the upper parts of the canyon at the far western and eastern branches (> 2000 m depth; one station at each end) than at the deeper (three stations < 3000 m depth) more central parts. The observed decrease in sPOM concentrations with water depth was also a common feature in both cases, attributed to the less energetic nature of oceanographic conditions at the deeper parts. sPOM in that study seemed to be fresh phytoplankton-derived as suggested by the low molar C/N ratios (4.1 – 7.7). In addition the same authors showed that the nutritional quality of sPOM was higher in the upper parts, as evidenced by the elevated concentrations of essential fatty acids, docosahexaenoic fatty acid (DHA) and eicosapentaenoic fatty acid (EPA) in sPOM. EPA and DHA are biosynthesized primarily by phytoplankton and they are pivotal in aquatic ecosystem functioning, as they largely control trophic transfer efficiency to higher trophic levels (Muller-Navarra, et al., 2004). In these locations of the upper canyon, these high concentrations and nutritional quality of sPOM (the latter is defined by the relatively high concentrations of EPA and DHA in sPOM; see Kiriakoulakis et al., 2011) seem to be responsible for the presence of a rich community consisting of cold-water corals and associated organisms (Huvenne et al., 2011; Morris et al., 2013).
contrast, in the deeper and more impoverished parts of the canyon, one finds no cold-water corals. Although the sPOM data in Huvenne et al. (2011) were from a small number of locations and the sampling only provided a ‘snapshot’ (sPOM was collected in early summer 2009 soon after the phytoplankton bloom), the presence of a flourishing *Lophelia pertusa* population is often linked to a supply of relatively fresh OM (Orejas et al., 2009; Wagner et al., 2011; Duineveld et al., 2012; Morris et al., 2013). The exact mechanism between the apparent coincidence *Lophelia* occurrence and the water column characteristics is not clear yet, but it has been suggested that downslope processes like resuspension by internal waves and tides (Ivanov et al., 2004), dense shelf water cascading, sediment gravity flows (Puig et al., 2012) and turbidity currents to greater depths, could result not only in canyon flushing, but also in focused enrichment and deposition of OM to greater depths (Duineveld et al., 2001; Masson et al., 2010). These mechanisms provide favourable environmental conditions (current regime, food input) to sustain the megafauna communities, even when they are outside the optimal depth and density envelopes reported elsewhere in the NE Atlantic.

Recently, Amaro et al. (2015) showed with a yearly deployment of sediment traps at the outer deeper (~4000 m depth) central part of the canyon (Whittard Channel) that the occurrence of mass aggregation of megafauna organisms is not necessarily the result of down-canyon transport of OM. Amaro et al. (2015) showed, and that the highest flux of fresh OM arriving at the deeper end of the Whittard Canyon is due to local settling of phytodetritus after the spring phytoplankton bloom. In their study gravity-driven episodic events, provided low nutritional quality material.

### 3.2. Sedimentary organic matter (SOM)

Duineveld et al. (2001) showed that the sedimentary organic carbon (SOC) content in the surficial sediments at the middle-lower central channels of the Whittard canyon (2735 to 4375 m water depth) was higher, (0.9--1.1% of dry sediment), than in the surface sediments of the open slope stations of the Goban Spur, (0.4--0.5% of dry sediment), although there was no clear downslope trend. Canyons acting as ‘traps’ of OM have been observed before in the European Margin (Masson et al., 2010). This was related to the high sedimentation rates in the canyon which promote carbon burial by reducing the oxygen exposure time (OET) of the sediment (Kiriakoulakis et al., 2011). The high SOC levels observed in Duineveld et al. (2001) persisted down core to 5 cm in the upper middle section, but deeper the SOC content dropped to levels comparable to the Goban Spur 2–3 cm below the surface. This was attributed to coarser grains sizes of the canyon sediments that increase OET and have a weaker mineral association with OM (Hedges and Keil, 1995). Other investigations (Huvenne et al., 2011; Amaro et al., 2015) showed that surficial sediments in several locations within the Whittard Canyon were practically indistinguishable from open slope values (0.1 -- 0.7% SOC of dry sediment). Both studies showed that the highest SOC values were closer to the Whittard Channel (i.e. the deep central section). Clearly the mechanisms for the often mentioned ‘OM enrichment’ in submarine canyons are not fully understood and perhaps cannot be universally applied. It appears likely that they vary both spatially and temporally in relation to the complex topography and its interaction with the current and tidal regime that could promote deposition or erosion of sediment (Huvenne et al., 2011), the nature of gravity flows (Houghton, 2009), the impact of the resident benthic fauna (Ingels et al., 2011; Amaro et al., 2015) and the supply and lability of OM (Huvenne et al., 2011; Kiriakoulakis et al., 2011).

The lability of sedimentary OM (SOM) from various locations within the Whittard Canyon has been investigated (Duineveld et al., 2001; Huvenne et al., 2011; Ingels et al., 2011; Amaro et al., 2015). The molar C/N ratios of the first 10 cm of sediments mostly show a marine unaltered (i.e. ‘fresh’) signal (most values 4-8), although there were occasionally higher (up to 20; Duineveld et al., 2001; Ingels et al., 2011). Microbial degradation, benthic bioturbation or episodic deposition of resuspended degraded material with high C/N ratios could all be likely reasons for this observation. In addition there was no consistent trend with depth emphasizing the complexity and the multitude of the transport processes affecting this vast system. Fewer studies have provided a more detailed insight on the bioavailability of SOM, mainly by investigating phytopigments, nucleic and fatty acids in selected locations. Duineveld et al. (2001) showed that concentrations of phytopigments and nucleic acids decreased both down slope and down core within the canyon, suggesting a lowering of OM bioavailability both in fine (vertical) and larger (distance from shelf)
scales. Ingels et al. (2011) supported the former observation by showing that small scale (vertical) heterogeneity in SOM quality (expressed mainly as relative contributions of phytopigments to Carbon) within the same core can explain much of the variation of the meiofaunal communities of the canyon. The importance of SOM (nutritional) quality to benthic communities has also been highlighted by Huvenne et al. (2011), and Amaro et al. (2015) who found appreciable concentrations of essential fatty acids (EPA and DHA) in the surficial sediments from several areas of the central upper and middle parts of the canyon. These seem to be associated with the presence of CWCs in the same areas. Similarly Amaro et al. (2015) showed that ‘fresh’ OM (using phytopigments as proxies) in sediments from the Whittard Channel was associated with abundant elpidiid holothurians. Latter organisms have been frequently found associated with favourable quality and quantity of sedimentary OM (De Wilde et al., 1998; Amaro, et al., 2010; Billett et al., 2010; De Leo et al., 2010). The same authors suggested that the SOM origin was related to overlying phytoplankton blooms rather than gravity driven processes through the canyon. When these were detected (using sediment traps) they resulted in accumulation of low quality degraded material.

4. CONCLUSION

This overview represents the first attempt to reveal the fuller picture of the flow of the OM transfer through Whittard Canyon and its effects on the megafauna communities. The Whittard Canyon seems to play a role in transfer of shelf production (and terrestrial carbon) to the deep sea. The OM quality seems to depend on the overlying production of the water masses and the distribution of the fresh OM seems to be coupled with processes in the canyon such as the gravity flow events. However, down the canyon and specifically on the Whittard channel, the fresh OM found in the area is decoupled from such processes and most of the OM supply is more likely linked to local phytodetritus deposition, concentrated within the topographic depression formed by the Whittard Channel after redistribution by bottom currents. The occurrence of abundant megafauna communities both in the upper canyon and channel is linked to OM quality and quantity. However, the data analysed here are only a snapshot of the conditions within the Whittard Canyon. There is a need to get more data on mega-macro-meiomega abundances in Whittard Canyon in relation to OM (quality, quantity) thru a multi-year study to understand the processes behind these patterns. In submarine canyons susceptible to being affected by dense shelf-water cascading events, simultaneous measurements of water temperature and salinity should be made to compute water density. Observations in submarine canyons should be combined with external forcing conditions (e.g., winds, surface waves, and river discharges) to correctly discern the mechanisms involved in shelf-to-canyon sediment delivery.

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