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Cold-water coral habitats in the Penmarc'h and Guilvinec Canyons (Bay of Biscay): Deep-water versus shallow-water settings

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Abstract :

In 1948, Le Danois reported for the first time the occurrence of living cold-water coral reefs, the so-called “massifs coralliens”, along the European Atlantic continental margin. In 2008, a cruise with R/V Belgica was set out to re-investigate these cold-water corals in the Penmarc'h and Guilvinec Canyons along the Gascogne margin of the Bay of Biscay. During this cruise, an area of 560 km2 was studied using multibeam swath bathymetry, CTD casts, ROV observations and USBL-guided boxcoring.

Based on the multibeam data and the ROV video imagery, two different cold-water coral reef settings were distinguished. In water depths ranging from 260 to 350 m, mini mounds up to 5 m high, covered by dead cold-water coral rubble, were observed. In between these mounds, soft sediment with a patchy distribution of gravel was recognised. The second setting (350–950 m) features hard substrates with cracks, spurs, cliffs and overhangs. In water depths of 700 to 950 m, both living and dead cold-water corals occur. Occasionally, they form dense coral patches with a diameter of about 10–60 m, characterised by mostly stacked dead coral rubble and a few living specimens. U/Th datings indicate a shift in cold-water coral growth after the Late Glacial Maximum (about 11.5 ka BP) from shallow to deep-water settings.

The living cold-water corals from the deeper area occur in a water density (sigma–theta) of 27.35–27.55 kg m− 3, suggested to be a prerequisite for the growth and distribution of cold-water coral reefs along the northern Atlantic margin. In contrast, the dead cold-water coral fragments in the shallow area occur in a density range of 27.15–27.20 kg m− 3 which is slightly outside the density range where living cold-water corals normally occur. The presented data suggest that this prerequisite is also valid for coral growth in the deeper canyons (> 350 m) in the Bay of Biscay.

Keywords : Bay of Biscay ; continental margin ; canyons ; cold-water corals ; *Lophelia* ; *Madrepora*

1. Introduction

Cold-water corals are widespread along the European Atlantic continental margin (Freiwald and Roberts, 2005; Freiwald et al., 2004; Roberts et al., 2006, 2009). Previous studies have already revealed a large amount of information about the distribution, significance and environmental setting of these ecosystems along the Norwegian margin (Fosså et al., 2005; Freiwald et al., 2002; Hovland et al., 1998; Lindberg and Mienert, 2005; Mortensen et al., 1995), and the continental margin off Ireland and the UK (De Mol et al., 2002; Dorschel et al., 2007; Huvenne et al., 2007; Kenyon et al., 2003; Masson et al., 2003; Mienis et al., 2007; Roberts et al., 2006; Van Weering et al., 2003; Wheeler et al., 2007). Cold-water corals are able to form habitats which vary in size from small patches (few metres in size) to large reef structures covering several kilometres (Freiwald et al., 1999; Roberts et al., 2005). In the Porcupine Seabight and Rockall Trough giant cold-water mounds up to 300 m high were observed (De Mol et al., 2002; Kenyon et al., 2003; Wheeler et al., 2007; Van Weering et al., 2003). In contrast to these well studied areas, coral occurrences within the Bay of Biscay, and more specifically the Armorican margin, are less investigated (Reveillaud et al., 2008).

The occurrence of cold-water corals in the Bay of Biscay was already reported by Joubin (1922) and Le Danois (1948). The latter study mainly observed the presence of living *Madrepora oculata* and *Lophelia pertusa*, mostly occurring in a patchy distribution but at some locations able to form a dense coral field with a maximum height of 2 m. Afterwards these cold-water corals were also reported at different locations in the Bay of Biscay by Altuna (1995), Alvarez-Claudio (1994), Zibrowius

(1980, 1985) and Zibrowius et al. (1975). In 1997, two areas along the north Atlantic margin in the Bay of Biscay were revisited by Freiwald and Henrich (1997), namely the Penmarc'h Bank and the Banc de la Chapelle, 160 km northwest of Penmarc'h Bank. On the Banc de la Chapelle, only dead colonies of *Lophelia pertusa*, *Madrepora oculata* and *Desmophyllum dianthus* were found in water depths of 340 to 790 m. Further south, on the Penmarc'h Bank living colonies of *Dendrophyllia cornigera* were observed (Reveillaud et al., 2008). The same authors also observed *Caryophyllia smithii* specimens which yielded calibrated U/Th ages of the end of the last glacial period (11-14 ka BP) (Schröder-Ritzrau et al., 2005). In 2008, Reveillaud et al. presented an overview of the cold-water coral distribution and diversity in the Bay of Biscay based on historical reports and more recent (pre-2008) data. However, it is still not known to which extent the available information represents the actual distribution of cold-water corals in the Bay of Biscay.

Cold-water corals occur in temperatures ranging between 4° and 12°C. This temperature zone corresponds with water depths between ~50 and 1000 m at high latitudes and up to 4000 m at low latitudes (Freiwald et al., 2004). Besides temperature several other environmental factors favour coral settlement and growth: hard substrates (e.g., boulders, moraine ridges, flanks of oceanic banks, seamounts, sedimentary mounds; Dodge and Vaisnys, 1977; Rogers, 1990), strong topographically guided bottom currents (Freiwald et al., 2004), nutrient-rich waters containing labile organic matter (Kiriakoulakis et al., 2004) and zooplankton (Freiwald et al., 2004), and the depth of the aragonite saturation horizon (Davies et al., 2008). Due to the presence of these conditions along the continental slope in the Bay of Biscay, this area is a potential habitat for cold-water coral ecosystems (Hall-Spencer et al., 2007; Reveillaud et al., 2008). The numerous canyons cutting the slope of the Bay of Biscay (Bourillet et al., 2003, 2006b; Le Suavé et al., 2000; Zaragosi et al., 2006) funnel sediment and labile organic matter from the continental shelf (~200 m) to the abyssal plain (~4000 m) (Freiwald et al., 2004). An additional major food source is provided by nutrient-rich waters (Freiwald et al., 2004). Recently, Dullo et al. (2008) discovered that water density also plays an important role in the distribution of cold-water corals. Along a transect stretching from 51 to 70°N (~3000 km), living cold-water corals (*Lophelia pertusa*) occur within a narrow density (sigma-theta) range of σ_{Θ} = 27.35 to 27.65 kg m^{-3}, independent from the surrounding water masses.

The data presented in this paper were collected during the BiSCOSYSTEMS cruise on board of the R/V Belgica from 25 May to 7 June 2008 within the framework of the EC FP6 IP HERMES and the ESF EuroDIVERSITY MiCROSYSTEMS projects. The main aim of the study was (1) to revisit one of the cold-water coral locations described by Le Danois (1948) in order to better understand their significance, distribution and environmental conditions, and (2) to test the hypothesis that cold-water corals only occur within the potential density range described by Dullo et al. (2008), also south of 51°N.

2. Regional setting

The continental margin in the Bay of Biscay can be subdivided in five main geographic areas (Fig.1A): the Celtic margin and Armorican margin in the north, and the Aquitaine margin, Cantabrian margin and Galician margin in the south. The Armorican margin has an orientation of 140° with a relatively broad continental shelf, up to 200 km wide, and a steep slope, with an average gradient between 2.86° and 5.15° (Lallemand and Sibuet, 1986; Le Suavé et al., 2000). The slope extends from a water depth of 200 m down to 4000 m. The morphology of the continental slope is characterised by spurs and canyons, organised in submarine drainage basins (Bourillet and Lericolais, 2003).

The water column stratification in the Bay of Biscay predominantly shows that water masses are of North Atlantic origin (Pollard et al., 1996). The uppermost water mass is the Eastern North Atlantic Central Water (ENACW) which extends down to water depths of 600 m. The ENACW is characterised by a cyclonic gyre with an average velocity of 4 $cm.s^{-1}$ (Pingree and Le Cann, 1989). Below a minimal density layer, probably due to the influence of the Sub Antarctic Intermediate Water (SAIW), the Mediterranean Outflow Water (MOW) is observed down to 1500 m water depth. Its circulation as a contour current is conditioned by seafloor irregularities and the Coriolis effect. MOW velocities have been measured in the Bay of Biscay at 8ºW and 6ºW with average values of 2-3 $cm.s^{-1}$ (Pingree and Le Cann, 1989). Between 1500 and 3000 m water depth, the North Atlantic Deep Water (NADW) is observed. It includes a core of Labrador Sea Water (LSW), recognised by a salinity minimum at 1800 to 2000 m, and the Iceland-Scotland Overflow Water (ISOW) which is identified by a small salinity maximum around 2600 m (González-Pola, 2006; McCartney, 1992; McCave et al., 2001; Pingree, 1973). Below the NADW, the Lower Deep Water (LDW) is identified (McCartney, 1992). A cyclonic recirculation cell over the Biscay Abyssal Plain is recognised with a characteristic poleward velocity near the continental margin of 1.2 (± 1.0) $cm.s^{-1}$ (Dickson et al., 1985; Paillet and Mercier, 1997).

Along the slopes of the Bay of Biscay strong, localised internal tides are reported, due to a combination of favourable water mass stratification, steep topography and strong barotrophic tidal currents (Huthnance, 1995; Pingree and Le Cann, 1989, 1990). These may be channelled and result in regions of locally increased flow and local circulations (Pingree and Le Cann, 1990). Internal tides are proposed to explain the enhanced levels of surface phytoplankton abundance (Holligan et al., 1985; Pingree and Griffiths, 1982).

3. Materials and methods

3.1. Multibeam echosounding

The multibeam echosounder used during the BiSCOSYSTEMS cruise is a Kongsberg Simrad EM1002 system, installed permanently on the R/V Belgica. The EM1002 has up to 111 receiver beams of 2° (across track) x 3.3° (along track) width. The high-resolution depth data was obtained with a nominal frequency of 95 kHz and a ping-rate of 4 to 6 Hz. Survey speed was between 4 and 6 knots depending on water depth and wave conditions. In total, an area of 560 km² along the Armorican margin was mapped in water depths between 160 m and 1000 m (Fig.1B).

The bathymetric information of the recorded files was extracted as xyz-data with the open source MB-Systems software (Caress and Chayes, 1995). Next, data editing occurred in the IVS Fledermaus software package resulting in a digital terrain model (DTM) with a 5-m grid resolution.

3.2. CTD measurements

Two CTD casts (CTD 03: 46°51.990'N/5°31.768'W at 1450 m water depth and CTD 04: 46°54.536'N/5°21.262'W at 1250 m water depth) were obtained in the Guilvinec Canyon using a SBE Seacat 19 in order to gain insight into the local water mass stratification and to calibrate the EM1002 echosounder for sound velocity. The raw data were binned at 1 m using the SBE Data Processing software (version 7.18c).

3.3. ROV observations

The Remotely Operated Vehicle (ROV) 'Genesis' from Ghent University is a Sub-Atlantic Cherokee-type ROV with an operational survey depth down to 1600 m. Imagery was obtained from one forward-looking colour camera, recorded with and without a navigational overlay. High-resolution still images were obtained from a Canon Powershot camera. Two parallel laser beams with a distance of 10 cm were used as a scale during seabed observations. The ROV positioning was obtained using the USBL (Ultra Short Base Line) IXSEA GAPS positioning system. This allowed subsurface positioning with an accuracy of about 2-3 m. The processing and interpretation of the dives was performed using OFOP (Ocean Floor Observation Protocol) version 3.2.0c (Huetten and Greinert, 2008). Based on the observations, a number of facies characteristic for the study area were identified. Each facies was given a colour-code and integrated into ArcGIS 9.1, resulting in a facies interpretation map.

3.4. Sedimentological analyses of boxcore samples

Boxcores were taken at different locations within the Guilvinec Canyon. For each boxcore, subsamples from different depths (mostly one sample from the surface and one from the bottom) and/or subcores (if possible) were taken for sedimentological analysis. Each subcore was sampled every 5 cm. The location of boxcores B08-1305-bc and B08-1306-bc was accurately determined by using the GAPS USBL system.

Subsamples were analysed for grain-size distribution with a Malvern Mastersizer 2000 (Marine Biology Section, Ghent University). First, the sediment was dried in a furnace at 60° for about 48h. After subsampling 1 cm^3 of sediment, the carbonate fraction was removed by adding 75 ml of 10% acetic acid (CH_3COOH). This process was performed twice in order to remove all carbonate fragments. Afterwards, the sample was rinsed twice with distilled water, each time followed by a 24 h settling period. Finally, the sediment was transferred in a 15 ml centrifuge tube together with 0.2% calgon (sodium hexametaphosphate, $(NaPO_3)_6$). Prior to analysis, the samples were rotated (20 rpm) for 24h. Afterwards, the results were processed with GRADISTAT (Blott and Pye, 2001) and the mean grain-sizes were calculated using the Folk and Ward (1957) method.

Six cold-water coral specimens (*Lophelia pertusa*) from the surface of different boxcores (B08-1301-bc, B08-1305-bc and B08-1306-bc) were sampled for U/Th dating.

The U-series measurements and age determination were carried out in the Laboratoire des Sciences du Climat et de l'Environnement (LSCE) in Gif-sur-Yvette using inductively coupled plasma source mass spectrometry (Thermo-Fisher X-Series). Preparation of corals, analytical procedures and physical measurement routines followed the detailed description by Frank et al. (2004, 2005) and Douville et al. (in press).

4. Results

4.1. Environmental setting of the canyons and spurs

4.1.1. Geomorphology

The morphology of the canyon head and SE flank of the Penmarc'h Canyon, the Guilvinec Canyon and the NW flank and canyon head of the Odet Canyon was studied in detail using multibeam mapping (Fig.1B). These canyons are orientated in a NE-SW direction and are separated by two spurs: the Penmarc'h Bank and the Odet Spur.

The Penmarc'h Canyon is a slightly asymmetric V-shaped canyon with a maximum width of 10 km. The SE flank has an average slope of 10° and is incised by WNW-ESE orientated gullies with average slopes varying between 9-14° (Fig. 1B).

The Guilvinec Canyon is an asymmetric V-shaped canyon with a maximum width of 16 km. The NW slope has an average slope of 8° whereas the SE slope is characterised by an average slope of 6°. The total length of the canyon from the canyon head until the abyssal plain is about 33 km and the maximum incision depth is 2 km. The slopes flanking the canyons show ENE-WSW orientated gullies on the SE flanks with an average slope of 8-11° and NW-SE orientated gullies on the NW flanks with an average slope of 10°. The width of the gullies varies between 600 and 1000 m.

The Odet Canyon is also an asymmetric V-shaped canyon with a maximum width of 9 km. The NW flank of the Odet Canyon has a constant average slope of about 11°, compared to the SE flank where an abrupt change in slope occurs around 1000 m water depth. The NW slope of the Odet Canyon shows NW-SE orientated gullies with an average slope of 8-12°.

The Penmarc'h Bank is a narrow spur with a minimum width of 4 km which goes up to 10 km close to the canyon heads. In contrast the Odet Spur has a maximum width of 14 km. Along both spurs, NE-SW orientated gullies occur with an average slope of 8-13°. In the shallow area on the western part of the Odet Spur between 200 and 300 m water depth, small mounds were observed with a diameter of approximately 100 m and a height of 5 to 10 m.

4.1.2. Hydrography

The stratification of the water masses does not change significantly over the study area (Fig. 2). The CTD casts show the presence of a seasonal thermocline down to 50 m water depth. A salinity minimum (35.58 psu) is observed at 550 m, separating the overlying ENACW from the MOW, which has its salinity maximum (35.76 psu) at about 1000 m. Below, the T/S (temperature versus salinity) profile gradually follows the 27.75 $kg.m^{-3}$ potential density gradient towards the LSW and NADW, as shown in González-Pola (2006) and Van Rooij et al. (submitted-b).

4.2. Shallow-water coral rubble fields on Odet Spur

Mini mounds were observed on the multibeam echosounder data on Odet Spur in water depths of 260 to 350 m. The gentle slope features an average gradient of 3-4° (Fig. 1B). ROV observations allowed to distinguish four different facies: (1) rippled soft sediment with a patchy distribution of dead cold-water corals (Fig. 3A), (2) rippled seabed with biogenic debris and a patchy distribution of dead cold-water corals, (3) rippled soft sediment covered with gravel or small pebbles (Fig. 3B), and (4) a dense cold-water coral rubble coverage, dominated by *Lophelia pertusa* and/or *Madrepora oculata* (Fig. 3C and Fig. 3D).

Figure 4A shows that the small mounds are covered by dead cold-water coral rubble. At the base of the mounds and in between them, an alternation of rippled soft sediment with a patchy distribution of dead cold-water corals and/or biogenic debris, and rippled soft sediment with gravel-sized particles was observed (Fig. 3A and Fig. 3B). The coral rubble consists of crushed coral fragments (Fig. 3C and Fig. 3D) and nearly no visible living fauna. The size of the coral rubble fields varies between 20 to 80 m. The undulatory N-S to NNW-SSE orientated sand ripples appear with wavelengths between 5 and 10 cm and have heights of about 3-5 cm.

Boxcore samples were taken along the track of ROV dive B08-03 resulting in two different lithofacies (Fig. 4B). Lithofacies 1 is characterised by olive brown to olive grey poorly-sorted, fine to medium sand with mean grain-sizes varying between 215 µm and 305 µm. Within this facies in boxcore B08-1302-bc fine laminations are observed between olive brown and olive grey sand. In contrast, a clear colour change is observed in boxcore B08-1305-bc at a depth of 5 cm. In boxcore B08-1303-bc, on top of a mini mound (Fig. 4A), only a very thin layer of lithofacies 1 is observed. The surface of all boxcores is covered with coarse biogenic debris and several *Lophelia pertusa* fragments (1-4 cm), up to 5 cm depth. At the surface of boxcore B08-1303 also large gravel fragments (up to 7 cm) were observed. Lithofacies 2 is characterised by olive grey very poorly to poorly-sorted, medium silt with grain-sizes varying between 8.9 µm and 12.6 µm. Within this unit black sediment spots, supposedly caused by reducing geochemical conditions, were observed. In boxcore B08-1303-bc a few sand lenses occur between 5 and 10 cm depth.

Boxcore B08-1304-bc had a penetration of only 5 cm (no subcoring). It consists of olive grey, well sorted sand (lithofacies 1) with coarse biogenic debris and robust coral fragments of *Lophelia pertusa* (several cm).

In addition, several coral fragments were dated using U-series: two coral fragments (*Lophelia pertusa*) were collected during ROV dive B08-03, one coral fragment (*Lophelia pertusa*) in boxcore B08-1301-bc and two coral fragments in B08-1305-bc. The resulting ages after correction are shown in Table 3.

4.3. Deep-water corals in the Penmarc'h and Guilvinec Canyons

The second setting features cold-water corals observed in the Penmarc'h and Guilvinec Canyons in water depths of 700 to 900 m. Both living and dead coral specimens occur, predominantly *Madrepora oculata*. In total, eleven different facies were defined during four ROV dives (Table 1). Facies 1 and 2 correspond to respectively even (Fig. 5A) and rippled soft sediment with at some locations intense bioturbation. Facies 3 and 4 correspond to respectively even and rippled soft sediment covered with a patchy distribution of cold-water corals (mostly *Madrepora oculata*) (Fig. 5B). Living as well as dead species occur. Soft sediment with a cover of biogenic debris was defined as facies 5 (Fig. 5C). No ripple marks were observed. Facies 6 and 7 are characterised by respectively even and rippled soft sediment covered with biogenic debris and a patchy distribution of cold-water corals (dead and living *Madrepora oculata*). Next, facies 8 consists of soft sediment with gravel (Fig. 5D). The gravel fragments reach sizes up to 10 cm. Facies 9 corresponds with outcropping hard substratum (Fig. 5E and Fig. 5F), colonised by living cold-water corals (*Madrepora oculata*) and sponges. At some locations, cracks filled with soft sediment were observed (Fig. 5G and Fig. 5H). Finally, facies 10 and 11 relate to the cold-water coral coverage. Facies 10 is characterised by a dense coverage of coral rubble (Fig. 6A) whereas facies 11 also features living species of *Madrepora oculata* and *Lophelia pertusa* on top of the coral rubble, creating dense coral fields (Fig. 6B, Fig. 6C and Fig. 6D). Facies 11 often coincides with a very rough seafloor and big boulders (20 cm up to 1 m). Boxcore B08-1306-bc was taken within this facies which delivered three coral pieces for U-series dating (Table 3). Grain-size analysis reveals very poorly sorted fine sand with a mean grain-size of 81 µm.

Four ROV dives were undertaken. Dive B08-01 is located on the SE flank of the Penmarc'h Canyon in water depths of 385 to 750 m. During this dive, an E-W downslope transect was made with an average slope gradient of 8-10°. A large part of the track consists of soft sediment with gravel (facies 8). At a water depth of 530 m the gravel disappears and strongly bioturbated soft sediment (facies 1) remains until a water depth of 720 m (Fig. 5A). Below 720 m, the first cold-water corals (facies 3) (*Lophelia pertusa* and *Madrepora oculata*), with a size of 10-20 cm width and about 15 cm high, appear on boulders with a diameter of 25 cm. Except for one living *Madrepora oculata*, all corals are dead.

Dive B08-02 on the NW flank of the Guilvinec Canyon has a U-shaped track starting with a first transect southwards from the NE flank of a gully at 712 m water depth and ending with a second transect on the SW flank of that gully. The slope of this part features an average gradient of 11°. During this dive many different facies were observed (Fig. 7). In the uppermost part of the slope, between 700 and 900 m, soft sediment alternates with coral fields which vary in diameter between 10 and 60 m (Fig. 6B). The soft sediment is sometimes covered with biogenic debris (Fig. 5C), gravel (Fig. 5D) and/or a patchy distribution of cold-water corals, mostly *Madrepora oculata*. Also big boulders with a diameter up to 1 m were observed, colonised with living cold-water corals (*Madrepora oculata*) and *Hexadella sp.* sponges (Fig. 6E and Fig. 6F). Between 800 and 900 m, asymmetric N-S orientated sand ripples appear with wavelengths between 10 and 20 cm and with heights of about 5 cm. Below 900 m water depth, mostly hard substratum (Fig. 5E and Fig. 5F) occurs with a patchy distribution of living cold-water corals (*Madrepora oculata*). NW-SE orientated cracks of 5 cm up to 40 cm occur in this area, and are filled with (rippled) soft sediment (Fig. 5G and Fig. 5H). At several locations, the rather smoothly sloping seabed is interrupted by the presence of small banks (Fig. 6G) or cliffs (Fig. 6H). Between 700 and 750 m water depth, these escarpments have an E-W orientation, while the deeper ones reveal a S-N or SSW-NNE orientation. The banks are generally few decimetres in height and thus much smaller than the cliffs, which vary in height between 2 and 4 m. At three locations, the escarpments are colonised by *Madrepora oculata* corals and *Neopycnodonte zibrowii* oysters, which are discussed in more detail in Van Rooij et al. (submitted-a).

Dive B08-04 is located on a small spur with dimensions of 200 by 400 m on the SE flank of the Guilvinec Canyon in water depths of 675 to 700 m. Only one facies was recognised: a dense cold-water coral coverage with dead and living species, predominantly *Madrepora oculata* (Fig. 6C and Fig. 6D). The living species grow on the dead coral rubble, which is built up by chunky coral fragments up to 40 cm.

Finally, dive B08-05 investigated the southern shoulder of a gully south of the spur that separates the Penmarc'h Canyon from the Guilvinec Canyon. The track follows a southern to western course between 300 and 750 m water depth with an overall slope gradient of 8-10°. This track does not show many different facies. Between 300 and 450 m a rippled seafloor with regionally some biogenic debris and/or gravel was observed.

The straight to gently undulatory SSE-NNW orientated sand ripples have a wavelength between 10 and 15 cm. The area between 450 and 730 m is characterised by soft sediment with bioturbations and a zone of low-relief rippled seabed. Close to a water depth of 480 m, some small escarpments are present. At 735 m, the gently dipping seafloor is interrupted by a 4 m high WSW-ENE escarpment, colonised by *Madrepora oculata* cold-water corals and *Neopycnodonte zibrowii* oysters (Van Rooij et al., submitted-a).

5. Discussion

5.1. Canyons as cold-water coral habitats

For the first time a cold-water coral habitat is mapped in detail within a canyon setting in the Bay of Biscay. Although deep-sea canyons may provide suitable environmental conditions for cold-water corals to grow, resulting deep-water habitats have not yet been described in detail. Canyons are transport ways of organic matter from the continental shelf down to the abyssal plain (Canals et al., 2006; Freiwald et al., 2004). During most of the ROV dives described here, an intense marine snow was observed, composed of suspended particulate material, ideal nutrients for scleractinians. In addition, the cold-water corals occur just above, in case of the shallow water setting, and just beneath, in case of the deep-water setting, the physical boundary between the Eastern North Atlantic Central Water (ENACW) and the Mediterranean Outflow Water (MOW) (Fig. 2). As De Stigter et al. (2007) already demonstrated, the mixing of both water masses results in enhanced suspended material thus favouring the feeding of scleractinians.

Moreover, the observations of ripple marks on the seabed, within the upper zone of the MOW, indicate the presence of an E-W bottom current with a speed around 10 to 40 $cm.s^{-1}$ (Stow et al., 2009). This elevated bottom current is beneficial for coral growth as it delivers nutrients to the polyps. Additionally, the asymmetry of the sand ripples shows a sediment transport direction away from the shelf edge into the canyon axis. Similar observations were made by Cunningham et al. (2005) in the canyons on the Celtic Margin between Goban Spur and Brenot Spur. Apart from the flow velocity of the MOW, the bottom currents may be enhanced by strong internal tides (White, 2007). Next to a favourable oceanographic environment, the sedimentological environment of deep-sea canyons provides hard substrates for living cold-water corals to settle on. Indeed, during the ROV dives, corals were observed on cliffs, outcropping hard substratum and on the numerous boulders which are scattered on the seabed. The dives also revealed a preferential erosion of the western flank of the canyons while the eastern flank is draped with soft sediment. This is attributed to the strong E-W bottom currents. The western slope will act as an obstacle for these enhanced currents intensifying the easterly bottom currents through isopycnal doming, which results in erosion (Hernandez-Molina et al., 2003; Iorga and Lozier, 1999; Van Rooij et al., submitted-a). Hence, the constant reworking by downslope (turbiditic) and alongslope (contouritic) current processes (Arzola et al., 2008; Bourillet et al., 2006b; Cunningham et al., 2005; Pingree and Le Cann, 1989; Toucanne et al., 2009) which occur along this slope will play an important role in the shaping of habitats suitable for coral settlement. This study indicates that canyons are perfectly suited for coral growth due to the food availability, strong bottom currents and the presence of hard substratum. More coral habitats might be discovered in a similar setting in the future.

5.2. Mini mounds on Odet Spur

The shallow area, located in water depths between 278 and 289 m, revealed a dense coverage of dead cold-water coral fragments on top of mini mounds and small ridges (Fig. 4A). Within the boxcores, cold-water coral fragments were only found in the uppermost 5 cm which suggests that these mini mounds were present before the settling of the cold-water corals. The fact that the boxcores only show a thin sand cover (1.5 cm) on top of the mini mound while at the base of the mound the sand cover increases to 11 cm, these mini mounds and ridges are probably the result of selective erosion of the clayey substrate due to strong bottom currents during interglacials and interstadials, as observed by Øvrebø et al. (2006) offshore Ireland. This observation highlights the importance of an elevated topography which acts as a template for coral settlement (Freiwald et al., 2004; Roberts et al., 2006). The lack of coral fragments deeper in the sediment of the mini mounds is a fundamental difference with the giant coral mounds observed along the Irish margin which are completely constructed by corals (Kano et al., 2007). In that aspect, the mini mounds on Odet Spur reveal strong similarities with the Darwin mounds in the northern Rockall Trough. The size of the coral topped Darwin mounds is similar (height: 5 m / diameter: 75 m) but they are located in a deeper water depth (1000 m). Coring revealed that corals are not a major contributor to mound building (Masson et al., 2003). The Moira mounds in the Porcupine Seabight which are characterised by diameters of 30-50 m and heights up to 5 m (Foubert et al., 2005; Wheeler et al., 2005) might also serve as an analogue for the mounds observed on Odet Spur.

5.3. Time and distribution of coral growth

The dating of the cold-water corals using U-series reveals that coral growth in the study area started at the beginning of the Holocene. The older age of the corals in the shallow (7.4-9.1 ka) compared to the deeper setting (1.2-2.3 ka) indicates a migration of the coral habitats towards greater water depths. Moreover, the fact that the corals observed in the shallow water setting are heavily bio-eroded and disintegrated, demonstrates that they are already exposed on the seabed for a significant amount of time. In contrast, the corals in the deeper setting are much better preserved suggesting a younger age for these species. The cause of the downslope migration of the corals is still uncertain. However, the changing sea level, influencing labile organic matter fluxes (Hall and McCave, 1998), and the rising temperatures, might have forced corals to deeper water depths, where they found better live conditions. A more dramatic hypothesis is that the shallow coral reefs were destroyed by bottom trawling since the shallower area is subject to intense fishing activity (Bourillet et al., 2006a). According to Hily et al. (2008), a great change has been observed in the benthic communities in the northern part of the Bay of Biscay since the 1960s due to bottom trawling. Bottom trawling could also explain the age difference between sample B08-03 C, with an age of 1.41 ± 0.17 ka, and the other samples with ages over 7 ka (Table 3). Due to the reworking effect of trawling, most of the coral reefs are turned upside down. However, no trawl marks were observed within the shallow water area during the ROV dive.

On a more regional scale, the U-series datings of the corals confirm a climate-driven influence. Since the Late Glacial Maximum (about 11.5 ka BP), extended living cold-water coral reefs appear along the European margin between 50° and 70° N (Frank et al., 2009). In contrast, during glacial times, the cold-water corals were only able to survive in the relatively more temperate Atlantic below 50° N (Frank et al., submitted). At present, only scarce coral occurrences are observed south of 50°N (Reveillaud et al., 2008; Wienberg et al., 2009), which is also confirmed by the results presented in this paper. The northern part of the Bay of Biscay, and more specifically the Armorican margin, can be seen as a transition zone between the eastern temperate Atlantic and the eastern North Atlantic between 50° and 70° N. This might explain why no successive mound growth occurred in the Bay of Biscay, resulting in the build up of giant coral mounds as discovered in the Porcupine Seabight (De Mol et al., 2002; Dorschel et al., 2007; Henriet et al., 1998; Huvenne et al., 2007, 2009; Wheeler et al., 2005) and the Rockall Trough (De Haas et al., 2009; Kenyon et al., 2003; Mienis et al., 2006; Van Weering et al., 2003).

5.4. Relation between potential density and cold-water coral occurrence

The results of the present study may add to the theory of Dullo et al. (2008) who concluded that the potential density (σ_Θ = sigma-theta), where cold-water corals are able to live and migrate along the Norwegian margin and in the Porcupine Seabight, needs to be between 27.35 and 27.65 $kg.m^{-3}$. The deeper canyon setting, where living cold-water corals have been observed, is located in this density range (27.35 and 27.55 $kg.m^{-3}$) (Fig.2) and thus supports the results of Dullo et al. (2008). In contrast, the dead shallow water corals fall within a density range of 27.15-27.20 kg.m^{-3} which is slightly outside the density range where living cold-water corals normally occur. This finding demonstrates that the density range of 27.35 and 27.65 kg.m^{-3} is also valid for the living cold-water corals in the Bay of Biscay. In addition, our results confirm that this density range is not only applicable for dense living *Lophelia pertusa* reefs but also accounts in this setting for living *Madrepora oculata* species.

6. Conclusions

Cold-water coral habitats along the Gascogne margin in the Bay of Biscay, earlier reported by Le Danois in 1948, were investigated. The R/V Belgica BiSCOSYSTEMS cruise was set out to better understand the significance and distribution of these cold-water coral ecosystems and the environmental controls on their living habitat.

The main conclusions are:

- Deep-sea canyons such as the Penmarc'h and Guilvinec Canyons are suitable habitats for the settlement of cold-water corals (*Madrepora oculata* and *Lophelia pertusa*).
- Two cold-water coral settings were distinguished within the canyons: a shallow setting in water depths of 280-290 m with only dead coral rubble (mostly *Lophelia pertusa*) and a deep-water setting (700-920 m) with mostly living *Madrepora oculata* species on top of coral rubble. The occurrence of the mini mounds at ~280 m water depth is an unusually shallow water depth compared to most other cold-water coral (reef) occurrences along the NE Atlantic margin.

- The Bay of Biscay can be considered as a transition zone between the temperate Atlantic (below 50°N) and the cold north-eastern Atlantic between 50° and 70°N. After the Late Glacial Maximum, cold-water corals started to grow along the Armorican margin but migrated likely during the mid Holocene to deeper water depths.
- The density range of 27.35 to 27.65 $kg.m^{-3}$ (Dullo et al., 2008) is also valid for the living cold-water corals (mostly *Madrepora oculata*) in the Bay of Biscay, which makes it a good prerequisite for the distribution and growth of living cold-water corals along the northeast Atlantic margin. It can be used as a predictive tool in order to discover more cold-water coral habitats along the European continental margin.

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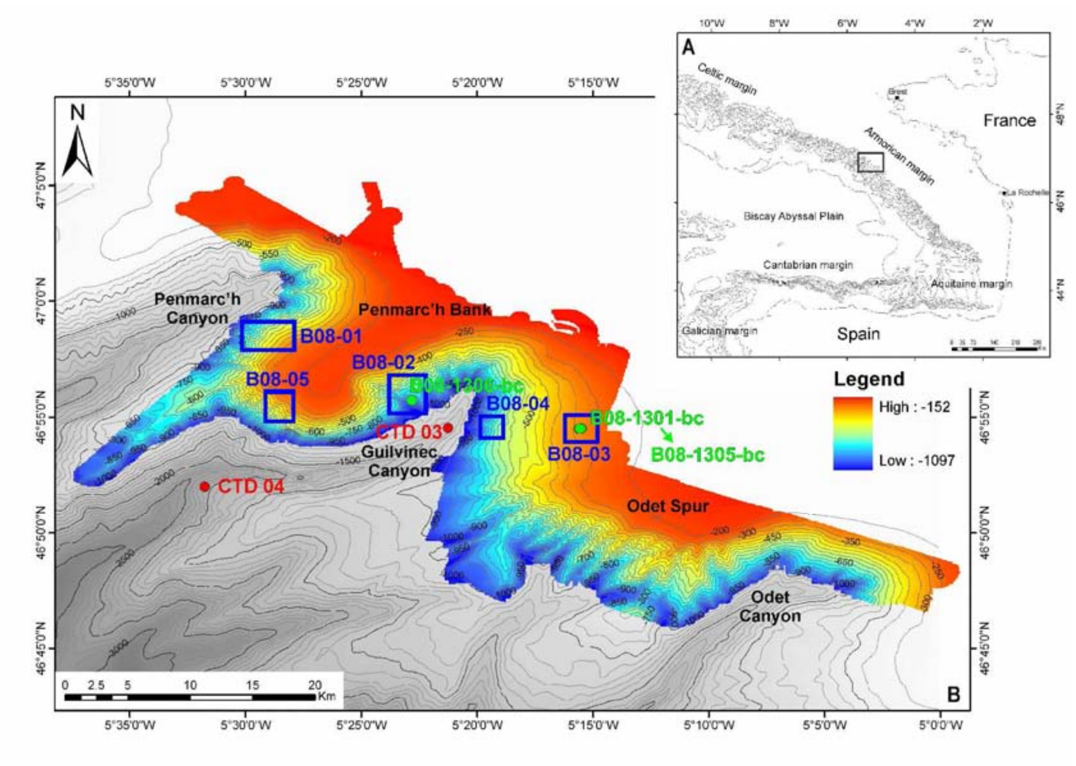
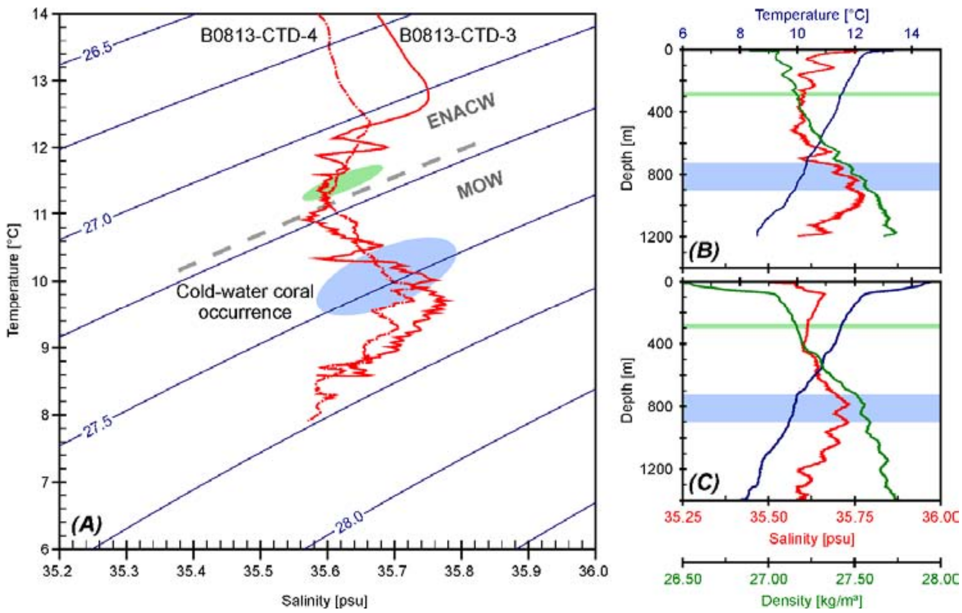
Figures

Figure 1.



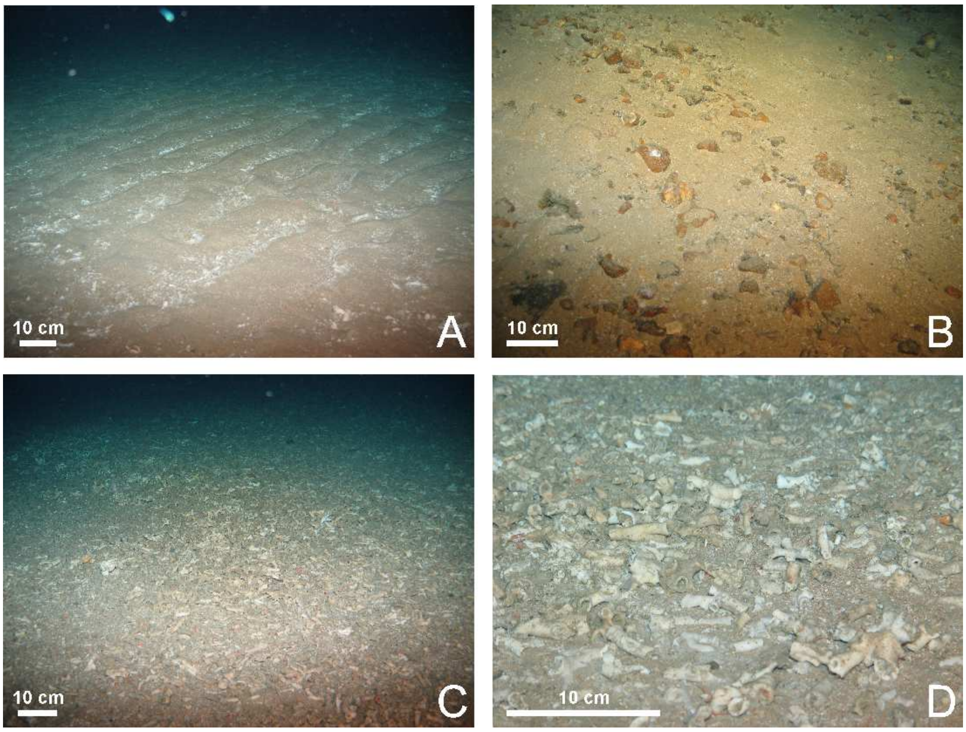
(A) Location of the study area along the French Atlantic continental margin (GEBCO bathymetry, contour lines every 500 m), (B) Detail of the study area with EM1002 bathymetry (contour lines every 50 m) and the location of the CTD casts (red), ROV dives (blue) and boxcores (green), collected during the R/V Belgica BiSCOSYSTEMS cruise (2008). As background a bathymetric map of IFREMER (Normand and Mazé, 2000) is used (contour lines every 100 m).

Figure 2.



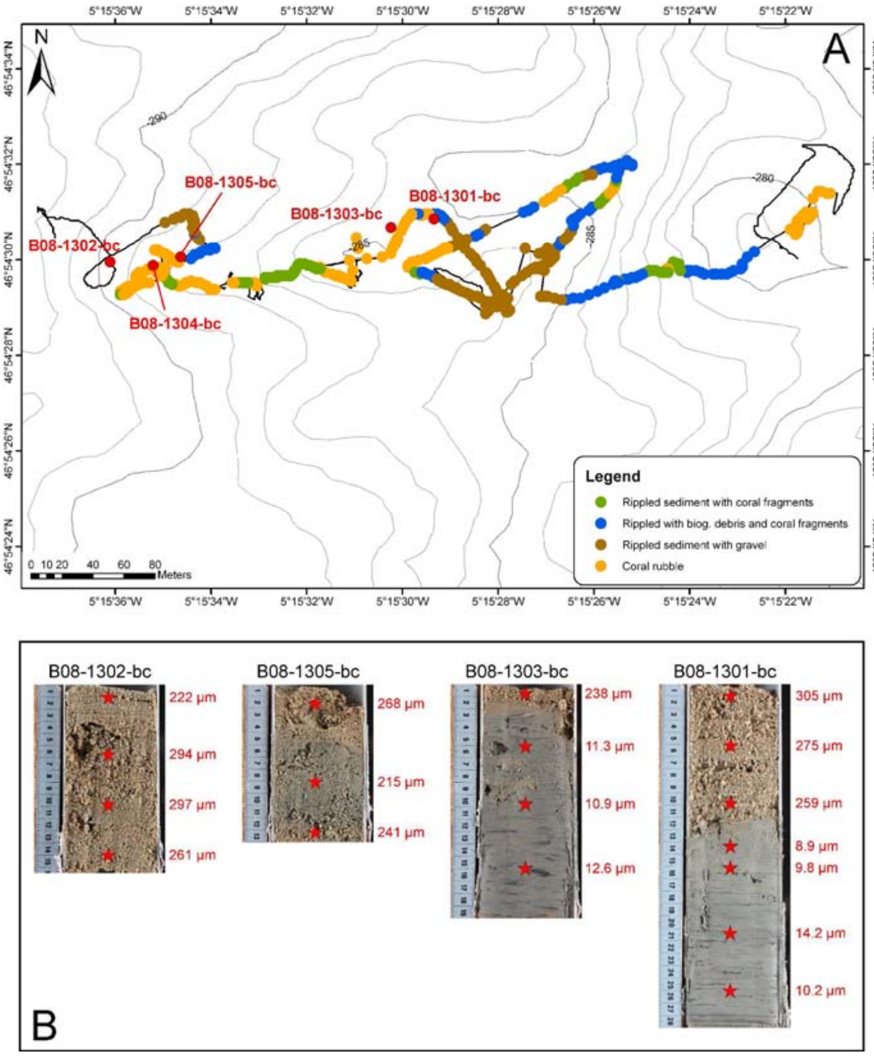
Hydrographic data of the Guilvinec Canyon. (A) Temperature/salinity plot for both CTD casts, with indication of the boundary (dashed grey line) between the Eastern North Atlantic Central Water (ENACW) and the Mediterranean Outflow Water (MOW). The estimated occurrence envelope of the shallow-water (green) and deep-water (blue) cold-water corals in the Penmarc'h and Guilvinec Canyons is based on the ROV observations, plotted on the CTD data of respectively (B) cast B0813-CTD-3 and (C) cast B0813-CTD-4.

Figure 3.



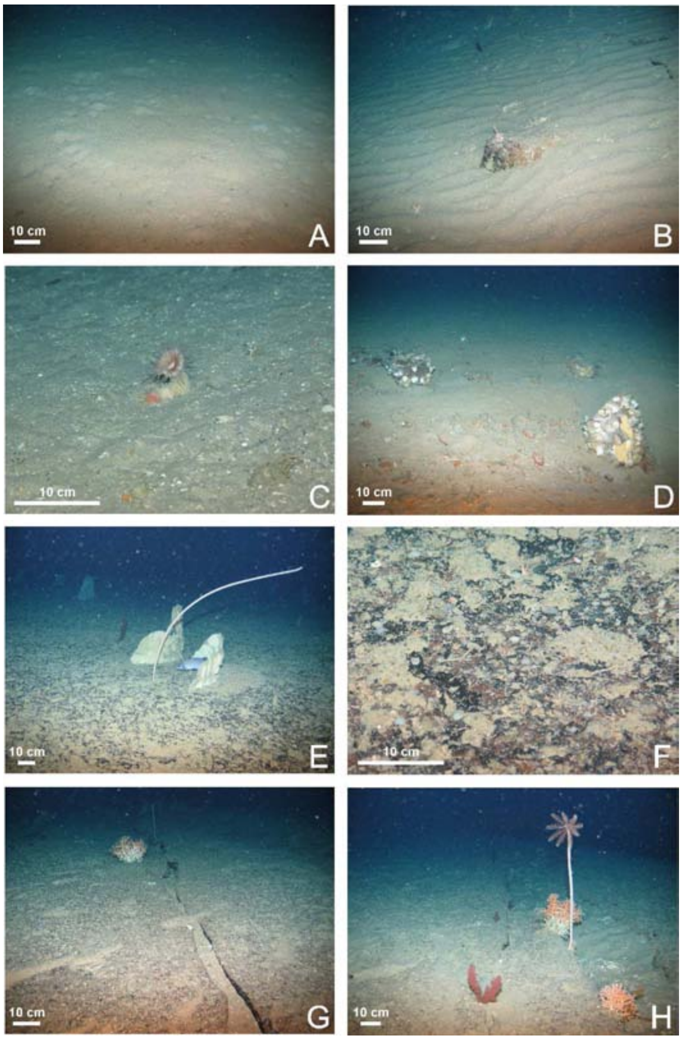
ROV images from the shallow-water setting (ROV dive B08-03): (A) rippled seabed with a patchy distribution of cold-water corals, (B) coarse sand with a high amount of gravel, (C) the dense cold-water coral rubble coverage on top of the small mounds, and (D) zoom in this coral rubble facies with predominantly *Lophelia pertusa*.

Figure 4.



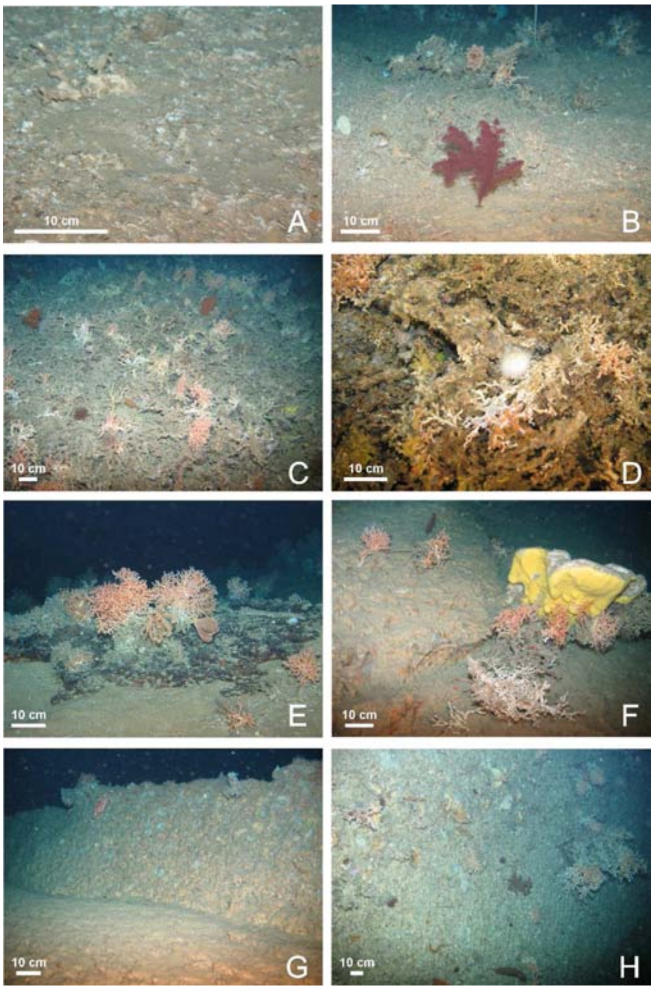
(A) Facies interpretation map of the shallow-water dive B08-03 on the southeastern flank of the Guilvinec Canyon in water depths between 278 and 289 m. (B) Photographs of the obtained boxcores in the shallow water area with the locations and mean grain-size values.

Figure 5.



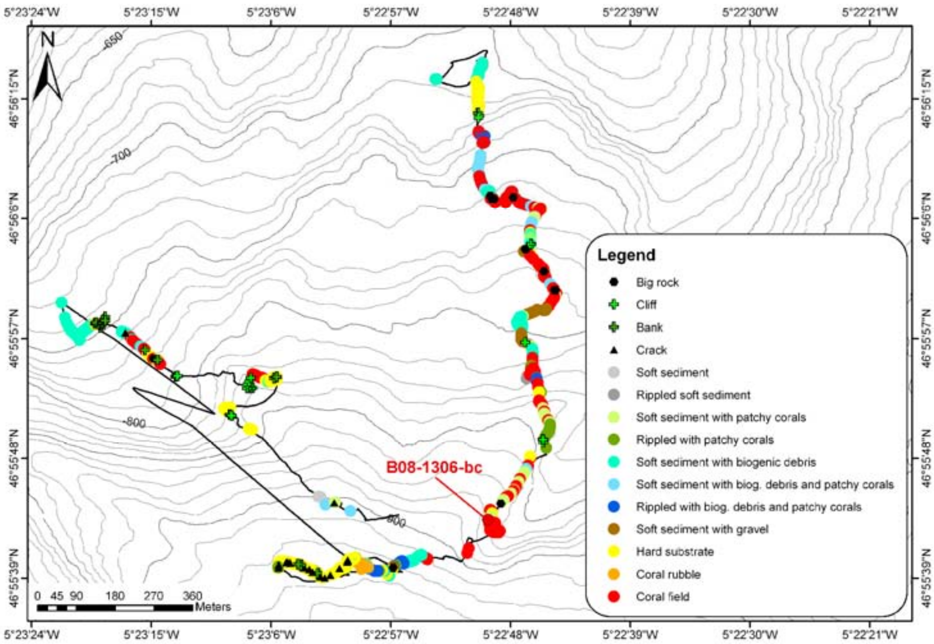
ROV stills imagery highlighting the most important facies and associated fauna in the deep-water setting: (A) soft sediment with bioturbations; (B) rippled soft sediment with gravel; (C) a seabed covered with biogenic debris; (D) soft sediment with a patchy distribution of gravel; (E) hard substrate with a patchy distribution of cold-water corals, sponges and a sea urchin; (F) zoom on the hard substrate; (G) hard substrate with a large crack and one *Madrepora oculata* species; (H) hard substrate with a crack filled up with rippled soft sediment, colonised by a crinoid and a few living *Madrepora oculata* corals.

Figure 6.



ROV stills imagery highlighting the different types of cold-water coral occurrences in the deep-water coral setting: (A) rippled seabed with coral rubble and biogenic debris; (B) example of a coral field with living and dead coral species; (C) a dense cold-water coral coverage with both living and dead species; (D) detailed zoom on the facies mentioned in A; (E) outcropping hard substratum with a few living coral species (*Madrepora oculata*) and Gorgonians; (F) outcropping hard substratum with the sponges *Geodia sp.* and *Topsentia sp.*, and again living and dead *Madrepora oculata* specimens; (G) a small bank with a height of 50 cm colonised by oysters and a few living coral species; (H) a vertical cliff colonised with oysters and living *Madrepora oculata*.

Figure 7.



Facies interpretation map of ROV dive B08-02 on the northwestern flank of the Guilvinec Canyon in water depths of 712 to 900 m.

Tables

Table 1. Names, locations and operational data of the ROV Genesis dives. Time in UTC.

Name	Area	Start track		End track	
		Time	Depth	Time	Depth
B08-01	South flank of Penmarc'h canyon	13:16:02	385 m	16:47:44	699 m
B08-02	North flank of Guilvinec canyon	11:24:46	712 m	15:46:00	900 m
B08-03	South flank of Guilvinec canyon: small mounds/ridges on the top	12:29:41	278 m	14:05:25	289 m
B08-04	Spur, south flank of Guilvinec canyon	15:51:10	676 m	16:38:51	691 m
B08-05	North flank of Guilvinec canyon	11:17:00	305 m	14:27:53	529 m

Table 2. Location, water depth and recovery length of the studied boxcores.

Core number	Latitude	Longitude	Water Depth	Recovery
B08-1301-bc	46°54.514' N	5°15.489' W	285 m	31 cm
B08-1302-bc	46°54.499' N	5°15.602' W	290 m	17 cm
B08-1303-bc	46°54.511' N	5°15.504' W	285 m	20 cm
B08-1304-bc	46°54.498' N	5°15.587' W	288 m	5 cm
B08-1305-bc	46°54.501' N	5°15.577' W	288 m	14 cm
B08-1306-bc	46°55.723' N	5°22.828' W	866 m	10-15 cm

Table 3. Overview of the U-series datings in the shallow water setting (left) and the deep-water setting (right).

Shallow water setting			Deep-water setting		
Sample name	Age (ka)	Error (ka)	Sample name	Age (ka)	Error (ka)
B08-1301-bc	7.35	0.45	B08-1306-bc A	1.32	0.52
B08-1305-bc A	7.78	0.71	B08-1306-bc B	1.21	0.13
B08-1305-bc A	9.07	0.25	B08-1306-bc C	2.27	0.30
B08-03 B	8.89	0.31			
B08-03 C	1.41	0.17			