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The Whittard Canyon – A case study of submarine canyon processes

by

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52
53
54 **ABSTRACT**

55 Submarine canyons are large geomorphological features that incise continental

56 shelves and slopes around the world. They are often suggested to be biodiversity and

57 biomass hotspots, although there is no consensus about this in the literature.

58 Nevertheless, many canyons do host diverse faunal communities but owing to our

59 lack of understanding of the processes shaping and driving this diversity, appropriate

60 management strategies have yet to be developed. Here, we integrate all the current

61 knowledge of one single system, the Whittard Canyon (Celtic Margin, NE Atlantic),

62 including the latest research on its geology, sedimentology, geomorphology,

63 oceanography, ecology, and biodiversity in order to address this issue. The Whittard

64 Canyon is an active system in terms of sediment transport. The net suspended

65 sediment transport is mainly up-canyon causing sedimentary overflow in some upper

66 canyon areas. Occasionally sediment gravity flow events do occur, some possibly the

67 result of anthropogenic activity. However, the role of these intermittent gravity flows

68 in transferring labile organic matter to the deeper regions of the canyon appears to be

69 limited. More likely, any labile organic matter flushed downslope in this way

70 becomes strongly diluted with bulk material and is therefore of little food value for

71 benthic fauna. Instead, the fresh organic matter found in the Whittard Channel mainly

72 arrives through vertical deposition and lateral transport of phytoplankton blooms that

73 occur in the area during spring and summer. The response of the Whittard Canyon

74 fauna to these processes is different in different groups. Foraminiferal abundances are

75 higher in the upper parts of the canyon and on the slope than in the lower canyon.

76 Meiofaunal abundances in the upper and middle part of the canyon are higher than on

77 adjacent slopes, but lower in the deepest part. Mega- and macrofauna abundances are

78 higher in the canyon compared with the adjacent slope and are higher in the eastern

79 than the western branch. These faunal patterns reflect the fact that the Whittard

80 Canyon encompasses considerable environmental heterogeneity, related to a

81 combination of organic matter trapping, current regimes (due to focused internal

82 tides) and different substrates. We conclude that coordinated observations of

83 processes driving faunal patterns are needed at a fine scale in order to understand the

84 functioning of communities in this and other submarine canyons.

85

1. INTRODUCTION

More than 9450 large submarine canyons have been identified along the World's continental margins (Harris et al., 2014), making them important features that affect the geology, sedimentology, oceanography, biology and ecology of our oceans. Their presence gives rise to complex physical oceanographic conditions that locally enhance primary productivity and increase particulate matter concentrations (Bosley et al., 2004; Ryan et al., 2005; Skliris & Denidi, 2006). They provide the main transport pathways between the shelf and the deep ocean, funnelling sediments, nutrients and organic matter (OM) (Puig et al., 2014) as well as pollutants and litter (e.g. Palanques et al., 2008; Pham et al., 2014) into the deep sea. These phenomena eventually lead to an enrichment in abundance and diversity of biological communities (Schlacher et al., 2007, Danovaro et al., 2009; Bianchelli et al., 2010; Vetter et al., 2010) including commercially important stocks of fish and shellfish (Puig et al., 2012). However, the processes controlling these phenomena are only partly understood. The interactions between oceanography, sediment transport, biogeochemistry and the resulting spatial distributions of biological communities are particularly unclear.

Submarine canyons, with their steep morphology, variable current speeds and occasional catastrophic flows, are challenging environments to study. Recent technological advances (e.g., the use of Remotely Operated Vehicles, gliders and robust landers) have driven an increase in the number and geographical spread of submarine canyon studies. However, a more complete picture of the processes acting and interacting in submarine canyon settings can only be obtained from concerted studies of individual canyons (Huvenne & Davies, 2014). The aim of this overview is therefore to integrate current knowledge of processes operating in the Whittard Canyon, one of the main submarine canyons along the Celtic Margin, NE Atlantic.

The Whittard Canyon is an interesting case study for several reasons. Firstly, the canyon head is located approximately 300 km from land (Fig. 1). This means that terrestrial sediment input is strongly reduced compared to canyons receiving direct river input (e.g. Kaikoura Canyon, off the coast of New Zealand) or canyons that have their heads close to the shoreline and hence act as traps for along-shore sediment transport (e.g., Nazaré Canyon, Iberian Margin). Hence, from this perspective, this canyon may appear inactive (Toucanne et al., 2008). However, the Whittard Canyon

120   still encompasses the complexities of a shelf-incising submarine canyon (as defined

121   by Harris & Whiteway, 2011): a dentritic morphology with multiple branches

122   converging into a single deep-sea channel, topography (steep and vertical walls), rich

123   and varied biological communities. Therefore, a broad range of typical canyon

124   processes (e.g. internal waves, small-scale slope failures, sediment gravity flows,

125   lateral transport, Allen & Durrieu de Madron, 2009; Puig et al., 2014) are still acting

126   here and can be studied without being obscured by repeated throughputs of

127   terrestrially-derived material. The Whittard Canyon has been the subject of a wide

128   range of specific studies over the past 10-15 years, covering many aspects of

129   submarine canyon research. By combining all the available data and insights obtained

130   by these individual investigations (Table 1), we aim to advance our understanding,

131   not only of the Whittard Canyon system as a whole but also of canyon processes in

132   general. As a framework for this integration, this paper will tackle the following

133   questions. 1) Is the Whittard Canyon active in terms of sediment transport? 2) If so, at

134   which temporal and spatial scale? 3) What impact does this (in)activity have on the

135   associated benthic fauna and their functioning?

136

137   **2. SETTING**

138

139   a) Geology of the Celtic Margin

140   The Celtic Margin is a WNW-ESE oriented passive margin that extends from

141   the Goban Spur to the Berthois Spur in the Bay of Biscay (Fig. 1). The adjacent

142   continental shelf is wide, whereas its continental slope is steep (average slope 8°).

143   The entire margin is cut by approximately 35 submarine canyons, with the Whittard

144   Canyon being the most westerly located (Bourillet et al., 2006; Mulder et al., 2012).

145   The Celtic spurs and canyons are associated with submarine drainage basins (Grande

146   Sole and Petite Sole), and feed the deep-sea Celtic fan through the Whittard and

147   Shamrock Canyons (Bourillet et al., 2006). During the last glacial period, they were

148   connected to an active palaeovalley system (Bourillet et al., 2003; Toucanne et al.,

149   2008), but its activity is now much reduced due to its distance from the present-day

150   shoreline (Reid and Hamilton, 1990). The canyon morphology was influenced by

151   existing NNW-SSE trending fault systems, older buried canyons and natural

152   depressions in the seafloor (Cunningham et al., 2005).

153   The Whittard Canyon is a deeply incising dendritic system, formed through

154   headward erosion and retrogressive slope failure, starting in the Plio-Pleistocene,

155   cutting deeply into Plio-Pleistocene aggradation and shelfal deposits, Miocene deltaic

156   deposits (Fig. 2; Little Sole, Cockburn and Jones formations; Bourillet et al., 2003;

157   Stewart et al., 2014) and the Cretaceous/Paleocene chalks (Evans and Hughes, 1984;

158   Cunningham et al., 2005). The most recent phase of canyon incision into the

159   continental slope commenced during a number of episodic sea level lowstands in

160   Plio-Pleistocene times (Fig. 2; Bourillet etal., 2003; Evans, 1990; Evans and Hughes,

161   1984). Fluvial connections to the Grande Sole and the Petite Sole drainage basins

162   were via the Celtic Sea and Fleuve Manche respectively, resulting in multiple

163   sediment sources for the Celtic deep-sea fan (Bourillet et al., 2003). Massive

164   deglaciation of the British and European ice-sheets (ca. 20-13 ka) resulted in a

165   significant increase in the fluvial flux to the Grande Sole drainage basin, and hence

166   the Whittard Canyon, with terrigenous input prolonged until 7000 years ago by

167   glacio-hydroisostatic uplift of the British Isles (Bourillet et al., 2003; Lambeck, 1996).

168   The linear tidal sand ridges that developed on the outer continental shelf of the Celtic

169   Sea (Praeg et al., 2015) between 20 and 12 ka years ago (Scourse et al., 2009) are also

170   proposed as a sediment source to the Celtic deep-sea fan through strong tidal transport

171   of sediments into the canyon heads (Bourillet et al., 2006; Scourse et al., 2009).

172   However, recent current measurements and oceanographic modelling results suggest

173   an opposite sediment transport direction (see below, and also in Cunningham et al.,

174   2005).

175   The Whittard Canyon system has four main V-shaped branches (Fig. 1), which

176   connect with the broad shelf at approximately 200 m water depth and merge at 3500

177   m into the wide flat-bottomed or U-shaped Whittard Channel, that flows out to the

178   Celtic Fan at 4500 m depth (Reid and Hamilton, 1990; Cunningham et al., 2005). The

179   orientation of the canyon branches at the shelf edge is predominantly NNW-SSE and

180   NNE-SSW (Cunningham et al., 2005). The canyon slope angles may increase to 40°

181   within the canyon heads and flanks, or possibly steeper, featuring steep cliffs and

182   overhangs (Huvenne et al., 2011; Robert et al., 2014; Stewart et al., 2014). Typically,

183   the upper flanks have complicated gully networks and numerous headwall scars from

184   slumps and slope failures, which caused gravity driven flows that widened the canyon

185   by retrogressive canyon wall failure. The seabed substratum is generally coarse-

186   grained or mixed on the interfluves, whereas towards the flanks, the sediment

5

187 becomes muddy, but with outcropping rocks within gullies or scars (Cunningham et
188 al., 2005; Stewart et al., 2014). Additionally, Stewart et al. (2014) reported small
189 mounds built of dead cold-water coral fragments on the Explorer and Dangeard
190 interfluves (Eastern branches). In contrast to the morphologically diverse canyon
191 walls, the canyon thalwegs are predominantly characterised by flat areas of soft
192 sediment (Robert et al., 2014).

193

194 b) Oceanography of the Celtic Margin

195   The structure of the upper-water column (1500 m) along the Celtic Margin is
196 characterised by central and intermediate water masses originating from sub-tropical
197 latitudes. Relatively warm and saline Eastern North Atlantic Water (ENAW), a winter
198 mode water with a source in the SW Bay of Biscay region, occupies the layer above
199 the permanent thermocline (e.g. Perez et al., 1995; Pollard et al., 1996) with
200 Mediterranean Outflow Water (MOW) present below the ENAW (e.g. van Aken,
201 2000; Van Rooij et al., 2010a). Flow characteristics are dominated by the European
202 Slope Current (ESC) carrying ENAW (Pingree and Le Cann, 1990; Xu et al., 2014),
203 and boundary flows associated with the MOW (Van Rooij et al., 2010a). The ESC is
204 typically directed northwest (poleward) with mean flow speeds of 0.05-0.1 ms^{-1}
205 (Pingree and LeCann, 1989; 1990) and varies seasonally, with a minimum in the
206 principal driving mechanism during the summer months (Xu et al., 2014). Spring and
207 autumn loss of slope-current continuity in the Whittard and Goban Spur region,
208 through slope-ocean exchange and mean current reversals, has been reported and
209 termed the SOMA (Sept-Oct-March-Apr) response (Pingree et al., 1999). Near the
210 seabed, observed currents generally have a tidally induced downslope mean
211 component balanced by Stoke transports (Pingree and LeCann, 1989). The possibility
212 of cascading cold dense water from the shelf edge in winter and early spring was
213 reported by Cooper and Vaux (1949), but has not subsequently been observed. In
214 deeper adjacent waters, significant mesoscale variability exists within the MOW
215 boundary flow and deeper (1600-2200 m) Labrador Sea Water layers (Bower et al.,
216 2002).

217   Along the Celtic Sea shelf edge, internal waves and tides are generated at the
218 shelf break by across-slope tidal flow (Pingree and Mardell, 1985; Holt and Thorpe,
219 1997). However, the direction of the propagating internal waves onto the shelf is quite
220 random (Holt and Thorpe, 1997), in contradiction to the generally accepted view that

221   across-shelf internal wave energy flux is controlled by the orientation of the shelf

222   break (Garrett and Kunze, 2007). This is likely due to the highly corrugated nature

223   (e.g. Nash et al., 2004) of the Celtic Sea shelf edge. Understanding the effect of the

224   Whittard Canyon on the internal wave field is therefore important in understanding

225   the internal wave dynamics within the larger Celtic Sea region. The semi-diurnal tide

226   has been observed to drive 28-48W m^{-1} of energy on-shelf (Hopkins et al., 2014),

227   with the positive on-shelf energy flux modulated by nonlinear interaction between the

228   vertical velocity associated with the semi-diurnal internal tide, and the vertical shear

229   of inertial oscillations, leading to an increase of 25-43% in the energy flux. Internal

230   solitary waves with amplitudes reaching a maximum of 105 m have also been

231   reported (Vlasenko et al., 2014). The internal tide generated at the shelf break has

232   been observed as a coherent signal up to 170 km onto the Celtic Sea shelf (Inall et al.,

233   2011). However, an estimated shoreward energy decay scale of 42 km implies that

234   much of the energy generated at the shelf edge is dissipated at or near the shelf break.

235   Primary productivity along the Celtic Sea margin is reasonably high, with

236   estimates between 100-250 g C m^{-2} yr^{-1} reported (Joint et al., 1986; Rees et al., 1999;

237   Wollast and Chou, 2001). Near the Whittard region, Wollast and Chou (2001) report a

238   value of 200 g C m^{-2} yr^{-1} decreasing to 140 g C m^{-2} yr^{-1} in deeper water 150 km from

239   the shelf edge, with potentially 30 g C m^{-2} yr^{-1} exported to the open slope and deep

240   ocean. Mixing by internal tides at the shelf edge is recognised as a significant driver

241   of nutrient fluxes and fuelling enhanced primary productivity (e.g. Holligan et al.,

242   1985; Sharples et al., 2007). Sharples et al. (2007) found a spring-neap modulation in

243   vertical nitrate fluxes across the seasonal thermocline. Neap tide fluxes were

244   sufficient to sustain significant new production, but a 3-6 increase in fluxes at spring

245   tide provided excess available nitrate.

246

247   b.1) Surface tides

248   Tides play an important role in submarine canyons, leading to rectified

249   barotropic flows, enhanced currents and mixing (Allen and Durrieu de Madron,

250   2009). Measurements of the barotropic tide close to Whittard Canyon (48°

251   34.59' N, 9° 30.69' W) over a spring-neap cycle show a variable depth-mean tidal

252   current regime, 0.2 m s^{-1} during neap and 0.5 m s^{-1} during spring (Sharples et al.,

253   2007). The semi-major axis of the depth-mean tidal flow is aligned approximately

254   perpendicular (NE-SW) to the orientation of the isobaths at the sampling

255   location and is confirmed by the TPXO 7.1 inverse model (Egbert, 1997; Egbert

256   and Erofeeva, 2002). This across-slope alignment facilitates internal tide

257   generation at the shelf edge and the upper reaches of the Whittard Canyon. In the

258   Celtic Sea region, about 90% of the total kinetic energy of currents is contained

259   in semi-diurnal frequencies, of which 75% can be attributed to the principal

260   lunar semi-diurnal component (M_2) (Pingree, 1980). This distribution of tidal

261   energy is also applicable to the Whittard Canyon.

262

263   b.2) Internal tides

264   The complex sloping topography associated with submarine canyons can

265   result in both the generation and reflection of internal waves and tides (Hickey,

266   1995). Scattering of barotropic (surface) tides from the sloping topography can

267   generate baroclinic (internal) tides (Baines, 1982), whilst reflection of existing

268   internal waves can lead to trapping and focusing of internal wave energy from

269   outside the canyon (Gordon and Marshall, 1976; Hotchkiss and Wunsch, 1982). The

270   type of reflection that occurs can be predicted from the topographic slope

271   gradient (S_{topog}) and the internal wave characteristic slope gradient (S_{wave}), the

272   latter dependant on local stratification, internal wave frequency and latitude

273   (Thorpe, 2005). Steep canyon walls typically cause supercritical reflection

274   ($S_{topog}/S_{wave} > 1$) resulting in internal waves above the canyon rim being focused

275   towards the canyon floor. Gently sloping canyon floors typically cause subcritical

276   reflection (< 1) resulting in offshore internal waves being focused toward the

277   canyon head. During both types of reflection, the separation between adjacent

278   internal wave characteristics narrows, focusing the wave energy into a smaller

279   volume and hence increasing energy density. In the case of near-critical reflection

280   ($\cong 1$), the energy is trapped against the boundary resulting in nonlinear effects

281   such as wave breaking, internal bores and turbulent mixing (e.g. Nash et al.,

282   2004).

283   Initial high-resolution simulations of the M_2 tide in Whittard Canyon using

284   a modified version of the Princeton Ocean Model (as used by Hall and Carter,

285   2011 and Hall et al., 2014 for Monterey Canyon) show that the depth-integrated

286   baroclinic energy flux within the canyon is elevated, but variable in different

287   branches (Fig. 3a) and that there is a significant flux from certain canyon

288   branches onto the shelf. Enhancement of near-bottom tidal currents is also seen

289 within the canyon (Fig. 3c), with peak velocities >0.4 m s^{-1} in the upper reaches,
290 and the current ellipses highly rectilinear along the canyon axes. In the lower
291 reaches, current velocities are lower, around 0.1 m s^{-1}, and the current ellipses
292 more circular. Enhanced tidal currents and breaking internal waves within
293 the canyon drive turbulent mixing, both in the bottom boundary layer and the interior
294 of the water column. Elevated bottom boundary layer mixing may increase sediment
295 and OM resuspension and along-canyon transport, potentially generate nepheloid
296 layers, and has implications for benthic biology and ecology. Meanwhile, elevated
297 interior mixing has the potential to enhance nutrient fluxes over the canyon, helping
298 to fuel the enhanced primary productivity observed at the Celtic Sea margin.
299
300 **3. CANYON ACTIVITY**
301
302 a) Nepheloid layers
303   Nepheloid layers are cloudy layers of suspended particulate material largely
304 driven by energetic hydrodynamics. They induce high turbidity compared to the
305 surrounding clear waters contributing significantly to the shelf edge exchange of
306 sediment (Mc Cave, 1986; Amin and Huthnance, 1999). They serve as a physical
307 link between productive shallow environments and the deep abyss (Puig and
308 Palanques, 1998), transporting biogenic and lithogenic material, supporting
309 unique benthic ecosystems and contributing to the deposition of carbon in marine
310 sediments.
311   Benthic (BNL) and intermediate nepheloid layers (INL) line the branches
312 of the Whittard Canyon (de Stigter et al., 2008a; Huvenne et al., 2011; Wilson et
313 al., 2015a). Wilson et al. (2015a) report INLs that occur at depths where the
314 benthic source could be attributed to enhanced seabed currents, particularly
315 associated with near-critical internal wave reflection, or the presence of the
316 permanent thermocline, and at depths where MOW cores impinge on the slope
317 (e.g. Van Rooij et al., 2010a). Locations of INLs sourced at the seabed in four
318 branches of Whittard Canyon based on observations from four consecutive
319 surveys (2011-2014) are highlighted in Fig. 3b. Extensive BNLs cover the upper
320 reaches of the branches down to 2500 m, likely maintained by canyon-enhanced
321 near-bottom tidal currents (Fig. 3c). Intermittent INL observations in some of the

322   branches of the Whittard Canyon (INLs observed in one survey only) may possibly

323   be related to lower internal tide energy fluxes (Fig. 3 b).

324

325   b) Current dynamics and tidally driven sediment transport

326   Near bottom current dynamics, in combination with temperature, salinity,

327   turbidity and sediment flux, were recorded at various locations within the Whittard

328   Canyon and Channel using the BOBO (BOttom BOundary; van Weering et al., 2000)

329   and ALBEX (Duineveld et al., 2004) benthic landers. A number of deployments were

330   carried out between 2007 and 2012 and lasted from a few days up to an entire year

331   (Fig. 1). The lander records show that in the upper canyon reaches, extending from

332   the shelf edge to about 2500 m depth, the near-bed current regime is indeed

333   dominated by moderate to strong semi-diurnal tidal currents, flowing alternately in

334   up- and down-canyon direction. Bottom water turbidity is generally observed to

335   increase during periods of enhanced current speed, indicating that bottom sediment is

336   resuspended and entrained by the tidal current (Fig. 4). Instantaneous horizontal

337   particulate fluxes, calculated by multiplying suspended sediment concentrations with

338   instantaneous current speed, reached values in the order of several grams m^{-2} s^{-1}

339   during tidal current peaks. Net suspended sediment transport driven by tidal currents

340   appeared to be generally in up-canyon direction, supporting the oceanographic

341   modelling results (Fig. 4). At greater depths in the canyon (deployments at 3566 and

342   3569 m) and in the adjacent deep-sea channel (4166 m), semi-diurnal tidal currents

343   appear very weak, not exceeding 0.1-0.15 m s^{-1} and with no sign of resuspension of

344   bottom sediment (Amaro et al., 2015). As also observed at shallower sites, net water

345   flow at deeper sites was in an up-canyon direction, once more indicating that tidal

346   currents do not contribute to down-canyon sediment transport (Mulder et al., 2012,

347   Amaro et al., 2015). Low current speeds in the lower reaches of the canyon and the

348   adjacent deep-sea fan area have previously been reported from short-term current

349   meter deployments by Reid and Hamilton (1990).

350

351   c) Recent sediment gravity transport

352   Apart from the prevailing tidal currents, the BOBO landers deployed at 1479

353   and 4166 m recorded several events of significant down-canyon suspended sediment

354   transport, which we interpret as representing sediment gravity flows (Fig. 4, Amaro et

355   al., 2015). Typically, these events were marked by a sharp increase in suspended

356   particulate matter (SPM) concentration, followed by a gradual decrease to normal

357   values in the course of several days. Sediment trap samples encompassing these

358   particular events recorded elevated sediment fluxes. In some cases the initial sharp

359   increase in SPM was also accompanied by a marked increase in current speed and

360   change to down-canyon flow. As illustrated by the 10-month BOBO record obtained

361   at 1479 m depth in the western branch of Whittard Canyon (Fig. 4), sediment gravity

362   flows occurring in the upper canyon reaches may be masked by the overall high

363   concentrations of SPM and high current speeds. On several occasions the current

364   speed at 1 m above bottom exceeded 0.7 m s^{-1}. Two high current speed events,

365   however, recorded on 15 November 2009 and 14 January 2010, showed

366   characteristics of a sediment gravity flow. During the most intense event in January

367   2010, the instantaneous near-bottom sediment flux during the peak of the event was

368   estimated to be in excess of 3.2×10^6 kg m^{-2} y^{-1} in down-canyon direction. For

369   comparison, the typical average rate of sediment accumulation at that depth as

370   determined from ^{210}Pb in sediment cores is in the order of 10 kg m^{-2} y^{-1}. During the

371   last recorded high current speed event on 19 July 2010, probably representing another

372   sediment gravity flow, the lander was dislodged from its anchors and was later

373   recovered drifting at the surface.

374   In the more quiescent lower canyon, where background suspended matter

375   concentrations is very low, the turbidity peaks representing sediment gravity flows

376   were obvious. In a 12-month record obtained from 4166 m depth in the Whittard

377   Channel, two sediment gravity flow events were recorded on 22nd March and 1st July

378   2011, marked by sharp increases in bottom water turbidity together with a strong

379   increase in sediment deposition (Amaro et al., 2015). Very similar high-turbidity

380   events also accompanied by high mass sediment flux have been reported from other

381   canyon systems considered to be active (e.g. Xu et al., 2002; de Stigter et al., 2007;

382   Martín et al., 2011). In the Whittard Canyon, storm depressions, common over the

383   Bay of Biscay, may be the most likely trigger for these events, comparable to

384   processes observed in other canyons (e.g. Martín et al., 2011; Sanchez-Vidal et al.,

385   2012).

386

387   d) Recent sediment deposition

388   Surface sediments from major branches of the Whittard Canyon (western and

389   eastern middle branch) and from the Whittard Channel, as well as from adjacent slope

390   and interfluve areas, were studied in boxcores and multicores collected between 2007
391   and 2011 (Fig. 1). Sediments from the upper reaches of the western and eastern
392   central branches and from the adjacent upper slope, down to depths of about 500 m,
393   appeared very similar, consisting of structureless silty sand composed for three
394   quarters of lithogenic material (Fig. 5) and about one quarter of $CaCO_3$. Toward
395   greater depths, sediments on the slope adjacent to the western canyon branch become
396   progressively depleted in lithogenic material, whilst $CaCO_3$ content increases until
397   constituting more than half of bulk sediment at depths below 3000 m on the lower
398   slope. Most likely the observed trend reflects a decreasing input of lithogenic material
399   with increasing distance from the shelf edge. In contrast to this, along the axis of the
400   western and eastern middle canyon branches, lithogenic fine sand and silt consistently
401   constitute the dominant sediment component down to 4000 m depth, suggesting
402   ongoing transport of shelf-derived material down to the lower canyon reaches. On the
403   interfluve adjacent to the eastern middle branch, lithogenic contents are also relatively
404   high, possibly indicating sediment spillover from the adjacent canyon branches.
405   Beyond 4000 m depth, where the lower canyon extends into the Whittard Channel,
406   lithogenic fine sand and silt occurs as thin layers of a few mm thick, alternating with
407   more carbonate-rich hemipelagic ooze. This indicates that down-canyon transport
408   occurs episodically by sediment gravity flows, punctuating prolonged intervals of
409   hemipelagic deposition. Sediment dating with ^{210}Pb in a core from the proximal
410   Whittard Channel showed that a number of these turbiditic layers were deposited
411   within the last century. Thin turbidite layers were also observed in surface sediments
412   draping the low banks to the east of the Whittard Channel, indicating spillover of
413   turbidity currents from the main channel (Amaro et al., 2015). The fact that sediments
414   on both sides of Whittard Channel contain distinctly more lithogenic material than
415   lower slope sediments from west of the Whittard Canyon is another indication that
416   spillover of turbidity currents contributes significantly to sediment deposition beyond
417   the bounds of Whittard Channel. Apart from the afore-mentioned thin-bedded
418   turbidites, one core from 4392 m depth in Whittard Channel contained a coarse sandy
419   turbidite layer and debris flow deposit, in which abundant fragments of scleractinian
420   corals were found. These corals must have been transported from the upper reaches of
421   the canyon and slope at 250-2000 m depth, where both living and dead corals have
422   been reported from ROV and towed video frame explorations (van Rooij et al., 2010a,
423   Huvenne et al., 2011, Johnson et al. 2013, Davies et al., 2014).

424

425   e) Organic matter (OM)

426   e.1. Suspended Particulate Organic Matter (sPOM)

427   Huvenne et al. (2011) showed that near bottom (<10 m altitude) sPOM

428   concentrations, measured using stand-alone pumps (SAPS – Challenger Oceanic),

429   were 2 to 3 times higher in the upper parts of the canyon (< 2000 m depth) than in the

430   deeper and more central parts (three stations > 3000 m depth). These values were

431   comparable to those found in canyons from the Iberian Margin (Tyler et al., 2009;

432   Kiriakoulakis et al., 2011). The observed decrease in sPOM concentrations with water

433   depth was attributed to the less dynamic nature of deeper parts of the canyon. sPOM

434   appeared to be fresh and phytoplankton-derived as suggested by the low molar C/N

435   ratios (4.1 – 7.7). In addition, they showed that the nutritional quality of sPOM was

436   higher in the upper canyon, as illustrated by the elevated concentrations of essential

437   fatty acids, docosahexaenoic fatty acid (DHA) and eicosapentaenoic fatty acid (EPA).

438   EPA and DHA are biosynthesized primarily by phytoplankton and are pivotal in

439   aquatic ecosystem functioning, as they greatly affect trophic transfer efficiency to

440   higher trophic levels (Muller-Navarra et al., 2000; Kiriakoulakis et al., 2004, 2011).

441   Recently Wilson et al. (2015b) also investigated the sPOM in the intermediate

442   and bottom nepheloid layers in the central upper branches of the Whittard Canyon.

443   Data were collected in early summer 2013, mainly by filtering water from CTDs and

444   to a lesser extent, from SAPS. Peaks in turbidity were detected with unusually high

445   concentrations of SPM, in some cases greater than an order of magnitude higher than

446   maximum values typically found in NLs. sPOM from these nepheloid layers was

447   strikingly different from that reported by Huvenne et al. (2011) both in concentration

448   and elemental composition. The suspended particulate organic carbon (sPOC)

449   concentrations were more than an order of magnitude higher in the Wilson study (up

450   to 690 μg L^{-1}; *vs*. 12 – 23 μg L^{-1} in similar canyon depths), indicating that an episodic

451   event had possibly taken place. The molar C/N ratios of the sPOM from these NLs

452   were highly variable, ranging from 1 to 27. Although care needs to be exercised in

453   comparing data from different sampling techniques (i.e. SAPS vs CTDs; see

454   Turnewitsch et al. 2007). The results clearly show that sPOM collected during this

455   study was highly heterogeneous, with possible contributions from clay-trapped

456   inorganic nitrogen, bacteria and zooplankton (see references in Kiriakoulakis et al.

457   2011) and degraded material (C/N ratios above 10 indicate degraded OM in the

13

458   absence of terrestrial inputs) in comparison to Huvenne et al. (2011). It is interpreted

459   that these NL are possibly influenced by bottom trawling (see section 5).

460   A further insight on OM fluxes in the canyon system was provided by Amaro

461   et al. (2015) based on the sediment trap record obtained from a one-year lander

462   deployment at 4166 m depth in the Whittard Channel. Sediment traps provide a time

463   series of particle fluxes suitable for investigating sinking material (White et al., 2015).

464   The study by Amaro et al. (2015) concluded that the highest flux of fresh OM arriving

465   in the Whittard Channel was due to local vertical settling and lateral transport of

466   phytodetritus, after the spring phytoplankton bloom, rather than through gravity-

467   driven episodic events, which provided material of low nutritional quality.

468

469   e.2. Sedimentary organic matter (SOM)

470   Canyons may act as 'traps' of organic matter (OM) as has been observed in

471   the Nazaré Canyon off the coast of Portugal (e.g. Masson et al., 2010). The high

472   sedimentation rates in Nazaré Canyon promote carbon burial by reducing the oxygen

473   exposure time of the sediment (Kiriakoulakis et al., 2011). Evidence about the

474   potential of other European canyons, such as the Whittard Canyon, to act as OM (and

475   hence carbon) sinks can be derived from total organic carbon (TOC) contents and the

476   elemental (i.e. C/N ratios; e.g. Meyers 1997) and molecular (e.g. Duineveld et al.,

477   2001; Kiriakoulakis et al., 2011; Amaro et al., 2015) composition of OM in the

478   sediment.

479   Duineveld et al. (2001) measured sedimentary TOC and total nitrogen (TN)

480   content in the upper 5 cm at three stations in the middle-lower central branches of the

481   Whittard Canyon (2735 - 4375 m water depth) and found that TOC (and TN) contents

482   in the upper cm of the canyon sediments were double the values than at corresponding

483   depths on the nearby open slope (Goban Spur). The shallowest station (2735 m) had

484   highest overall TOC and TN content throughout the upper 5 cm, whereas at the two

485   deeper stations levels sharply dropped below 2-3 cm. Duineveld et al. (2001)

486   attributed this drop in TOC and TN at the deeper stations to a subsurface layer of

487   coarse sand most likely originating from a gravity flow event. In general, coarser

488   grains increase oxygen exposure and thus oxidation of SOM (Hedges and Keil 1995).

489   Extensive surveys of SOM in surface sediments (0-1 cm) along the axes of the

490   western and eastern middle branches of Whittard Canyon showed that TOC and TN

491   content generally increases towards the deeper part (~ 4000 m) of the canyon and

492   decreases from the proximal to more distal areas of the Whittard Channel and
493   adjacent deep-sea fan area (Fig. 6). This apparent increase of the TOC content in the
494   deeper locations could be due to a corresponding decrease of the sediment particle
495   size. However, no significant relationship was found between median grain size and
496   TOC in cores from seven locations in the canyon axes of the upper middle branches,
497   which were sectioned every cm down to 10 cm (Spearman's Test, r=0.450, p=0.224).
498   Alternatively, the higher TOC contents in the lower canyon reaches and proximal part
499   of the Whittard Channel could be explained by intermittent sediment gravity flows
500   flushing fine-grained sediments enriched in SOM down the canyon. Less frequent
501   occurrence of sediment gravity flows further down the Whittard Channel could then
502   explain the decreasing OC contents towards more distal areas. However, in some
503   locations within the Whittard Canyon (depths between 650 to 4450 m from eastern to
504   western branches), surficial sediments are practically indistinguishable from open
505   slope values at the same depth (0.1 – 0.7% TOC of dry sediment) (Huvenne et al.
506   (2011). TOC content presented in surface sediments and sediment traps (Fig. 6) from
507   the Whittard Canyon branches in part supports the analyses presented by Amaro et al.,
508   (2015). This could be due to the complexity and spatial and temporal variability of the
509   canyon processes that are as yet poorly understood.

510   As a crude measure of lability of SOM its molar C/N ratios from various
511   locations in and outside the Whittard Canyon has been investigated by several authors
512   (Duineveld et al., 2001; Huvenne et al., 2011; Ingels et al., 2011a; Amaro et al., 2015;
513   de Stigter et al., 2008b). Molar C/N ratios of surface sediments show no consistent
514   differences between canyon and slope sites, nor any consistent trends from the upper
515   canyon and slope to the lower canyon and slope (Fig. 7). This, in combination with
516   consistently low C/N ratios, suggests that the bulk of the OC preserved in surface
517   sediments is broadly of relatively unaltered marine origin (Meyers 1997 and reference
518   therein). The TOC contents of particulate matter collected in sediment traps close to
519   the seabed in the western and eastern middle branches were significantly higher than
520   in the nearby surface sediments (1.09±0.51 and 0.47±0.20 respectively; T-test,
521   p<0.05), while molar C/N ratios were significantly (if only slightly and still indicating
522   marine origin) lower (8.12±1.23 and 8.80±1.68 respectively; T-test, p<0.05). It is
523   unclear, however, whether the differences are due to modification of settling OM by
524   benthic organisms, as suggested by Amaro et al., (2015), or by dispersal of slightly

525   degraded OM from the shelf across the canyon and slope or a combination of both
526   processes.

527   Few studies have investigated phytopigments, nucleic and fatty acids (and
528   hence the bioavailability of sedimentary organic matter) in the Whittard Canyon.
529   Duineveld et al. (2001) showed that concentrations of phytopigments and nucleic
530   acids decreased, both down slope and down core within the canyon, suggesting a
531   lowering of OM bioavailability with canyon and core depth. In contrast to bulk
532   sediment and TOC distributions and concurrent with the observations described for
533   sPOM, there is not yet any evidence for systematic down-canyon transport of labile
534   organic material. Whilst current meter and fluorometer data recorded with a benthic
535   lander in the upper canyon indicate resuspension and transport of phytodetritus by
536   oscillating tidal currents (Fig. 8), the net transport of resuspended material appears to
537   be in up- rather than in down-canyon direction. Up-canyon transport of phytodetritus,
538   as well as proximity to shelf surface production, may well contribute to the high
539   phytopigment concentrations reported by Duros et al. (2011) from the upper canyon.
540   Even where intermittent gravity flows have been recorded, such as in the proximal
541   Whittard Channel (Amaro et al., 2015), their role in transferring labile OM to lower
542   slope regions appears very limited. More likely, the labile organic material flushed
543   down-canyon by gravity flows, becomes strongly diluted with bulk sediment
544   entrained by the flow, rendering it of little value for consumption by fauna in the area
545   of deposition. Gravity flows through the canyon occasionally detected in sediment
546   traps, resulted in accumulation of low quality degraded material.

547

548   **4. FAUNAL ASSEMBLAGES**

549

550   a) Foraminifera

551   Most of the information on foraminifera in the Whittard Canyon and adjacent
552   areas derives from the study of Duros et al. (2011), who analysed sediment samples
553   obtained from 18 stations for benthic foraminifera (>150 μm fraction). (Fig.1, Table
554   1). Densities of Rose-Bengal stained foraminifera, indicating living specimens, were
555   positively related to phytopigment concentrations and to proxies for food availability,
556   leading to higher standing stocks in the upper parts of the canyon and on the slope
557   than in the lower canyon (Duros et al., 2011). Many of these upper canyon stations

558   (328-525 m, 1109 m) were characterised by a dominance of species (notably *Bolivina*

559   spp., *Bulimina marginata*, *Cassidulina carinata*, *Trifarina angulosa* and *Uvigerina*

560   *peregrina*) that are typical for organically enriched settings. The deepest site (3002 m

561   in the western branch) was dominated (62% of fauna) by *Quinqueloculina seminula*.

562   Agglutinated species (*Reophax* spp., *Lagenammina difflugiformis*) typical of tranquil

563   deep-water environments are common together with *Bulimina costata* and *B. inflata*.

564   At shallower sites (mainly < 600 m) in both canyon branches, particularly the eastern

565   branch, there was a strong concentration of stained foraminifera in the upper 0.5 cm

566   sediment layer, reflecting the shallow oxygen penetration depth associated with a high

567   OM input. At deeper sites, stained foraminifera followed oxygen in tending to

568   penetrate further into the sediment. However, shallow-infaunal species, which

569   typically occur in surficial sediment layers, were also encountered in deeper core

570   layers, for example, at 515 m in the western branch and 328 m in the eastern middle

571   branch. This is probably a result of bioturbation by macro- and mega-fauna.

572   Foraminiferal densities decreased with water depth on the slope adjacent to the

573   eastern and western branches. Assemblage composition changed accordingly and was

574   largely different from that observed in the canyon, particularly at shallower depths.

575   *Uvigerina mediterranea* (considered to be an opportunistic species that responds to

576   phytodetritus pulses) was dominant (48%) at 498 m depth on the western slope, *U.*

577   *mediterranea*, *U. peregrina* and *Melonis barleeanum* were abundant around 1000 m

578   on both slopes, *U. peregrina* was joined by *Hoeglundina elegans*, *Cibicidoides*

579   *kullenbergi*, *Gavelinopsis translucens* and *Gyroidina orbicularis* at 1500-2000 m,

580   while the deepest slope sites (2950-3000 m) were characterised by species of

581   *Reophax*, *Lagenammina* and *Ammobaculites agglutinans*. This sequence reflects

582   increasingly food-depleted conditions with increasing water depth, as is typical on

583   continental margins. The distribution of stained specimens within the sediment profile

584   is more consistent with depth on the slope than in the canyon. However, as expected,

585   sediment penetration still tended to be deeper at the deeper sites. Comparison between

586   stained and dead assemblages reveals evidence for the transport of dead foraminiferal

587   tests within the canyon (Duros et al., 2012). Species that are confined to the stained

588   assemblage in the upper canyon are found as dead tests at deeper sites. In addition, the

589   dead tests of species (*Ammonia beccarii* and *Haynesina germanica*) that are restricted

590   to coastal settings occur at shallow (328 and 535 m) sites in the eastern canyon

591   branch. These have probably been carried into the upper canyon by bottom currents,

592 gravity flows or transported on floating algae. Differences between stained and dead

593 assemblages in the area of the Whittard Canyon can also reflect seasonal population

594 fluctuations. Thus, *Epistominella exigua*, an opportunistic species that responds with

595 rapid population growth to inputs of phytodetritus (Gooday, 1988), represents 13% of

596 the dead fauna, but only 2% of the living fauna collected at 2995 m on the western

597 slope in June 2007 (Duros et al., 2012). Many of these dead tests are presumed to

598 have been generated during a reproductive burst earlier in the year.

599 An earlier study by Weston (1985) provided species-level information on

600 benthic foraminifera from the Whittard Canyon in a study that also encompassed the

601 nearby Shamrock Canyon and Meriadzek Terrrace and the more tranquil environment

602 of the Porcupine Seabight. Weston (1985) studied Rose Bengal-stained and dead

603 assemblages (>125-µm fraction) in grab and anchor dredge samples collected at

604 depths between 255 m and around 2000 m depth in the canyon. Standing stocks of

605 stained tests were considerably higher in the Whittard Canyon than at comparable

606 depths in the Porcupine Seabight and there were substantial differences in both the

607 stained and dead faunas from the two areas. For example, certain species, notably

608 *Cassidulina carinata* but also *Trifarina angulosa*, *T. bradyi*, *Brizalina spathulata* and

609 *B. subaenariensis*, were considerably more abundant in the stained assemblage, and

610 occurred at greater depths, in the Whittard Canyon than in the Porcupine Seabight. As

611 a result, the latter area displayed a much clearer zonation of species with depth than

612 the canyon. Many of the species reported by Weston from the Whittard Canyon are

613 the same as those in Duros et al. (2011, 2012). However, she also records attached

614 species (*Cibicides lobatulus*, *C. refulgens*, *Planulina ariminensis*, *Paromalina*

615 *crassa*), not reported by Duros et al. (2011, 2012), living on various hard substrates

616 (e.g. pebbles, ascidians, agglutinated foraminiferan tubes, sponge spicules) between

617 700 and 1400 m depth.

618

619 b) Meiofauna

620 Ingels et al. (2011a) reported meiofaunal abundance and biodiversity (as

621 nematode genera) at two stations (ca. 700 and 1000 m depth), within the western

622 middle branch of the Whittard Canyon. Data collected by Gambi and Danovaro

623 (2016) between 1483 and 2939 m in the eastern middle branch have allowed to

624 identify meiofaunal patterns along a wider bathymetric range in the middle branches

625 of the Whittard canyon. To assess differences in terms of meiofaunal abundance and

626   nematode diversity (as expected number of genera for 51 individuals) among the

627   stations selected here, we used one-way permutational analyses of variance

628   (PERMANOVA) under unrestricted permutation of raw data. The analyses were

629   carried out using Station as 5 fixed levels (700m, 1000m, 1483m, 1938m, 2939m) and

630   data of abundance and diversity were in three replicates. Significant terms were

631   investigated using a posteriori pair-wise comparisons with the PERMANOVA t

632   statistic and 999 permutations. Because of the restricted number of unique

633   permutations in the pairwise tests, P values were obtained from Monte Carlo

634   samplings (Anderson and Robinson, 2003). The PERMANOVA analyses were

635   performed using the routines included in the PRIMER6 & Permanova software

636   (Clarke and Gorley, 2006). The results of the statistical analyses reveal that

637   meiofaunal abundance does not change between 700m and 1938m depth (p=0.287)

638   while differences are observed between 700m and 2939m and between 1483m and

639   2939m (p<0.05) and between 1000m and 2939m and between 1938m and 2939m

640   (p<0.01; Fig. 9a). Meiofaunal abundances in the upper and middle part of the

641   Whittard Canyon are generally higher than those reported from the open slopes of the

642   Atlantic Ocean (Celtic and Portuguese margins) and of the Mediterranean Sea

643   (Catalan and South Adriatic margins) (Bianchelli et al., 2010; Ingels et al., 2009,

644   2011a, b, c, 2013a; Romano et al., 2013) at similar depths. Meiofaunal abundances at

645   3000 m depth in the Whittard Canyon are lower than values reported at comparable

646   depths in Nazaré and Cascais Canyons along the Portuguese margin (Ingels et al.

647   2009, 2011b, c). Meiofaunal diversity (at the level of higher taxa) did not display a

648   clear spatial pattern with increasing water depth (Fig. 9b). This lack of bathymetric

649   pattern has been observed in several canyons, independent of geographical region or

650   canyon-scale environmental conditions (Bianchelli et al., 2010; Ingels et al., 2013;

651   Romano et al., 2013; Leduc et al., 2014; Pusceddu et al., 2013) and is likely

652   reminiscent of canyon heterogeneity and associated environmental variability exerting

653   influence on benthic assemblages. More important are small-scale environmental

654   conditions that act on the scale of meiofauna and nematodes, such as those associated

655   with sediment grain size and sediment depth, or the amount and availability of food

656   (Ingels and Vanreusel, 2013, Leduc et al., 2012, 2014). Ingels et al. (2011a) supported

657   the former observation by showing that small-scale (vertical) heterogeneity in SOM

658   quality (expressed mainly as relative contributions of phytopigments) within the same

659   core could explain much of the variation of the meiofaunal communities of the

660 canyon. In the middle branches of the Whittard Canyon fourteen meiofaunal taxa

661 have been identified: Nematoda, Copepoda (including their nauplii), Polychaeta,

662 Kinorhyncha, Bivalvia, Ostracoda, Turbellaria, Oligochaeta, Tardigrada, Gastrotricha,

663 Isopoda, Tanaidacea, Acarina and Aplacophora. Meiofaunal community structure

664 displays a typical composition of deep-sea assemblages with few dominant taxa:

665 nematodes dominate (92-96%) all stations, followed by copepods (3-7%),

666 kinorhynchs (0-3%) and polychaetes (0-1%). All other taxa can be considered as rare

667 (*sensu* Bianchelli et al., 2010), since their contribution to the overall community

668 composition is <1%, and their number displays a clear decreasing pattern at depth

669 >1000 m. The results of the statistical analyses described above, reveal that, contrary

670 to the spatial pattern observed for meiofaunal diversity in general, nematode diversity

671 (as expected richness of genera for 51 individuals) decreases between 700m and

672 1000m (p<0.05), among 700m and all other sampling depths, expect for 1483m, and

673 progressively decreases between 1483m and 2939m (p<0.05), except for between

674 1939m and 2939m (Fig. 10a). No differences in nematode diversity at species level

675 (both as species richness and expected species number for 51 individuals) are

676 observed between 1483 m and 2939 m in the middle eastern branch of the Whittard

677 Canyon (Gambi and Danovaro, 2016). The present analysis of nematode assemblages

678 in the middle branches of the Whittard Canyon reveals the presence of 119 nematode

679 genera among a total of ca. 1400 individuals investigated from ca. 100 individuals

680 from each of three replicate samples of each station. Ingels et al. (2011a) reported the

681 dominance of the genera *Leptolaimus* and *Molgolaimus* at 700 m-depth and

682 *Astomonema* at 1000 m depth, respectively while in the deepest stations the dominant

683 genera are: *Halalaimus* (16%), *Acantholaimus* (8%) and *Daptonema* (6%).

684 Differences in genus dominance between the investigation by Gambi and Danovaro

685 (2016), and Ingels et al. (2011a) are mostly caused by differences in bathymetric

686 ranges considered in the two studies. These results are consistent with the patterns

687 observed along other canyon systems and open slopes in which, the turnover of

688 nematode genera (and species) is generally very high among sampling sites at greater

689 water depths (Danovaro et al., 2009, 2014, Ingels et al., 2011a, Gambi and Danovaro,

690 2016). Different drivers can be invoked to explain these patterns. Ingels et al (2011a),

691 indeed, revealed that the high variability of nematode genera composition was mainly

692 explained by grain size and food availability (both quality and quantity) inside the

693 canyon system. The analysis of nematode trophic structure at genus level does not

694   display clear patterns along the bathymetric gradient in the middle branches of the
695   Whittard Canyon (Fig.10b). Deposit feeders are always the dominant trophic guild, as
696   observed for deep-sea sediments worldwide (Soetaert and Heip, 1995; Gambi et al.,
697   2003; Vanhove et al., 2004; Danovaro et al., 2008; Vanreusel et al., 2010; Gambi et
698   al., 2014). However, epistrate feeders contribute substantially to trophic composition
699   at all stations and this could be related to the amount of "fresh" material in the canyon
700   system deriving from the highly productive surface waters of the Celtic margin (Joint
701   et al., 2001, Duros et al., 2011 and this manuscript). The relative contribution of
702   predators is low and decreases progressively with increasing water depth. Predators
703   represent a limited portion of the overall nematode trophic structure in the Whittard
704   Canyon in comparison to their relevant contribution observed in the adjacent open
705   slopes (Gambi and Danovaro, 2016) and in the oligotrophic sediments of the deep
706   Mediterranean Sea (Danovaro et al., 2008, Gambi et al., 2014). Interesting to note is
707   also the relatively high numbers of chemosynthetic *Astomonema* nematodes,
708   particularly at 1000 m water depth, suggesting reduced sedimentary conditions akin to
709   seep environments. These conditions may be caused by very high sedimentation rates
710   and consequent enhanced respiration and organic carbon burial conditions, which
711   allow these nematodes to thrive (Ingels et al., 2011a, Tchesunov et al., 2012). Such
712   sedimentary conditions may be caused by sedimentary overflow on the interfluves of
713   the canyon head.

714

715   c) Macrofauna

716   Duineveld et al. (2001) published the first study of macrofauna from the
717   Whittard Canyon. Samples obtained at 2735 and 3760 m water depth yielded similar
718   densities (2717 ind m^{-2} and 1339 ind m^{-2}) to those found on the nearby Goban Spur, c.
719   150 km northeast of the canyon (3039 ind m^{-2} at 2200 m and 2420 ind m^{-2} at 3600 m).
720   The same was true for the sample taken on the canyon fan at 4375 m depth (canyon
721   fan 696 ind m^{-2}; Goban Spur 807 ind m^{-2} at 4500 m) (Duineveld et al. 2001, Fig. 11).
722   On the other hand, biomass values were elevated inside the canyon (4739, 1877 and
723   1592 mg m^{-2} wet weight at 2735, 3760 and 4375 water depth, respectively) compared
724   with the Goban Spur (3039, 1256, 886 mg m^{-2} wet weight at 2200, 3600 and 4500 m
725   water depth, respectively). This increase was consistent with higher levels of OM and
726   pigments found in the surface sediments of the canyon compared with the slope.

727   In a recent study, Gunton et al. (2015b) compared macrofauna assemblages at

728 3500 m water depth in three different branches of the Whittard Canyon (Fig. 1) and

729 the adjacent slope to the west of the canyon. The canyon had a higher macrofaunal

730 density than the slope (canyon average $4536 \pm$ SD 1676 ind m^{-2}; slope $2744 \pm$ SD 260

731 ind m^{-2}). Density varied throughout the branches of the canyon, increasing across the

732 sites from west to east (western branch 2900 ± 538 ind m^{-2}; eastern middle branch

733 $4461 \pm$ SD 856 ind m^{-2}; eastern branch $6249 \pm$ SD 1363 ind m^{-2}). This is consistent

734 with the data of Hunter et al. (2013) who sampled macrofauna at a similar water depth

735 (3500 m) in the canyon. They recorded higher macrofaunal densities in the eastern

736 branch ($5352 \pm$ SD 2583 ind m^{-2}) compared with the western branch ($3416 \pm$ SD 2069

737 ind m^{-2}) (Fig. 11). As seen in section 3, disturbance regimes and the quantity and

738 quality of OM vary throughout the canyon branches and this may have led to the

739 different faunal densities reported in both studies. However, as the stations analysed

740 for the quantity and quality of OM (section 3) are different from those where

741 macrofauna were sampled, we can only make assumptions and a more coordinated

742 sampling programme should be carried out in the future, so that observations from all

743 disciplines can be better integrated.

744   Gunton et al. (2015b) also found that the Whittard Canyon macrofauna

745 exhibited considerable variability at the higher taxon level. Polychaeta was the

746 dominant taxon at 3500 m and represented > 50 % of the assemblage in the three

747 main canyon branches. However, the ranking of the second and third most abundant

748 taxa varied between branches and were respectively Sipunculida (12.5%) and

749 Bivalvia (8.4 %) in the western branch; Isopoda (16.2 %) and Tanaidacea (7.3 %) in

750 the eastern middle branch; Isopoda (10.7 %) and Bivalvia (8.6 %) in the eastern

751 branch. Hunter et al. (2013) also noted a difference in macrofaunal composition

752 between canyon branches at 3500 m. In the eastern branch macrofaunal-sized

753 nematodes (> 50 %) and polychaetes (cirratulids and spionids) contributed most to the

754 assemblage, whereas in the western branch crustaceans (tanaids and harpacticoid

755 copepods) and polychaetes dominated. The differences between the two studies may

756 reflect the sampling gear and sampling processing techniques used. Gunton et al.

757 (2015b) used a megacorer and a 300 μm sieve, whereas Hunter et al. (2013) used

758 ROV push cores and a 250 μm sieve. A megacorer will collect a larger sediment

759 sample, while a larger sieve would retain fewer animals. Furthermore, Hunter et al.

760 (2013) included nematodes in their macrofaunal analysis, but Gunton et al. (2015b)

761 only included macrofauna *sensu stricto*. Polychaete family assemblage composition
762 also varied throughout the canyon. Hunter et al. (2013) reported that the western
763 branch had a high proportion of Amphinomidae, whereas Cirratulidae and Spionidae
764 contributed most to the assemblage in the eastern branch. Gunton et al. (2015b)
765 reported high numbers of Amphinomidae (all *Paramphinome jeffreysii*) in the
766 western, central and eastern branches. The abundance of *P. jeffreysii* increased across
767 sites from the western (21.2 %) to the eastern branch (39.6 %) (Gunton et al., 2015a).
768 *Aurospio* sp. was ranked second in the western and eastern middle branches whereas
769 juvenile Opheliidae were ranked second in the eastern branch. This within-canyon
770 faunal heterogeneity is probably explained by a combination of variable organic
771 enrichment and hydrodynamic activity, both of which can be influenced by the
772 topographic profile of individual canyon branches (Gunton et al. 2015b and section 3
773 of this paper).

774 Although the macrofauna at all three stations in the study by Duineveld et al.
775 (2001) were numerically dominated by deposit-feeders, the proportion of filter-
776 feeders (mainly sabellid polychaetes) was highest at the deeper canyon station (3760
777 m). This was unexpected since more quiescent conditions, favouring deposit feeders
778 rather than filter feeders, would normally be expected at greater depths. At slightly
779 shallower depths (3500 m), polychaete feeding groups displayed a shift across the
780 canyon, with a higher abundance of omnivores and macrophagous feeders reported in
781 the eastern branch compared with more microphagous feeders in the western branch
782 (L. Gunton unpublished observations). Macrofaunal-sized nematodes displayed a
783 similar trend, the eastern branch was characterised by high numbers of predators and
784 scavengers (e.g. *Paramesacanthion*) and the western branch by epigrowth feeders.
785 Again, this shift in feeding groups may be linked to the different environmental
786 characteristics of individual branches, as mentioned above.

787 Local macrofaunal diversity appears to be depressed inside the Whittard
788 Canyon compared with the adjacent slope (Gunton et al., 2015a). Rarefied polychaete
789 richness was similar in the western ($E[S_{47}] = 18.5$), eastern middle ($E[S_{47}] = 19.9$) and
790 eastern ($E[S_{47}] = 18.4$) branches, but higher at the slope site to the west of the canyon
791 ($E[S_{47}] = 21.2$). The Simpson ($1-\lambda'$) and Shannon (H' ($\log_2$)) indexes were likewise
792 highest at the slope site ($1-\lambda' = 0.918$, H' ($\log_2$) = 4.104), intermediate in the western
793 and eastern middle branches ($1-\lambda' = 0.880$ and 0.856, H' ($\log_2$) = 3.706 and 3.891,
794 respectively) and lowest in the eastern branch ($1-\lambda' = 0.814$, H' ($\log_2$) = 3.656).

795 Dominance was also higher inside the canyon (Rank 1 dominance canyon average

796 33.1, slope 18.7). Depressed diversity and increased dominance may be caused by

797 high numbers of opportunistic species. As mentioned above, *P. jeffreysii* and juvenile

798 Opheliidae were particularly abundant in the eastern branch of the canyon, perhaps as

799 a result of an opportunistic response to a possible recent input of OM. Forty-six

800 polychaete species that were not present on the open slope, were found in the

801 Whittard Canyon, suggesting that the canyon may enhance diversity at a regional

802 scale (Gunton et al., 2015a). However, the sampling effort on the adjacent slope was

803 not sufficient to confirm that the canyon acts to increase regional diversity.

804

805 d) Megafauna

806 Megafaunal abundances have been found to be higher in the eastern as

807 opposed to the western branch of the Whittard Canyon, but species richness appears

808 to be similar (Ismail, 2016). Only one Agassiz trawl sample is available from the

809 Whittard Canyon. A single trawl at a similar depth (3700 m) on the Goban Spur in

810 1995, repeated in 1996, revealed only minor differences in overall megafauna density,

811 biomass and indeed the distribution of feeding guilds on the open slope as compared

812 to the Whittard Canyon (Duineveld et al., 2001). By combining visual (ROV)

813 observations on megafauna with habitat characteristics in General Additive Models

814 (GAMs), higher megafauna abundance in the Whittard Canyon was found at

815 shallower depths (<1000m), with small peaks at ~2200 and 3000m, while a peak in

816 species richness occurred at ~1200 m (Robert et al., 2014). Some of these peaks may

817 be associated with the interface of water masses present within the region (van Aken,

818 2000a, b; section 2 of this paper). At a finer scale, increased abundance, species

819 richness and diversity were associated with steep slopes and topographic highs, and

820 decreased towards the thalweg (5). Video analysis of 17 transects (500-4000 m in

821 depth) identified ~210 morphospecies (5), of which 31 putative species were corals

822 (based on 13 transects). The most commonly observed species in the outer branches

823 of the Whittard Canyon were xenophyophores (probably *Syringammina fragilissima*),

824 *Pentametrocrinus* sp., *Acanella* sp., *Lophelia pertusa*, cerianthids and *Anthomastus*

825 sp. (Robert et al. 2014). Examination of beta diversity indicated a high species

826 turnover with transects showing species similarities below 40% (Robert et al., 2014),

827 but many of these species have also been reported from other nearby banks, canyons

828 and continental slopes, and are likely not to represent distinct communities (Tyler and

829   Zibrowius 1992, Roberts et al. 2008, Howell 2010, Narayanaswamy et al. 2013,

830   Davies et al. 2015). In terms of cold-water corals (CWC), the most abundant coral

831   species found in a series of dive transects covering depths from 520 – 4703 m were

832   *Acanella* sp., *Anthomasthus* sp. and *L. pertusa* (Morris et al., 2013). Although Morris

833   et al. (2013) did not have a stratified random sampling scheme, the studied transects

834   did cover a wide range of depths throughout the canyon and the coral distribution

835   appeared to be driven by substratum type. The highest density of corals has been

836   found along an overhanging vertical wall (1600 m long x 120 m high) at 1350 m

837   water depth, mapped by Huvenne et al. (2011), where faunal coverage, mostly *L.*

838   *pertusa*, was estimated at ~70%. Despite corals on vertical walls representing the

839   habitat with the highest abundance and species richness, octocoral richness tended to

840   be low (Morris et al. 2013,Robert et al., 2014). Species commonly found in this

841   habitat included; the bivalve *Acesta excavata*, unidentified feather stars and an

842   anemone species, possibly *Actinauge* sp. The frequently observed crinoids found in

843   association with *L. pertusa*, (Robert et al., 2014) may represent a variant of the

844   described '*L. pertusa* and crinoids on bedrock' biotope as listed by Davies et al.

845   (2014). At depths between 633-762 m, *A. excavata* was found to be highly abundant

846   and form a different vertical-wall assemblage with the deep-sea oyster

847   *Neopycnodonte zibrowii* (Johnson et al. 2013). Other commonly observed species

848   found within this assemblage included the cup coral *Desmophyllum dianthus*,

849   unidentified feather stars and unidentified pink cerianthids. Another smaller wall has

850   been found in the western branch at ~1650 m, colonised by *Primnoa* sp. and possibly

851   *Solenosmilia variabilis* (Huvenne et al., 2011). At the foot of these walls, high

852   concentrations of SPM and the presence of bottom nepheloid layers have been

853   recorded (Huvenne et al., 2011, Johnson et al., 2013). The potential increased mixing

854   following the occurrence of down-canyon sediment gravity flows or the presence of

855   internal waves (Wilson et al., 2015a) may explain why *Lophelia* within Whittard

856   Canyon tend to occur outside the sigma-theta density envelope of 27.35-27.65kg m^{-3}

857   proposed by Dullo et al. (2008) and Flögel et al. (2014) for optimal *Lophelia* growth

858   (Whittard Canyon coral wall: ~27.80kg m^{-3}; Huvenne et al. 2011). Moreover and as

859   mentioned in section 3, Huvenne et al. (2011) showed appreciable concentrations of

860   essential fatty acids (EPA and DHA) in the surficial sediments from several areas of

861   the upper and middle parts of the canyon, which can explain the presence of CWCs in

862   the same areas. Protection against excessive sedimentation and increased food

863   availability were suggested as potential drivers for the colonisation of vertical cliffs;
864   cliff habitats may act as refuges from fishing activities, play a role in providing
865   nursery habitats and protection against predation, and add complexity beneficial for
866   other filter feeders (Huvenne et al. 2011, Johnson et al. 2013).

867   In the deepest part of the canyon (4166-4349 m) and in the Whittard Channel
868   (4321-4448m), dense aggregations of elpidiid holothurians have been observed
869   (Duineveld et al., 2001; Amaro et al., 2015). Since members of the
870   *Amperima*/*Peniagone* species complex are among those deep-sea organisms that
871   select the freshest type of phytodetritus (FitzGeorge-Balfour et al. 2010), their
872   presence is most likely associated with favourable quantities of trophic resources
873   (Amaro et al., 2010; Billett et al., 2010; Jamieson et al. 2011) and their high densities
874   in areas like the Whittard Channel confirm the presence of highly valuable food for
875   the rest of the deep-sea benthos. As discussed above, this fresh OM is most probably
876   derived from vertical settling, transported by bottom currents from adjacent lower
877   slope areas and trapped in the topographic depressions incised by the canyon and
878   channel rather than being flushed down-canyon by gravity flows, which appear to
879   dilute the organic matter with bulk sediment.

880   The Dangeard and Explorer canyons (SW Approaches) are shallower canyons
881   which feed into the Whittard Canyon (Fig. 1; Stewart et al., 2014). Davies et al.
882   (2014) identified and mapped 12 megabenthic assemblages (biotopes) from imagery
883   data (acquired between 184-1059 m), which revealed that these canyons are
884   dominated by soft sediment assemblages. Although no similar biotope analysis is
885   available for the Whittard Canyon, dense sea pen aggregations (particularly
886   *Kophobelemnon*) and *Lophelia* and/or *Madrepora* cold-water coral reef structures
887   have also been observed between 400 and 1050 m water depth in the eastern middle
888   branch (van Rooij et al., 2010a; ICES WGDEC 2012; Robert et al., 2014, Ingels et al.,
889   unpublished data).   *Kophobelemnon stelliferum* has been recorded from the
890   neighbouring Porcupine Seabight and so is not restricted to the canyons (Rice et al.,
891   1992).

892   Many of the coral species observed in the Whittard Canyon have been also
893   observed in the Dangeard and Explorer canyons including *Acanella* sp.,
894   *Anthomasthus* sp. and *L. pertusa*. Although CWC reef structures have been observed
895   in the main branches of the Whittard Canyon, only one highly sedimented '*L. pertusa*

896 reef' (795-940 m) has been observed on a steep flute feature on the floor of Explorer
897 Canyon.

898   Interestingly areas of cold-water coral mini-mounds (up to 3 m high and 50-
899 150 m in diameter) were found on the interfluves of Dangeard and Explorer canyons
900 (250-410 m); but such features have not been recorded from the Whittard Canyon
901 itself. Mini-mound provinces have also been recorded from the Guilvinec Canyon
902 (2008, Armorican margin, De Mol et al., 2011) and between the Ferrol and A Coruña
903 Canyon (van Rooij et al., 2009, Cantabrian margin, unpublished data) and so may be
904 related to presence of the canyon, however mini-mounds have also been documented
905 from the Porcupine Seabight upper slope (2003, Irish margin, Wilson et al., 2007).

906

907 **5. ANTHROPOGENIC INFLUENCES**

908

909   Recorded litter densities in Whittard Canyon are lower than in other nearby
910 canyons of the same continental margin. Derelict fishing gear represents ~28% of the
911 observed litter suggesting anthropogenic impacts in this canyon system might be
912 substantial, although in nearby Dangeard and Explorer Canyons this figure reached
913 72%. Approximately 42% of the litter was plastic, which will degrade slowly (Pham
914 et al. 2014).

915   For nearly a decade, the influence of anthropogenic activity (i.e. bottom
916 trawling) on sediment transport has been highlighted in numerous studies in
917 Mediterranean canyon systems (e.g. Martín et al., 2008; Puig et al., 2012; Martín et
918 al., 2014). Recently, evidence has been presented suggesting that trawling similarly
919 may influence SPM concentrations at the Whittard Canyon (Wilson et al., 2015b).
920 ROV video survey footage (van Rooij et al., 2010b; Robert et al., 2014) has shown
921 areas in the upper canyon (448-1119 m) that are draped by fine, loose sediment. This
922 could suggest high rates of sedimentation and potentially overflow from sediment
923 gravity events or tidal-driven sediment suspension, but could also be indicative of
924 anthropogenic activity (i.e. bottom trawling). During a survey in 2013, concentrations
925 of SPM in enhanced nepheloid layers (ENLs) were significantly higher (typical an
926 order of magnitude) than the mean maximum in nepheloid layers normally observed
927 in the Whittard Canyon (Wilson et al., 2015a). Wilson et al. (2015b) showed that
928 vessel monitoring system (VMS) data indicated high spatial and temporal activity of
929 trawling vessels coinciding with the occurrence of ENLs. Although only one study,

930 the data would suggest that bottom trawling on the smooth adjacent spurs is triggering
931 sediment gravity flows at the steeper rims of the canyon. The increased resuspended
932 sediment induced by such activity maybe the cause of the episodic events detected by
933 Amaro et al. (2015) and may explain the higher C/N ratios of sPOM suggestive of
934 degradation detected during the Wilson study in comparison to Huvenne et al.,
935 (2011). Episodic trawl-induced resuspension events could potentially have
936 detrimental effects on local ecosystems, introducing high inorganic particle loading,
937 which smothers filter feeders and provides nutritional unsuitable material (Puig et al.,
938 2012).

939
940 **6. CONCLUSION AND FUTURE DIRECTIONS**

941

942 The following main conclusions emerge from the research results reviewed
943 here.

944 1) The Whittard Canyon is currently still active in terms of sediment transport,
945 although less so than during the last deglaciation. Intermediate and bottom nepheloid
946 layers can be found throughout the (upper) canyon reaches, and benthic landers have
947 recorded significant volumes of transported material, even in the deep Whittard
948 Channel.

949 2) The net suspended sediment transport is mainly up-canyon, but sediment gravity
950 flow events do occur (potentially due to anthropogenic activities) and carry shallow-
951 water sediments and foraminiferal tests to greater depths. However, the down-canyon
952 transport of labile OM by means of gravity flows appears to be limited. The fresh OM
953 found in deeper regions, particularly the Whittard Channel, appears to arrive through
954 the vertical deposition and lateral transport of settling phytodetritus from
955 phytoplankton blooms that occur during spring and summer.

956 3) The active sediment transport and trapping of OM influences the benthic fauna. In
957 general, meiofauna, macrofauna and foraminifera showed increased abundances
958 and/or biomass inside the canyon compared to the continental slope (adjacent slope,
959 Goban Spur or nearby Porcupine Seabight), although this pattern could not be
960 conclusively demonstrated for the megafauna. Similarly meiofaunal and foraminiferal
961 abundances were higher in the upper than in the lower canyon. These patterns are
962 related to a local increase of OM, food availability or food quality in the canyon

963   compared to on the slope and in the upper canyon compared to the lower cayon.

964   Megabenthic filter feeders, such as sponges, anemones, crinoids and corals, are found

965   in higher densities inside the canyon (especially on the walls) than on the open slope.

966   They are higher in the eastern than in the western branch. A similar east-west pattern

967   has been reported for macrofauna, and again appears to be linked to OM quality and

968   quantity. There is no evidence for a contrast in megafaunal densities inside versus

969   outside the canyon, although data are very limited to a single trawl sample and should

970   be treated with caution.

971   4) Biodiversity patterns are less consistent than abundance patterns between faunal

972   groups and seem more influenced by local effects within the canyon branches.

973   Nematode diversity at genus level decreased progressively with increasing water

974   depth in the western middle branch of the Whittard Canyon; this was not the case for

975   meiofauna higher taxa diversity. Local macrofaunal diversity appeared to be

976   depressed inside the Whittard Canyon compared to the adjacent slope, but was

977   characterised by an increase in opportunistic species not seen on the slope. This

978   suggests that the canyon may still enhance diversity at a regional scale and exert an

979   important influence on macrofaunal abundance, biomass and diversity patterns both

980   locally and regionally. The multiple patterns of biodiversity compared to the open

981   slope are generated by the complex, localised interactions of several environmental

982   drivers and the different response of organisms and populations. Megafauna diversity

983   increased on steep slopes and topographic highs and decreased towards the thalweg.

984   However, there is little evidence of a canyon endemic megafauna. Most species

985   observed in the canyon also occur on the neighbouring continental slope, although

986   comparative studies are needed to conclusively test this.

987   5) Elevated current velocities keep food for filter feeders in suspension and also

988   expose hard substrata to which organisms can attach. Constriction of across-canyon

989   tidal currents by the steep canyon walls and compensating amplification of along-

990   canyon velocities is one mechanism by which elevated and spatially variable current

991   regimes may occur. A second is enhancement of near-bottom currents associated with

992   the focusing of internal tides in the canyon. The complex bathymetry of Whittard

993   Canyon (with sub-, super- and near-critical reflection regimes) and the likely presence

994   of short but energetic nonlinear waveforms means that the internal tide field needs to

995   be observed and modelled at high resolution in order to map current variability at the

996   same scale as biological observations. Further complications arise from temporal

997   changes to the internal tide field in response to the spring-neap cycle and on longer

998   timescales in response to mesoscale activity and seasonal changes in stratification.

999   6) The continuous sediment resuspension due to fishing, specifically bottom trawling

1000   in the Whittard Canyon can gradually reshape seafloor community structure and

1001   biodiversity (i.e. enhancing SPM fluxes, which smothers filter feeders and provides

1002   nutritional unsuitable material) reducing its original complexity.

1003   Overall, this review has shown that perhaps the definition of an 'active'

1004   submarine canyon should not just be linked to the frequency of large-volume

1005   sediment flows and to unidirectional sediment transport from shallow waters to the

1006   deep-sea. A wide range of more frequent physical processes is 'active' in Whittard

1007   Canyon, both in terms of oceanography and sediment dynamics. Those equally

1008   contribute to the canyon formation and maintenance, and have a direct influence on

1009   the ecosystem functioning. It can be argued that those (tidal, seasonal) processes may

1010   be as important as, if not even more important than, large episodic events in shaping

1011   communities in submarine canyons. The spatial and temporal scales at which they

1012   occur are closer to the intrinsic scales of the biological patterns and ecological

1013   functioning within canyons, even if the latter ones are not well known yet. It is

1014   precisely a better insight in these intrinsic scales of biological patterns that is now

1015   urgently needed in order to fully understand the interaction between physical

1016   processes and biological observations, between environmental drivers and community

1017   distributions. Some of the complex patterns observed in Whittard Canyon are difficult

1018   to interpret based on existing observations. Further coordinated studies are therefore

1019   necessary to clarify the processes responsible for these highly variable faunal

1020   distributions. Sampling along bathymetric transects within branches of the Whittard

1021   Canyon and across the adjacent open slopes is limited, inconsistent between

1022   disciplines and faunal groups, and often confined to a single time point. Further

1023   advances will require concerted interdisciplinary research based on samples and

1024   observations made at the same locations, as well as better temporal coverage based on

1025   long-term observation and time-series programs. Ultimately, other submarine canyon

1026   systems, potentially with different 'activity' regimes, need to be investigated through

1027   similar large, multi-scale, multidisciplinary and well-coordinated studies to allow

1028   global insights in canyon processes to be reached. Although seemingly homogenous,

1029   nearby canyons may differ tremendously.

1030   A good understanding of the fundamental active processes governing submarine

1031   canyons, including their spatial and temporal scale, is also of major importance in
1032   order to correctly evaluate the impact of human activities. Although most active
1033   canyons may exhibit broad ecosystem patterns similar to those observed in the
1034   Whittard Canyon, the shelf-to-canyon sediment delivery mechanisms are often
1035   different. The Whittard Canyon head is located ~300 km from land, which means
1036   terrestrial sediment input is reduced compared to, for example, the Nazaré or
1037   Kaikoura Canyon. The effects of nepheloid layers and sediment flows caused by
1038   bottom trawling on canyon flanks may be very different in submarine canyons like
1039   Whittard Canyon, that are driven by tidal resuspension and limited downslope
1040   sediment flows, compared to systems with regular flows such as river-fed canyons.
1041   Equally, more indirect human impacts such as changes in water column temperature
1042   and density structure, caused by global warming, may have different impacts on the
1043   generation and propagation of internal tides, and hence on the crucial canyon
1044   'activity' driving biodiversity and ecosystem functioning. Also acidification, reduced
1045   oxygen levels and the introduction of chemical pollutants are expected to have major
1046   effects on submarine canyon systems, and may cause reductions in faunal biomass
1047   and diversity. Major decreases in biomass will cause a widespread change in benthic
1048   ecosystems and the functions and services they provide, causing unprecedented
1049   challenges for the sustainable management of canyon systems. The more insights can
1050   be obtained into the activity and functioning of submarine canyons by means of
1051   integrated studies, the better such challenges can be answered in the future.
1052
1053   **7. ACKNOWLEDGEMENTS**

1062
1063

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