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5 The Whittard Canyon – A case study of submarine canyon processes

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by

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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

86 1. INTRODUCTION

87

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

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

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

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 $28\text{-}48\text{ W m}^{-1}$ 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 $100\text{-}250\text{ g C m}^{-2}\text{ yr}^{-1}$ 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 $200\text{ g C m}^{-2}\text{ yr}^{-1}$ decreasing to $140\text{ g C m}^{-2}\text{ yr}^{-1}$ in deeper water 150 km from
239 the shelf edge, with potentially $30\text{ g C m}^{-2}\text{ yr}^{-1}$ 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, $9^{\circ} 30.69'$ 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 ($S_{\text{topog}}/S_{\text{wave}} > 1$) 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 $>0.4 \text{ m s}^{-1}$ 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 $\text{grams m}^{-2} \text{s}^{-1}$
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 $0.1\text{-}0.15 \text{ m s}^{-1}$ 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 $3.2 \times 10^6 \text{ kg m}^{-2} \text{ y}^{-1}$ 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 $10 \text{ kg m}^{-2} \text{ y}^{-1}$. 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 interfluvial 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 CaCO₃. Toward
395 greater depths, sediments on the slope adjacent to the western canyon branch become
396 progressively depleted in lithogenic material, whilst CaCO₃ 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 interfluvial 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 ²¹⁰Pb 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 $\mu\text{g L}^{-1}$; vs. 12 – 23 $\mu\text{g L}^{-1}$ 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

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., *Lagenammia 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*, *Lagenammia* 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 Terrace and the more tranquil environment
602 of the Porcupine Seabight. Weston (1985) studied Rose Bengal-stained and dead
603 assemblages (>125- μ m 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, except 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 interflaves 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 $4536 \pm \text{SD } 1676 \text{ ind m}^{-2}$; slope $2744 \pm \text{SD } 260$
731 ind m^{-2}). Density varied throughout the branches of the canyon, increasing across the
732 sites from west to east (western branch $2900 \pm 538 \text{ ind m}^{-2}$; eastern middle branch
733 $4461 \pm \text{SD } 856 \text{ ind m}^{-2}$; eastern branch $6249 \pm \text{SD } 1363 \text{ ind m}^{-2}$). 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 ($5352 \pm \text{SD } 2583 \text{ ind m}^{-2}$) compared with the western branch ($3416 \pm \text{SD } 2069$
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 (tanais 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 $300 \mu\text{m}$ sieve, whereas Hunter et al. (2013) used
758 ROV push cores and a $250 \mu\text{m}$ 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 27.35-27.65 kg m⁻³
857 proposed by Dullo et al. (2008) and Flögel et al. (2014) for optimal *Lophelia* growth
858 (Whittard Canyon coral wall: ~27.80 kg 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 canyon.
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

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1063

1064 **8. REFERENCES**

- 1065 Allen, S. and Durrieu de Madron, X. (2009). A review of the role of submarine
1066 canyons in deep-ocean exchange with the shelf. *Ocean Science*, 5, 607-620.
- 1067 Amaro, T., Bianchelli, S., Billett, D. S. M., Cunha, M. R., Pusceddu, A., and
1068 Danovaro, R. (2010). The trophic biology of the holothurian *Molpadia musculus*:
1069 implications for organic matter cycling and ecosystem functioning in a deep
1070 submarine canyon. *Biogeosciences*, 7: 1-14.
- 1071 Amaro, T., de Stigter, H., Lavaleye, M. & Duineveld, G. (2015). Organic matter
1072 enrichment in the Whittard Channel (northern Bay of Biscay margin, NE Atlantic); its
1073 origin and possible effects on benthic megafauna. *Deep-Sea Research Part I*. 102, 90-
1074 100.
- 1075 Amin, M. and Huthnance, J.M. (1999). The pattern of cross-slope depositional fluxes.
1076 *Deep Sea Research Part I: Oceanographic Research Papers*, 46, 1565-1591.
- 1077 Baines, P. G. (1982). On internal tide generation models. *Deep Sea Research Part A*.
1078 *Oceanographic Research Papers*, 29,307-338.
- 1079 Anderson, M.J., Robinson, J.; Generalised discriminant analysis based on distances.
1080 *Aust NZ J Stat* 45, 2003, 301 – 318.
- 1081 Bianchelli S, Gambi C, Zeppilli D, Danovaro, R. (2010) Metazoan meiofauna in
1082 deep-sea canyons and adjacent open slopes: a large-scale comparison with focus on
1083 the rare taxa. *Deep-Sea Research I*, 57: 420-433
- 1084 Billett, D.S.M., Bett, B.J., Reid, W.D.K., Boorman, B., Priede, M. (2010). Long-term
1085 change in the abyssal NE Atlantic: The ‘Amperima Event’ revisited, *Deep-Sea*
1086 *Research II* 57, 1406–1417.
- 1087 Bourillet, J.F., Reynaud, J.Y., Baltzer, A., Zaragosi, S. (2003). The 'Fleuve Manche':
1088 the submarine sedimentary features from the outer shelf to the deep-sea fans. *Journal*
1089 *of Quaternary Science* 18, 261-282.
- 1090 Bourillet, J.F., Zaragosi, S., Mulder, T. (2006). The French Atlantic margin and deep-
1091 sea submarine systems. *Geo-Marine Letters* 26, 311-315.
- 1092 Bosley, K. L., Lavelle, J. W., Brodeur, R. D., Wakefield, W. W., Emmett, R. L.,
1093 Baker, E. T., & Rehmke, K. M. (2004). Biological and physical processes in and
1094 around Astoria submarine Canyon, Oregon, USA. *Journal of Marine Systems*, 50(1),
1095 21-37.
- 1096 Bower, A. S., Lecann, B., Rossby, T., Zenk, W., Gould, J, Speer, K, Richardson, P.L.,
1097 Prater, M.D. and Zhang, H.-M (2002). Directly measured mid-depth circulation in the
1098 northeastern North Atlantic Ocean. *Nature*, 419, 603-607.

- 1099 Clarke, K.R., Gorley, R.N.; Primer v6: user manual/tutorial. PRIMER-E, Plymouth,
1100 2006.
- 1101 Cooper L.H.N. and Vaux D. (1949). Cascading over the continental slope of water
1102 from the Celtic Sea. *Journal of the Marine Biology Association of the United*
1103 *Kingdom*, 28, 719–750.
- 1104 Cunningham, M.J., Hodgson, S., Masson, D.G., Parson, L.M. (2005). An evaluation
1105 of along- and down-slope sediment transport processes between Goban Spur and
1106 Brenot Spur on the Celtic Margin of the Bay of Biscay. *Sedimentary Geology* 179,
1107 99-116.
- 1108 Danovaro R, Bianchelli S, Gambi C, Mea M, Zeppilli, D. (2009) α -, β -, γ -, δ and ϵ -
1109 diversity of deep-sea nematodes in canyons and open slopes of E-Atlantic and
1110 Mediterranean margins. *Marine Ecology Progress Serie*, 396: 197-209.
- 1111 Danovaro, R., Snelgrove, P.V. and Tyler, P.; Challenging the paradigms of deep-sea
1112 ecology. *Trends Ecol Evol* 29, 2014, 465–475.
- 1113 Danovaro R, Gambi C, Lampadariou N, Tselepides, A. (2008) Deep-sea biodiversity
1114 in the Mediterranean Basin: testing for longitudinal, bathymetric and energetic
1115 gradients. *Ecography* 31: 231-244.
- 1116 Davies, J. S., Howell, K. L ; Stewart, H. A. , Guinan, J. and Golding, N. (2014).
1117 Defining biological assemblages (biotopes) of conservation interest in the submarine
1118 canyons of the South West Approaches (offshore United Kingdom) for use in marine
1119 habitat mapping. *Deep Sea Research II*, 104, 208-229.
- 1120 Davies, J.S., Stewart, H.A., Narayanaswamy, B.E., Jacobs, C., Spicer, J., Golding, N.,
1121 Howell, K.L. (2015). Benthic assemblages of the Anton Dohrn Seamount (NE
1122 Atlantic): defining deep-sea biotopes to support habitat mapping and management
1123 efforts with a focus on Vulnerable Marine Ecosystems. *PLoS ONE*. . DOI:
1124 10.1371/journal.pone.0124815.
- 1125 De Mol, L., Van Rooij, D., Pirlet, H., Greinert, J., Frank, N., Quemmerais, F. and
1126 Henriët, J.-P. (2011). Cold-water coral habitats in the Penmarc'h and Guilvinec
1127 Canyons (Bay of Biscay): Deep-water versus shallow-water settings. *Marine*
1128 *Geology*, 282 (1-2), 40-52.
- 1129 de Stigter, H.C., Boer, W., de Jesus Mendes, P.A., Jesus, C.C., Thomsen, L., van den
1130 Bergh, G.D., van Weering, T.C.E. (2007). Recent sediment transport and deposition
1131 in the Nazaré Canyon, Portuguese continental margin. *Marine Geology* 246, 144–164.
- 1132 de Stigter, H., Lavaleye, M., Duineveld, G. and van Weering, T. (2008a). Sediment
1133 dynamics of the Whittard Canyon, Celtic Margin. Presentation at the 3rd HERMES
1134 workshop, Carvoeiro, Portugal, March 2008.

- 1135 de Stigter, H.C. and shipboard scientific party (2008b). Report of cruise 64PE269
1136 with RV Pelagia, Portimão – Cork, 19 May – 11 June 2007. Dispersal of
1137 anthropogenic lead in submarine canyons. NIOZ – Royal Netherlands Institute for
1138 Sea Research, Texel, The Netherlands, 65 pp.
- 1139 Duineveld G., Lavaleye M.S.S., Berghuis E.M., de Wilde P. (2001). Activity and
1140 composition of the benthic fauna in the Whittard Canyon and the adjacent continental
1141 slope (NE Atlantic). *Oceanologica Acta*, 24, 69–83.
- 1142 Duineveld, G.C.A., Lavaleye, M.S.S., and Berghuis, E.M.; Particle flux and food
1143 supply to a seamount cold-water coral community (Galicia Bank, NW Spain). *Mar.*
1144 *Ecol. Prog. Ser.* 277, 2004, 13–23.
- 1145 Dullo, W.-C., S. Flögel, and A. Rüggeberg (2008). Cold-water coral growth in
1146 relation to the hydrography of the Celtic and Nordic European continental margin.
1147 *Marine Ecology Progress Series*:165-176.
- 1148 Duros, P., Fontanier, C., Metzger, E., Pusceddu, A., Cesbron, F., De Stigter, H.C.,
1149 Bianchelli, S., Danovaro, R., Jorissen, F.J. (2011). Live (stained) benthic foraminifera
1150 in the Whittard Canyon, Celtic margin (NE Atlantic). *Deep-Sea Research Part I*:
1151 *Oceanographic Research Papers* 58, 128–146.
- 1152 Duros, P., Fontanier, C., de Stigter, H.C., Cesbron, F., Metzger, E., Jorissen, F.J.
1153 (2012). Live and dead benthic foraminiferal faunas from Whittard Canyon (NE
1154 Atlantic): focus on taphonomic processes and paleo-environmental applications.
1155 *Marine Micropaleontology* 94-95: 25-44.
- 1156 Egbert, G. D. (1997). Tidal data inversion: interpolation and inference. *Progress in*
1157 *Oceanography*, 40, 53-80. *Tidal Science In Honour of David E. Cartwright*.
- 1158 Egbert, G. D. and Erofeeva, S. Y. (2002). Efficient inverse modeling of barotropic
1159 ocean tides. *Journal of Atmospheric and Oceanic Technology*, 19, 183-204.
- 1160 Evans, C.D.R. (1990). The geology of the western English Channel and its western
1161 approaches. HMSO for the British Geological Survey, London.
- 1162 Evans, C.D.R., Hughes, M.J. (1984). The Neogene succession of the South Western
1163 Approaches, Great Britain. *Journal of the Geological Society of London* 141, 315-
1164 326.
- 1165 FitzGeorge-Balfour, T., Billett, D. S. M., Wolff, G. A., Thompson, A., and Tyler, P.
1166 A.; Phytopigments as biomarkers of selectivity in abyssal holothurians; inter-species
1167 differences in responses to a changing food supply. *Deep Sea Research II*, 57, 2010,
1168 1418–1428.
- 1169 Flögel, S., Dullo, W. C., Pfannkuche, O. Kiriakoulakis, K. and Rüggeberg, A. (2014).
1170 Geochemical and physical constraints for the occurrence of living cold-water corals.
1171 *Deep Sea Research Part II: Topical Studies in Oceanography* 99:19-26.

- 1172 Gambi, C., Vanreusel, A., Danovaro, R. (2003). Biodiversity of nematode
1173 assemblages from deep-sea sediments of the Atacama Slope and Trench (Southern
1174 Pacific Ocean). *Deep-Sea Research I*, 50, 103-117.
- 1175 Gambi C, Pusceddu A, Benedetti-Cecchi L, and Danovaro R (2014). Species richness,
1176 species turnover, and functional diversity in nematodes of the deep Mediterranean
1177 Sea: searching for drivers at different spatial scales. *Global ecology and*
1178 *biogeography*, 23, 24-39
- 1179 Gambi C., Danovaro R. (2016). Biodiversity and life strategies of deep-sea meiofauna
1180 and nematode assemblages in the Whittard canyon (Celtic margin, NE Atlantic
1181 Ocean). *Deep Sea Research Part I* 108, 13-22.
- 1182 Garrett, C. and Kunze, E. (2007). Internal tide generation in the deep ocean. *Annual*
1183 *Review. Fluid Mech.*, 39, 57-87.
- 1184 Gooday, A.J. (1988). A response by benthic foraminifera to phytodetritus deposition
1185 in the deep sea. *Nature*, 332: 70-73.
- 1186 Gordon, R. L. and Marshall, N. F. (1976). Submarine canyons - internal wave traps.
1187 *Geophysical Research Letters*, 3, 622-624.
- 1188 Gunton, L.M., Gooday, A.J., Glover, A.J., Bett, B.J. (2015a) Macrofaunal abundance
1189 and community composition at lower bathyal depths in different branches of the
1190 Whittard Canyon and on the adjacent slope (3500m; NE Atlantic). *Deep Sea Research*
1191 *Part I* 97, 29-39
- 1192 Gunton, L.M., Neal, L., Gooday, A.J., Bett, B.J., Glover, A.G. (2015b). Local and
1193 regional variation in deep-sea polychaete diversity: canyon influence (Whittard
1194 Canyon system, NE Atlantic). *Deep Sea Research Part I* 106, 42-54. .
- 1195 Hall, R. A. and Carter, G. S. (2011). Internal Tides in Monterey Submarine Canyon.
1196 *Journal of Physical Oceanography*, 41, 186-204.
- 1197 Hall, R. A., Alford, M. H., Carter, G. S., Gregg, M. C., Lien, R.-C., Wain, D. J., and
1198 Zhao, Z. (2014). Transition from partly standing to progressive internal tides in
1199 Monterey Submarine Canyon. *Deep-Sea Research II* 104, 164-173.
- 1200 Harris, P.T., Whiteway, T., (2011). Global distribution of large submarine canyons:
1201 geomorphic differences between active and passive continental margins. *Marine*
1202 *Geology* 285, 69-86.
- 1203 Harris, P.T., MacMillan-Lawler, M., Rupp, J., Baker, E.K.; Geomorphology of the
1204 oceans. *Marine Geology* 352, 2014,4-24
- 1205 Hickey, B. M. (1995). Coastal submarine canyons. Topographic effects in the ocean.
1206 SOEST Special publications, 95-110.

- 1207 Holligan, P. M., Pingree, R. D., & Mardell, G. T. (1985). Oceanic solitons, nutrient
1208 pulses and phytoplankton growth. *Nature*, 314, 348-350.
- 1209 Holt, J. and Thorpe, S. (1997). The propagation of high frequency internal waves in
1210 the celtic sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 4, 2087-
1211 2116.
- 1212 Hopkins, J. E., Stephenson, G. R., Green, J., Inall, M. E., and Palmer, M. R. (2014).
1213 Storms modify baroclinic energy fluxes in a seasonally stratified shelf sea: Inertial-tidal
1214 interaction. *Journal of Geophysical Research: Oceans*, 119, 6863-6883.
- 1215 Hotchkiss, F. S. and Wunsch, C. (1982). Internal waves in hudson canyon with
1216 possible geological implications. *Deep-Sea Research Part a-Oceanographic Research*
1217 *Papers*, 29, 415-442.
- 1218 Howell, K. L. (2010). A benthic classification system to aid in the implementation of
1219 marine protected area networks in the deep/high seas of the NE Atlantic. *Biological*
1220 *Conservation* 143:1041-1056.
- 1221 Hunter, W.R., Jamieson, A.J., Huvenne, V., Witte, U. (2013). Sediment community
1222 responses to marine vs. terrigenous organic matter in a submarine canyon.
1223 *Biogeosciences* 10, 67-80.
- 1224 Huvenne, V.A.I., Tyler, P.A., Masson, D.G., Fisher, E.H., Hauton, C., Hühnerbach,
1225 V., Le Bas, T.P., Wolff, G.A. (2011). A Picture on the Wall: Innovative Mapping
1226 Reveals Cold-Water Coral Refuge in Submarine Canyon. (J.M. Roberts, Ed.). *Plos*
1227 *One* 6, e28755.
- 1228 Huvenne, Veerle A.I.; Davies, Jaime S. (2014). Towards a new and integrated
1229 approach to submarine canyon research. Introduction. *Deep Sea Research Part II:*
1230 *Topical Studies in Oceanography*, 104. 1-5.
- 1231 ICES-NAFO Joint Working Group on Deep-Water Ecology (WGDEC). (26/03/2012 -
1232 30/03/2012. Copenhagen (Dinamarca)). 2012. ICES CM/2012/ACOM:29I
- 1233 Inall, M., Aleynik, D., Boyd, T., Palmer, M., and Sharples, J. (2011). Internal tide
1234 coherence and decay over a wide shelf sea. *Geophysical Research Letters*, 38,
1235 L23607, doi:10.1029/2011GL049943.
- 1236 Ingels, J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A. (2009). Nematode diversity
1237 and its relation to the quantity and quality of sedimentary organic matter in the deep
1238 Nazare Canyon, Western Iberian Margin. *Deep-Sea Research Part I-Oceanographic*
1239 *Research Papers* 56(9), 1521-1539.
- 1240 Ingels J., Tchessunov A.V., Vanreusel A. (2011a) Meiofauna in the Gollum Channels
1241 and the Whittard Canyon, Celtic Margin - How Local Environmental Conditions
1242 Shape Nematode Structure and Function. *Plos One* 6 (5), 1-15.

- 1243 Ingels, J., Billett, D., Van Gaever, S., Vanreusel, A. (2011b) An insight into the
1244 feeding ecology of deep-sea canyon nematodes - Results from field observations and
1245 the first in-situ C-13 feeding experiment in the Nazare Canyon. *Journal of*
1246 *Experimental Marine Biology and Ecology* 396(2), 185-193.
- 1247 Ingels, J., Billett, D.S.M., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A. (2011c).
1248 Structural and functional diversity of Nematoda in relation with environmental
1249 variables in the Setúbal and Cascais canyons, Western Iberian Margin. *Deep Sea*
1250 *Research Part II: Topical Studies in Oceanography* 58(23-24), 2354-2368.
- 1251 Ingels, J., Vanreusel, A., Romano, C., Coenjaerts, J., Mar Flexas, M., Zúñiga, D.,
1252 Martin, D., 2013. Spatial and temporal infaunal dynamics of the Blanes submarine
1253 canyon-slope system (NW Mediterranean); changes in nematode standing stocks,
1254 feeding types and gender-life stage ratios. *Progress in Oceanography* 118, 159-174.
- 1255 Ingels, J., and Vanreusel, A., 2013. The importance of different spatial scales in
1256 determining structural and functional characteristics of deep-sea infauna communities.
1257 *Biogeosciences* 10(7), 4547-4563.
- 1258 Ismail, K.,(2016). Marine landscape mapping in submarine canyons. University of
1259 Southampton, Ocean & Earth Science, Doctoral Thesis, 2016, 154pp.
- 1260 Joint, I.R., Owens, N.J.P. and Pomroy, A.J. (1986). Seasonal production of
1261 photosynthetic picoplankton and nanoplankton in the Celtic Sea. *Marine Ecology*
1262 *Progress Series*, 28, 251-258.
- 1263 Joint I, Wollast R, Chou L, Batten S, Elskens M, et al. (2001) Pelagic production at
1264 the Celtic Sea shelf break. *Deep-Sea Research Part II: Topical Studies in*
1265 *Oceanography* 48: 3049–3081
- 1266 Jamieson, A.J., Kilgallen, N.M., Rowden, A.A., Fujii, T., Horton, T., Lorz, A.-N.,
1267 Kitazawa, K. and Priede, I.G. (2011). Bait-attending fauna of the Kermadec Trench,
1268 SW Pacific Ocean: evidence for an ecotone across the abyssal-hadal transition zone.
1269 *Deep-Sea Research Part I* 58, 49–62.
- 1270 Johnson, M. P.; White, M.; Wilson, A.; Würzberg, L.; Schwabe, E.; Folch, H. and
1271 Allcock, A. L. (2013). A vertical wall dominated by *Acesta excavata* and
1272 *Neopycnodonte zibrowii*, part of an undersampled group of deep-sea habitats. *PLoS*
1273 *ONE* 8:e79917.
- 1274 Kiriakoulakis K., White M., Bett B.J. and Wolff G.A.; Organic biogeochemistry of
1275 the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic. *Deep Sea*
1276 *Research I* 51(12), 2004, 1937-1954.
- 1277 Kiriakoulakis K., Blackbird S., Ingels J., Vanreusel A., Wolff G.A. (2011). Organic
1278 geochemistry of submarine canyons: The Portuguese margin, *Deep Sea Research Part*
1279 *II*, 58, 2477-2488.

- 1280 Lambeck, K., (1996). Glaciation and sea-level change for Ireland and the Irish Sea
 1281 since Late Devensian/Midlandian time. *Journal of the Geological Society of London*
 1282 153, 853-872.
- 1283 Leduc, D., Rowden, A.A., Probert, P.K., Pilditch, C.A., Nodder, S.D., Vanreusel, A.,
 1284 Duineveld, G.C.A., Witbaard, R. (2012). Further evidence for the effect of particle-
 1285 size diversity on deep-sea benthic biodiversity. *Deep Sea Research Part I:*
 1286 *Oceanographic Research Papers*, 63, 164-169.
- 1287 Leduc, D., Rowden, A., Nodder, S., Berkenbusch, K., Probert, P., Hadfield, M.
 1288 (2014). Unusually high food availability in Kaikoura Canyon linked to distinct deep-
 1289 sea nematode community. *Deep Sea Research Part II: Topical Studies in*
 1290 *Oceanography* 104, 310-318.
- 1291 Lins, L., Vanreusel, A., van Campenhout, J., Ingels, J. (2013). Selective settlement of
 1292 deep-sea canyon nematodes after resuspension - an experimental approach. *Journal of*
 1293 *Experimental Marine Biology and Ecology*, 441, 110-116.
- 1294 Martín, J., Puig, P., Palanques, A., Masqué, P., García-Orellana, J. (2008). Effect of
 1295 commercial trawling on the deep sedimentation in a Mediterranean submarine
 1296 canyon. *Marine Geology* 252, 150-155.
- 1297 Martín, J., Palanques, A., Vitorino, J., Oliveira, A., de Stigter, H.C. (2011). Near-
 1298 bottom particulate matter dynamics in the Nazaré submarine canyon under calm and
 1299 stormy conditions. *Deep-Sea Research Part II, Topical Studies in Oceanography* 58,
 1300 2388-2400.
- 1301 Martín, J., Puig, P., Palanques, A., and Ribó, M. (2014). Trawling-induced daily
 1302 sediment resuspension in the flank of a Mediterranean submarine canyon. *Deep Sea*
 1303 *Research Part II: Topical Studies in Oceanography*, 104, 174-183.
- 1304 Masson D.G., Huvenne V.A.I., de Stigter H., Wolff G.A., Kiriakoulakis K., Arzola
 1305 R.G., Blackbird S. (2010). Efficient burial of carbon in a submarine canyon. *Geology*,
 1306 38, 831–834.
- 1307 McCave, I.N. (1986). Local and global aspects of the bottom nepheloid layers in the
 1308 world ocean. *Netherlands Journal of Sea Research* 20, 167-181.
- 1309 Meyers, P. A. (1997) Organic geochemical proxies of paleoceanographic,
 1310 paleolimnologic and paleoclimatic processes. *Organic Geochemistry*, 27, 213–250.
- 1311 Morris K.J., Tyler R.A., Masson D.G. Huvenne V.I.A. and Rogers A. (2013).
 1312 Distribution of cold water corals in the Whittard Canyon NE Atlantic. *Deep Sea*
 1313 *Research II*, 92, 136-144.
- 1314 Muller-Navarra D.C., Brett M.T., Liston A.M. and Goldman C.R. (2000). A highly
 1315 unsaturated fatty acid predicts carbon transfer between primary producers and
 1316 consumers. *Nature*, 403, 74–77.

- 1317 Mulder, T., Zaragosi, S., Garlan, T., Mavel, J., Cremer, M., Sottolichio, A., Sénéchal,
1318 N., Schmidt, S. (2012). Present deep-submarine canyons activity in the Bay of Biscay
1319 (NE Atlantic). *Marine Geology*, 295–298, 113-127.
- 1320 Narayanaswamy, B. E., Hughes, D. J., Howell, K. L., Davies, J., and Jacobs, C.
1321 (2013). First observations of megafaunal communities inhabiting George Bligh Bank,
1322 Northeast Atlantic. *Deep Sea Research Part II: Topical Studies in Oceanography*.
- 1323 Nash, J. D., Kunze, E., Toole, J. M., and Schmitt, R. W. (2004). Internal tide
1324 reflection and turbulent mixing on the continental slope. *Journal of Physical*
1325 *Oceanography*, 34, 1117-1134.
- 1326 Palanques, A., Guillé'n, J., Puig, P., and Durrieu de Madron, X.; Storm-driven shelf-
1327 to-canyon suspended sediment transport at the southwestern end of the Gulf of Lions,
1328 *Cont. Shelf Res.*, 28, 2008, 1947–1956.
- 1329 Pérez, F. F., Ríos, A. F., King, B. A., Pollard, R. T. (1995). Decadal changes of the θ -
1330 S relationship of the Eastern North Atlantic Central Water. *Deep Sea Research Part I:*
1331 *Oceanographic Research Papers*, 42, 1849-1864.
- 1332 Pham, C.K., Ramirez-Llodra, E.R., Alt, C., Amaro, T., et al. (2014) Marine litter
1333 distribution and density in European seas, from the shelves to deep basins. *PLoS ONE*
1334 9(4):e95839.
- 1335 Pingree, R. (1980). *Physical oceanography of the celtic sea and english channel.*
1336 Elsevier Oceanography Series, 24, 415-465.
- 1337 Pingree, R. and Mardell, G. (1985). Solitary internal waves in the celtic sea. *Progress*
1338 *in Oceanography*, 14, 431-441.
- 1339 Pingree R.D. and LeCann, B. (1989). Celtic and Armorican slope and shelf residual
1340 currents *Progress in Oceanography*, 23, 303–338.
- 1341 Pingree, R. D., Sinha, B., Griffiths, C.R. (1999). Seasonality of the European slope
1342 current (Goban Spur) and ocean margin exchange. *Continental Shelf Research* 19,
1343 929-975.
- 1344 Pingree, R.D. and Le Cann, B. (1990). Structure, strength and seasonality of the slope
1345 currents in the Bay of Biscay region. *Journal of the Marine Biological Association of*
1346 *the United Kingdom*, 70, 857-885.
- 1347 Pollard, R. T., Griffiths, M. J., Cunningham, S. A., Read, J. F., Pérez, F. F., Ríos, A.
1348 F. (1996). Vivaldi 1991-A study of the formation, circulation and ventilation of
1349 Eastern North Atlantic Central Water. *Progress in Oceanography*, 37, 167-192.
- 1350 Praeg, D., McCarron, S., Dove, D., Ó Cofaigh, C., Scott, G., Monteys, X., Facchin,
1351 L., Romeo, R., Coxon, P. (2015). Ice sheet extension to the Celtic Sea shelf edge at
1352 the Last Glacial Maximum. *Quaternary Science Reviews*, 111, 107-112.

- 1353 Puig, P. and Palanques, A., (1998). Temporal variability and composition of settling
 1354 particle fluxes on the Barcelona continental margin (Northwestern Mediterranean).
 1355 *Journal of Marine Research*, 56, 639-654.
- 1356 Puig, P., Canals, M., Company, J.B., Martín, J., Amblas, D., Lastras, G., Palanques,
 1357 A., Calafat, A.M. (2012). Ploughing the deep sea floor. *Nature* 489, 286–289.
- 1358 Puig, P., Palanques, A., Martín, J. (2014). Contemporary Sediment-Transport
 1359 Processes in Submarine Canyons. *Annual Review of Marine Science*, 6, 53-77.
- 1360 Pusceddu A, Mea M, Canals M, Heussner S, Durrieu de Madron X, Sanchez-Vidal A,
 1361 Bianchelli S, Corinaldesi C, Dell'Anno A, Thomsen L, Danovaro R (2013) Major
 1362 consequences of an intense dense shelf water cascading event on deep-sea benthic
 1363 trophic conditions and meiofaunal biodiversity. *Biogeosciences* 10(4): 2659-2670
- 1364 Reid, G.S., Hamilton, D. (1990). A Reconnaissance Survey of the Whittard Sea Fan,
 1365 Southwestern Approaches, British-Isles. *Marine Geology* 92, 69–86.
- 1366 Rees, A.P., Joint, I. and Donald. K.M. (1999). Early spring bloom phytoplankton-
 1367 nutrient dynamics at the Celtic Sea Shelf Edge. *Deep Sea Research*, 46, 483-510.
- 1368 Rice, A. L., Tyler, P. A., & Paterson, G. J. L. (1992). The pennatulid *Kophobelemnon*
 1369 *stelliferum* (Cnidaria: Octocorallia) in the porcupine seabight (north-east Atlantic
 1370 Ocean). *Journal of the Marine Biological Association of the United Kingdom*, 72(02),
 1371 417-434.
- 1372 Roberts, J. M., L. A. Henry, D. Long, and J. P. Hartley (2008). Cold-water coral reef
 1373 frameworks, megafaunal communities and evidence for coral carbonate mounds on
 1374 the Hatton Bank, north east Atlantic. *Facies*, 54, 297-316.
- 1375 Robert, K., D. O. B. Jones, P. A. Tyler, D. Van Rooij and V. A. I. Huvenne (2014).
 1376 Finding the hotspots within a biodiversity hotspot: fine-scale biological predictions
 1377 within a submarine canyon using high-resolution acoustic mapping techniques.
 1378 *Marine Ecology*, 36(4), 1256-1276. DOI: 10.1111/maec.12228.
- 1379 Romano, C., Coenjaerts, J., Mar Flexas, M., Zúñiga, D., Vanreusel, A., Company,
 1380 J.B., Martin, D. (2013). Spatio-temporal variability of meiobenthic density in the
 1381 Blanes submarine canyon (NW Mediterranean). *Progress in Oceanography* 118, 144-
 1382 158.
- 1383 Ryan, J. P., Chavez, F. P., & Bellingham, J. G. (2005). Physical-biological coupling
 1384 in Monterey Bay, California: topographic influences on phytoplankton ecology.
 1385 *Marine Ecology Progress Series*, 287, 23-32.
- 1386 Sanchez-Vidal, A., Canals, M., Calafat, A.M., Lastras, G., Pedrosa-Pàmies, R.,
 1387 Menéndez, M., Medina, R., Company, J.B., Hereu, B., Romero, J., Alcoverro, T.
 1388 (2012). Impacts on the Deep-Sea Ecosystem by a Severe Coastal Storm. *PlosOne* 71,
 1389 e30395.

- 1390 Scourse, J., Uehara, K., Wainwright, A. (2009). Celtic Sea linear tidal sand ridges, the
 1391 Irish Sea Ice Stream and the Fleuve Manche : palaeotidal modelling of a transitional
 1392 passive margin depositional system. *Marine Geology*, 259, 102-111.
- 1393 Sharples, J., Tweddle, J. F., Mattias Green, J., Palmer, M. R., Kim, Y.-N., Hickman,
 1394 A. E., Holligan, P. M., Moore, C. M., Rippeth, T. P., Simpson, J. H., et al. (2007).
 1395 Spring-neap modulation of internal tide mixing and vertical nitrate fluxes at a shelf
 1396 edge in summer. *Limnology and Oceanography*, 52, 1735-1747.
- 1397 Soetaert, K. and Heip, C. (1995) Nematode assemblages of deep-sea and shelf break
 1398 sites in the North Atlantic and Mediterranean Sea. *Marine Ecology Progress Series*
 1399 125: 171-183.
- 1400 Skliris, N. and Denidi, S. (2006). Plankton dynamics controlled by hydrodynamic
 1401 processes near a submarine canyon off NW corsican coast: a numerical modelling
 1402 study. *Continental Shelf Research*, 26, 1336-1358.
- 1403 Schlacher T. A, Schlacher-Hoenlinger M. A, Williams A., Althaus F., Hooper J. N.
 1404 A., Kloser R., Richness and distribution of sponge megabenthos in continental margin
 1405 canyons off southeastern Australia. *Mar. Ecol. Prog. Ser.* 340, 2007, 73–88.
- 1406 Stewart, H.A., Davies, J.S., Guinan, J.C., Howell, K.L. (2014). The Dangeard and
 1407 Explorer Canyons, South-West Approaches, UK: Geology, sedimentology and newly
 1408 discovered cold-water coral mini-mounds. *Deep-Sea Research II* 104, 230-244.
- 1409 Tchesunov, A.V., Ingels, J., Popova, E.V. (2012). Marine free-living nematodes
 1410 associated with symbiotic bacteria in deep-sea canyons of north-east Atlantic Ocean.
 1411 *Journal of the Marine Biological Association of the United Kingdom* 92(6), 1257-
 1412 1271.
- 1413 Thorpe, S. A. (2005). *The Turbulent Ocean*. Cambridge University Press.
- 1414 Toucanne, S., Zaragosi, S., Bourillet, J.F., Naughton, F., Cremer, M., Eynaud, F.,
 1415 Dennielou, B., (2008). Activity of the turbidite levees of the Celtic-Armorican margin
 1416 (Bay of Biscay) during the last 30,000 years: Imprints of the last European
 1417 deglaciation and Heinrich events. *Marine Geology*, 247, 84-103.
- 1418 Turnewitsch R., Springer B. M., Kiriakoulakis K., Vilas J. C., Arístegui J., Wolff G.
 1419 A., Peine F., Werk S., Graf G., Waniek. J. (2007). Approaching the true concentration
 1420 of particulate organic carbon in seawater: the relative methodological importance of
 1421 artificial organic carbon gains and losses in two-filtration-based techniques. *Marine*
 1422 *Chemistry*, 105, 208-228.
- 1423 Tyler, P. A., and H. Zibrowius (1992). Submersible observations of the invertebrate
 1424 fauna on the continental-slope southwest of Ireland (NE Atlantic-ocean). *Oceanologica*
 1425 *Acta* 15:211-226.

- 1426 Tyler P., Amaro T., Azorla R., Cunha M., de Stigter H., Gooday A., Huveene V.,
 1427 Ingels J., Kiariakoulakis K., Lastras G., Masson D., Oliveira A., Pattenden A.,
 1428 Vanreusel A., van Weering T., Vitorino J., Witte U., Wolff G.A. (2009). Europe's
 1429 'Grand Canyon': the Nazaré Submarine Canyon. *Oceanography*, 22, 46-57.
- 1430 Vanhove, S., Vermeeren, H. and Vanreusel, A., (2004). Meiofauna towards the south
 1431 Sandwich Trench (750-6300 m), focus on nematodes. *Deep-Sea Research Part II*, 51,
 1432 1665-1687.
- 1433 Vanreusel, A., Fonseca, G., Danovaro, R., da Silva, M., Esteves, A., Ferrero, T., Gad,
 1434 G., Galtsova, V., Gambi, C., Genevois, V., Ingels, J., Ingole, B., Lampadariou, N.,
 1435 Merckx, B., Miljutin, D., Miljutina, M., Muthumbi, A., Netto, S., Portnova, D.,
 1436 Radziejewska, T., Raes, M., Tchesunov, A., Vanaverbeke, J., Van Gaever, S.,
 1437 Venekey, V., Bezerra, T., Flint, H., Copley, J., Pape, E., Zeppilli, D., Martinez, P.,
 1438 Galeron, J. (2010). The contribution of deep-sea macrohabitat heterogeneity to global
 1439 nematode diversity. *Marine Ecology-an Evolutionary Perspective* 31(1), 6-20.
- 1440 van Aken, H. M. (2000a). The hydrography of the mid-latitude northeast Atlantic
 1441 Ocean: I: The deep water masses. *Deep Sea Research Part I: Oceanographic Research*
 1442 *Papers* 47:757-788.
- 1443 van Aken, H. M. (2000b). The hydrography of the mid-latitude Northeast Atlantic
 1444 Ocean: II: The intermediate water masses. *Deep Sea Research Part I: Oceanographic*
 1445 *Research Papers* 47:789-824.
- 1446 van Rooij, D., Iglesias, J., Hernández-Molina, F.J., Ercilla, G., Gomez-Ballesteros,
 1447 M., Casas, D. Llave, E., De Hauwere, A., Garcia-Gil, S., Acosta, J. and Henriët, J.P.
 1448 (2010a). The Le Danois Contourite Depositional System: interactions between the
 1449 Mediterranean outflow water and the upper Cantabrian slope (North Iberian
 1450 margin). *Marine Geology*, 274, 1-20.
- 1451 van Rooij, D., de Mol, L., Ingels, J., Versteeg, W., Ruggeberg, A., Jauniaux, T., party,
 1452 the shipboard scientific party (2010b) Cruise Report Belgica 10/17b, Belgica
 1453 BiSCOSYSTEMS II, Leg 2, Whittard Canyon. Renard Centre of Marine Geology &
 1454 Marine Biology Research Group, Ghent University, Belgium, pp. 39.
- 1455 van Weering, T.C.E., Thomsen, L., van Heerwaarden, J., Koster, B., Viergutz, T.
 1456 (2000). A seabed lander and new techniques for long term in situ study of deep-sea
 1457 near bed dynamics. *Sea Technology* 41, 17-27.
- 1458 Vetter E. W., Smith C. R., De Leo F. C., Hawaiian hotspots: enhanced megafaunal
 1459 abundance and diversity in submarine canyons on the oceanic islands of Hawaii. *Mar.*
 1460 *Ecol.* 31, 2010, 183-199.
- 1461 Vlasenko, V., Stashchuk, N., Inall, M. E., and Hopkins, J. E. (2014). Tidal energy
 1462 conversion in a global hot spot: On the 3-d dynamics of baroclinic tides at the celtic
 1463 sea shelf break. *Journal of Geophysical Research: Oceans*, 119(6):3249-3265.

- 1464 Weston, J. (1985). Comparison between Recent benthic foraminiferal faunas of the
1465 Porcupine Seabight and Western Approaches continental slope. *Journal of*
1466 *Micropaleontology*. 4: 165-183.
- 1467 White M., Mohn C., Kiriakoulakis K., 2015. Environmental Sampling. In: *Biological*
1468 *sampling in the deep-sea: An (illustrated) manual of tools and techniques* (eds: Clark
1469 M., Consalvey M., Rowden A.) Wiley-Blackwell.
- 1470 Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C. & Grehan, A.J. (2007).
1471 *Multiscale Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on*
1472 *the Continental Slope. Marine Geodesy*, 30, 3-35.
- 1473 Wilson, A.M., Raine, R., Mohn,C. and White, M. (2015a). Nepheloid layer
1474 distribution in the Whittard Canyon, NE Atlantic Margin. *Marine Geology*, 367,130-
1475 142.
- 1476 Wilson, A.M., Raine, R., Gerritsen, H., Kiriakoulakis, K., Blackbird, B., Allcock, L.
1477 and White, M. (2015b) Anthropogenic influence on sediment transport in the
1478 Whittard Canyon, NE Atlantic. *Marine Pollution Bulletin* 101, 320-329..
- 1479 Wollast, R. and Chou, L. (2001). The carbon cycle at the ocean margin in the northern
1480 Gulf of Biscay. *Deep Sea Research Part II*, 48, 3265-3293.
- 1481 Xu, J.P., Noble, M.A., Eitrem, S.L., Rosenfeld, L.K., Schwing, F.B., Pilskaln, C.H.,
1482 2002. Distribution and transport of suspended particulate matter in Monterey Canyon,
1483 California. *Marine Geology* 181, 215-234.
- 1484 Xu, J. P., Sequeiros, O. E.; Noble, M. A.; Sediment concentrations, flow conditions,
1485 and downstream evolution of two turbidity currents, Monterey Canyon, USA. *Deep*
1486 *Sea Research Part I* 89, 2014, 11-3.