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Environmental setting of deep-water oysters in the Bay of Biscay

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Abstract :

We report the northernmost and deepest known occurrence of deep-water pycnodontine oysters, based on two surveys along the French Atlantic continental margin to the La Chapelle continental slope (2006) and the Guilvinec Canyon (2008). The combined use of multibeam bathymetry, seismic profiling, CTD casts and a remotely operated vehicle (ROV) made it possible to describe the physical habitat and to assess the oceanographic control for the recently described species *Neopycnodonte zibrowii*. These oysters have been observed in vivo in depths from 540 to 846 m, colonizing overhanging banks or escarpments protruding from steep canyon flanks. Especially in the Bay of Biscay, such physical habitats may only be observed within canyons, where they are created by both long-term turbiditic and contouritic processes. Frequent observations of sand ripples on the seabed indicate the presence of a steady, but enhanced bottom current of about 40 cm/s. The occurrence of oysters also coincides with the interface between the Eastern North Atlantic Water and the Mediterranean Outflow Water. A combination of this water mass mixing, internal tide generation and a strong primary surface productivity may generate an enhanced nutrient flux, which is funnelled through the canyon. When the ideal environmental conditions are met, up to 100 individuals per m² may be observed. These deep-water oysters require a vertical habitat, which is often incompatible with the requirements of other sessile organisms, and are only sparsely distributed along the continental margins. The discovery of these giant oyster banks illustrates the rich biodiversity of deep-sea canyons and their underestimation as true ecosystem hotspots.

Research Highlights

►*Neopycnodonte zibrowii* oysters occur in a bathymetric range between 350 and 846 m. ►*N. zibrowii* habitat requires steep slopes with overhanging banks and escarpments. ►This underestimated deep-water community occurs almost exclusively in canyons. ►Suitable habitats created by interplay between turbiditic and contouritic processes.

Keywords : Bay of Biscay ; Deep-water oysters ; Canyons ; Habitat ; Resuspension ; MOW ; *Neopycnodonte zibrowii*

1. Introduction

Ocean margins are dynamic environments which host valuable deep-water benthic ecosystems. Along the Eastern Atlantic margin from Morocco to Norway, several „dæp-water ecosystem hotspots' have been identified in association with a complex interplay of oceanography, geology, seabed morphology, sediment and nutrient supply (Weaver and Gunn, 2009). Cold-water coral reefs and canyon environments are receiving particularly close attention (Arzola et al., 2008; Canals et al., 2006; De Mol et al., accepted; de Stigter et al., 2007; Dorschel et al., 2009; Mienis et al., 2007; Palanques et al., 2009; Wienberg et al., 2009). Cold-water coral occurrences have been identified over virtually the entire European margin and their reefs feature a high biodiversity (Freiwald et al., 2004; Reveillaud et al., 2008; Roberts et al., 2006). They belong to the Earth's most precious and endangered ecosystems, threatened by fisheries and ocean acidification (Freiwald et al., 2004; Halpern et al., 2008; IPCC, 2007; Roberts et al., 2006). The main driver for this ecosystem is a carefully balanced hydrodynamic environment controlling sediment and nutrient supply (Dorschel et al., 2009; Mienis et al., 2007; Roberts et al., 2006). Canyons play a critical role since they are the most important mechanism of nutrient input into the deep marine environment (Canals et al., 2006; de Stigter et al., 2007; Duineveld et al., 2001; Palanques et al., 2009). Moreover, due to frequent incisions during glacial sea-level lowstands (Bourillet et al., 2006; Cunningham et al., 2005; Toucanne et al., 2009; Zaragosi et al., 2000), the eroded canyon flanks may offer a peculiar environment which is beneficial for settling of sessile organisms since they profit from the enhanced nutrient flux. Already in the late 19th and the mid-20th century fisheries research had demonstrated the presence of cold-water corals in the vicinity of the canyons in the northern Bay of Biscay (Reveillaud et

al., 2008). A first mapping and description of these *Massifs coralliens* (Fig. 1) was published by Le Danois (1948). Sporadically, scientists and fishermen also reported dredged oysters from this part of the margin, which was not given the appropriate attention at that time. Oysters are commonly referred to as typical shallow-water and occasionally reef-forming molluscs, but a number of samples have also been recovered from the deeper realm (Wisshak et al., 2009a). The existence of the deep-water oyster *Neopycnodonte zibrowii* was formally described in Wisshak et al. (2009a) based on submersible observations and sampling in the Azores archipelago between 2002 and 2007.

In this paper, we report and describe the physical and oceanographic setting of the northernmost and deepest occurrence of *Neopycnodonte zibrowii* oysters within two canyons along the French Atlantic margin (Fig. 1). Seabed observations with the Remotely Operated Vehicle (ROV) *Genesis* resulted in the discovery of giant deep-water oyster banks and cliffs in depths between 540 to 846 m (Table 1). These observations were performed with R/V Belgica during the HERMES Geo cruise in June 2006 (La Chapelle continental slope) and the BiSCOSYSTEMS cruise in June 2008 (Guilvinec canyon). The observed spatial distribution of the molluscs in relation to the slope morphology and local hydrographic regime gives an insight in the habitat requirements of this new species. This will be compared to the habitat requirements of another successful reef-forming organism: scleractinian cold-water corals.

2. Regional setting

The NE Atlantic continental margin in the Bay of Biscay can be divided in five main areas: the Celtic and the Armorican margin in the north, and the Aquitaine, Cantabrian and Galician margin in the south (Fig. 1). The morphology of the continental slope is characterized by spurs and canyons, organized in drainage basins and actively feeding the Celtic, Armorican and Cap Ferret deep-sea fans (Bourillet et al., 2003; Zaragosi et al., 2000). However, between the Delesse (47°N) and Conti Spur (45°N), no significant deep-sea fans are observed at the mouth of the lower (southern) valleys; only small channel-levee complexes, slumps and small lobes are present (Bourillet et al., 2006).

Most of the water masses in the Bay of Biscay are of North Atlantic origin (Pollard *et al.*, 1996). The uppermost water mass is the Eastern North Atlantic (Central) Water (ENAW), which extends to depths of about 400 to 600 m. Although this water mass has a salinity of 35.6, according to Pollard et al. (1996) there is a core of low density water around 500 m water depth due to the lateral influence of the Subarctic Intermediate Water (SAIW). Between 400 to 500 m and 1500 m water depth, the Mediterranean Outflow Water (MOW) follows the continental slope as a contour current. Its circulation is conditioned by seafloor irregularities and the Coriolis effect. MOW velocities have been measured in the Bay of Biscay at 8ºW and 6ºW with minimum values of 2-3 cm/s. Iorga and Lozier (1999) show that the MOW splits into two branches as it passes Galicia Bank, and turns into the Bay of Biscay as a cyclonic recirculation. Low salinity values observed on the Armorican continental slope may reflect a depletion of the MOW core (Van Aken, 2000). Between 1500 and 3000 m water depth the North Atlantic Deep Water (NADW) is recognized. It includes a core of the Labrador Sea Water (LSW) at a depth of about 1800 m down to 2000 m

(McCartney, 1992; McCave et al., 2001; Vangriesheim and Khripounoff, 1990). Below the NADW, the Lower Deep Water is identified, which mainly seems to result from the mixing of the deep Antarctic Bottom Water and the Labrador Deep Water (Botas et al., 1989; Haynes and Barton, 1990; Pingree and Le Cann, 1992; Van Aken, 2000).

Along the slopes of the Bay of Biscay strong, localized internal tides are reported, resulting from a combination of favourable water mass stratification, steep topography and strong barotropic tidal currents (Huthnance, 1995; Pairaud et al., 2008; Pingree and Le Cann, 1989, 1990). As the slope is intersected with canyons, these tidally induced transports may be channelled and result in regions of locally increased flow and local circulations (Pingree and Le Cann, 1990). A dominant effect caused by internal tides from the upper slope is proposed to explain the enhanced levels of surface phytoplankton abundance (Holligan et al., 1985; Pingree et al., 1982).

3. Material and methods

The data for this study was acquired during two R/V Belgica expeditions in the Bay of Biscay. A first cruise, HERMES Geo, focussed during only 3 days in June 2006 on the La Chapelle continental slope (Fig. 1b). In June 2008, the BiSCOSYSTEMS cruise surveyed the vicinity of the Guilvinec Canyon (Fig. 1c). During both cruises a geophysical survey (multibeam bathymetry and seismic profiling) and CTD profiling (Fig. 2) preceded the ROV observations.

3.1 Geophysical survey

Initial swath bathymetry coverage of both study areas was performed using the R/V Belgica hull-mounted SIMRAD EM1002 multibeam echosounder. On the La Chapelle continental slope, an area of 71.7 km² was mapped in water depths ranging from 200 to 950 m (Fig. 1b) and processed using the IFREMER CARAIBES software. In 2008, an area of 584 km² was mapped around the Guilvinec canyon in water depths ranging from 180 to 1000 m (Fig. 1c). The 2008 dataset was processed using MB-Systems and IVS Fledermaus software. Both datasets were gridded to a cell size of 20 by 20 m and visualized using GMT version 4.2 (Wessel and Smith, 1991).

In order to obtain insight in the sedimentary processes and the thickness of the sediment cover, single channel seismic profiles were acquired using a SIG sparker source at a velocity of 3 knots (Figs. 1c and 3). The source was triggered every 3 s, reaching 500 J energy. The vertical resolution of the profiles varies between 1 and 2 m. A basic processing (band-pass filtering, automatic gain control) was applied using PROMAX software.

3.2 Water mass characterization

At both sites, information regarding the water mass stratification was obtained using a SEACAT SBE 19 CTD down to water depths of about 1400 m (Table 2, Fig. 2). The raw data was binned at 1 m using SBE Data Processing (version 7.16a). The obtained temperature (°C), salinity and potential density (sigma-theta, kg/m^3) were used to identify the water masses and to indicate the relationship between deep-water oyster occurrence and hydrography (Fig. 2).

3.3 ROV observations

The ROV observations (Table 1, video files as online supplementary material) were performed using Ghent University's ROV *Genesis*, a Sub Atlantic Cherokee type ROV with a Tethered Management System (TMS) allowing investigations down to 1400 m water depth. The underwater positioning was obtained using an IXSEA GAPS USBL system, allowing an accuracy in the order of 2 m. Seafloor observations were made by means of a forward-looking colour zoom and black & white video camera, assisted by > 250 Watt Q-LED illumination. A laser marker was added to the camera head for scale (10 cm spacing). High-resolution images were acquired using a digital Canon Powershot stills camera. Unfortunately, due to a malfunctioning during the June 2006 campaign, images were derived from video capture instead of the stills camera. The processing and interpretation of dive B06-02 was performed in an ArcGIS environment, expanded with the Adélie extension for ArcGIS 9.0 developed at IFREMER (http://www.ifremer.fr/flotte/systemes_sm/adelie/index.html). Dives B08-02 and B08-05 were interpreted using OFOP (Ocean Floor Observation Protocol) version 3.2.0c (Huetten and Greinert, 2008) and integrated into ArcGIS.

4. Results

4.1 Environmental setting

4.1.1 Hydrography

The CTD casts show a similar water mass stratification in both study areas (Fig. 2). The seasonal thermocline is recognized down to 50 m water depth (Figs. 2b-c). A salinity minimum (± 35.58) at about 550 m separates the upper Eastern North Atlantic Water (ENAW) from the saline Mediterranean Outflow Water (MOW), which has its salinity

maximum (± 35.76) at about 1000 m. Below, the T/S profile gradually follows the 27.75 kg/m^3 potential density gradient towards the LSW and NADW.

4.1.2 Geomorphology

The morphology of the La Chapelle continental slope is characterized by spurs and canyons (Fig. 1b). This study was carried out around a central, yet unnamed spur, flanked by deep canyons and thalweg channels in surveyed water depths from 150 to 1100 m. It has a main NE-SW orientation and an average inclination of 2°. Based on our discoveries, we suggest the name *Ostrea Spur* for this morphological feature. The slopes flanking the spur show a „herringbone' pattern of WNW-ESE orientated gullies on the western slope (13-15°) and NNW-SSE orientated gullies on the eastern slope (16°).

The Armorican margin near the Guilvinec Canyon is characterised by a heavily incised slope with NE-SW oriented canyons and spurs (Fig. 1). The Guilvinec Canyon is 14 km wide and bound to the northwest by the Penmarc'h Spur. The main part of this spur is relatively flat (0-2°) until 250 m water depth. Here, the gradient towards the Guilvinec Canyon is rather abrupt (10°), especially along its relatively steep northern to north-western flanks (30-40°). This flank contains about 4 large dendritic gully systems with a NNW-SSE orientation. In contrast, the eastern flank of the canyon is much smoother (and less incised) with slope gradients ranging from 5 to maximum 20°. This asymmetry is also observed on the seismic profiles (Figs. 1c and 3). Figure 3b shows a seismic profile through the largest (1 km wide) and steepest (17-35°) gully, which was also the subject of ROV dive B08-02 (Fig. 1c). Exclusively on the SE flank, a large

(200-400 ms TWT) sigmoidal depositional sequence can be observed which explains the smoother slope texture. A comparison with other regional seismic stratigraphic studies (Bourillet et al., 2003; Paquet et al., 2010) suggests that this sequence may be correlated with the Pliocene to Pleistocene Little Sole Formation. On the other hand, almost the entire NW flank is covered with diffraction hyperbolae, suggesting erosive steep slopes, irregular topography or outcropping hard substratum. These deeper strata may have a Miocene origin, belonging to the Jones or Cockburn Formations (Bourillet et al., 2003). Along the south-western tip of the spur, 6 more gullies can be observed within the prolongation of the spur's axis. These gullies are approximately 400-500 m wide and have a gradient between 10 to 25°.

4.2 ROV observations

4.2.1 Dive B06-02: Eastern flank of Ostrea Spur

Dive B06-02 followed a SW-NW, 2800 m long track over the eastern flank of the Ostrea Spur, parallel to its elongation, crossing several of the steep (16°) NNW-SSE orientated gullies on the eastern slope (Fig. 4). The main observations were carried out on the central gully between 7°20'00"W and 7°19'40"W, allowing a more comprehensive view on the gully environment.

A large part of the dive trajectory (57%) showed sandy bioturbated sediments with ripple marks on the relatively flat gully shoulders (Figs. 4 and 5a). These fairly straight NW-SE oriented sand ripples have wavelengths of approximately 10-20 cm and are less than 10 cm high. On other locations outside the gully axis, an enigmatic pale-coloured facies was observed featuring decimetric to metric blocks or knolls inferred to be

carbonated material (Fig. 5b). No recent sediment cover was observed and frequently yellow *Hexadella* sp. sponges were noticed on top these blocks, which were observed over 25% of the track length.

Protruding banks with a thickness ranging from 10 to 30 cm were observed regularly, especially on the steep slopes within the central part of the dive between 620 and 680 m (Figs. 5c-d). They form steps down to the central gully thalweg along a NNE-SSW to NW-SE orientation (Fig. 4). In total, 20 laterally variable banks were encountered over 60 m depth. Towards the centre of the gully they disappear into a large N-S oriented escarpment between 630 and 650 m water depth (Fig. 5f). Based on our observations, this escarpment cliff is at least 10 m high. The ensemble of this steep environment represents about 16% of the track length. At the base of this cliff and above the larger banks, accumulated debris provides settling sites for sessile organisms, whilst the escarpment and the larger protruding banks are sporadically colonized by medium to dense communities of giant (10-15 cm) *Neopycnodonte zibrowii* oysters (Figs. 5d-e), forming a 3D assemblage with occasional dead cold-water corals (*Lophelia pertusa*), which occur very rarely. The oysters only occur in high densities (up to 100 individuals per m²) near the centre of the gully between 620 and 680 m, while they were also observed in a similar setting at 4 other locations between 540 to 680 m (Fig. 4). Most typically, at the side of the gully, they only occur underneath overhanging banks which protrude far enough (10-15 cm) from the seafloor. Only 9 of the observed banks were large enough to offer sufficient space for closely stacked shells, literally hanging in a density of about 30 individuals per m² (Fig. 5e). Near the escarpment, they act as a high-density vertical wall pavement (Fig. 5f). Many oyster individuals are still articulated and

alive, or, where the free right valve is detached, show the non-degraded and locally still dark-coloured endostracum indicating that these oysters died only recently (Fig. 5e).

4.2.2 Dive B08-02: North-western flank of Guilvinec Canyon

Dive B08-02 covered 3700 m of seafloor observations along a U-shaped track starting with the first "leg" southwards from the NE flank of a gully at 700 m water depth and ending with a second "leg" parallel to the gully axis (Figs. 1c and 6). The seabed slope along this track has an average gradient of 11°.

Along the main part of the dive track, a featureless bioturbated sandy seafloor was observed. Nevertheless, the easternmost part of the track which is roughly following 5°22'50"W, revealed the presence of abundant yellow *Hexadella* sp. sponges, live *Madrepora oculata* patches or fossil *Lophelia pertusa* debris (Fig. 6). Since the distribution, diversity and habitat settings of cold-water corals along this part of the Armorican margin are discussed in detail by De Mol et al. (accepted), only their occurrence and substratum are described in this section. These are predominantly solitary cold-water corals and represent about 40% of the observations. The present-day community is not forming close reef-like structures, but can be found on dead cold-water coral rubble "graveyards" (De Mol et al., accepted). Further observed substrates for the cold-water corals include a sandy rippled seabed, buried biogenic rubble and erratic boulders. Common, co-occurring organisms associated to the cold-water corals are sea-pens, sea-urchins, sponges and soft corals (De Mol et al., accepted).

Between 800 and 950 m, a rippled seabed was frequently encountered (10% of the observations). Especially below 900 m, straight and sometimes sinuous N-S oriented low-relief sand ripples were observed with wavelengths ranging between 10-20 cm and heights of approximately 5 cm (Figs. 6 and 7c). Additionally, relatively intense flocculation was noted (Fig. 7c).

Only sporadically (less than 5% of the observations), the rather smoothly sloping seabed is interrupted by small banks or escarpments (Figs. 6 and 7a-b). These escarpments are long "ruptures" in the seabed, showing a consolidated subtrate and having an E-W orientation between 700 and 750 m, while the ones located deeper than 750 m, usually show a S-N or SSW-NNE orientation. Generally, the banks have a decimetric scale, while the heights of the escarpments range between 2 to 4 m. On only at three out of nine locations (Figs. 6 and 7a-c), the escarpments were colonized by *Neopycnodonte zibrowii* oysters and, in lesser degree, by *Madrepora oculata.* However, compared to dive B06-02 on Ostrea Spur, the abundance of *Neopycnodonte zibrowii* on the escarpments (Figs. 7a-b), is far less with 10 to 30 individuals per m². A relatively abundant community of deep-water oysters (100 individuals per m²) is only observed at a water depth of 744 m at the leeward side of a 1 m high W-E overhanging escarpment. Here, the top 40 cm underneath the edge is colonized. *Madrepora oculata* was observed on top of the escarpment's edge.

4.2.3 Dive B08-05: Western flank of Guilvinec Canyon

Dive B08-05 mainly investigates the southern shoulder of a gully south of the spur that separates the Guilvinec from the Penmarc'h Canyon (Figs. 1c and 8). The 3100 m long

track followed a southwest course between 300 and 750 m water depth. The overall gradient of the slope is 8-10°.

In contrast with the other dive tracks, this last track does not show a lot of variability in the encountered facies (Fig. 8). Between 300 and 450 m, the gently dipping slope is characterized by the presence of straight to gently undulatory sand ripples with a wavelength between 10 to 15 cm and a general SSE-NNW orientation (Fig. 9a), making up 37% of the observations. Sometimes coarser sand was observed in between the ripples. From 450 to 730 m, a relatively flat and bioturbated silty to sandy seafloor is observed with some small escarpments near 480 m and a low-relief rippled seabed (Fig. 8).

Only at the very end of Dive B08-05, the gentle slope is abruptly interrupted by a large, laterally continuous 4 m high WSW-ENE rocky escarpment at 735 m. The first meter of this escarpment is a 50 cm deep overhanging cliff underneath which a thriving community of *Neopycnodonte zibrowii* oysters, singular *Madrepora oculata* and some sponges can be observed (Figs. 9b-c). Figure 9d shows the typical high-density assemblage of *Neopycnodonte zibrowii* which seem to have grown on top of each other. Their size amounts to 10 cm on the smallest axis and 15 cm on the largest axis. The density is estimated at 63 individuals per m². Both the oysters as the occasional corals are hanging "upside down", concentrated near the most overhanging end of the cliff.

5. Discussion

The main part of the discussion is based on the observations made during ROV dive B06-02 along the La Chapelle continental margin, since it has provided the best overview of the occurrence of *Neopycnodonte zibrowii* in relation with the canyon environment (Fig. 10). The observations from Guilvinec canyon will be used as additional information. The habitat in which these giant deep-water oysters are thriving is dependent on both specific morphological and environmental conditions.

5.1 The occurrence of deep-water oysters in the Atlantic Ocean

These large deep-water oysters (up to 20 cm) belong to the recently described species *Neopycnodonte zibrowii* (Wisshak et al., 2009a, 2009b), which so far has only been documented alive from the Azores. The use of ROV technology enabled detailed observations of its deep-water habitat in a sheltered environment. Unfortunately, during none of the two R/V Belgica cruises samples could be acquired for morphological or molecular taxonomy. Nevertheless, corresponding alive oysters were observed and sampled with submersible aid at the Azores and were described – together with material recovered during R/V Thalassa expeditions in the early seventies from the southern Bay of Biscay – as a new species of *Neopycnodonte* by Wisshak et al. (2009b). Previous observations of mostly dead or sub-fossil specimens were only reported from dredge samples or fisheries by-catch (Le Danois, 1948; Reveillaud et al., 2008). Further isolated records of this species stem from the Gorringe Bank off Portugal (Auzende et al., 1984), south of Madeira (Hoernle et al., 2001) and in the Central Mediterranean Sea where they occur as prominent (sub-) fossil oyster banks (Gofas et al., 2007). This „living fossil' oyster is most unusual with respect to its habitat, size, geochemical signature and its particularly pronounced centennial longevity (Wisshak et al., 2009a,

2009b). It stands in strong contrast to all other extant oyster species which are relatively short-lived and predominantly occupy shallow to marginal marine settings, where they occasionally form reefal structures. From the upper slope (200-500 m) of the Bay of Biscay, the related but smaller (4-5 cm) *Neopycnodonte cochlear* has been reported (Le Danois, 1948). The latter is usually associated with hard substrates and in certain places colonizes *Dendrophyllia cornigera* coral reefs (Le Danois, 1948). *N. cochlear* certainly features the largest distribution worldwide, both in palaeo- (Videt and Neraudeau, 2003) and present-time environments (Harry, 1981). *Neopycnodonte zibrowii,* observed alive along the La Chapelle continental slope, the Guilvinec Canyon and off the Azores can be regarded as a distinct deep-sea relative of *N. cochlear* with specific adaptations allowing it to thrive in upper bathyal depths (now confirmed down to 846 m), and it can be expected that further direct seabed observations will considerably enhance the known biogeographic distribution of this unusual bivalved mollusc. Most recently, Delongueville and Sciallet (2009), reinvestigated two unusually large specimens sampled alive from the Bay of Biscay margin, previously addressed as *Neopycnodonte cochlear* (Delongueville and Sciallet, 1999), which can now be attributed to *Neopycnodonte zibrowii*. Interestingly, they were recovered from a water depth of only 350 to 400 m, expanding the known bathymetrical range of this species in the Bay of Biscay from 350 to 846 metres. In contrast to the Azores, both Biscay pycnodontines overlap in their bathymetrical range.

5.2 Influence of the physical environment on deep-water oyster colonization

Up to now, the occurrence of the deep-water oyster *Neopycnodonte zibrowii* within the Bay of Biscay has only been observed on hard substrates. More specifically, the area

underneath overhanging cliffs, banks or steep escarpments seem to be the most successful colonization surface (Figs. 5, 9 and 7). This is in contrast with the local occurrence of other sessile organisms such as cold-water corals (*M. oculata* and *L. pertusa*) and sponges, which are abundantly present on open parts of the slope (Fig. 6). They have settled on sandy substrate, biogenic debris and on top of elevated substrates, such as documented for this area by De Mol et al. (accepted) and along the NW European margin (Dorschel et al., 2009; Freiwald et al., 2004; Huvenne et al., 2005; Wheeler et al., 2007). Only occasionally, and in reduced numbers, they can be found on identical substrates colonized by the deep-water oysters (Figs. 7b and 9b). In this case, such vertical substrates and overhangs could be considered as a challenging surface to be colonized by cold-water corals. Such specific substrates can be considered as limited along the continental margins and are specifically concentrated within deep-sea canyons, where they still are relatively sparsely distributed (less than 5% in this dataset).

Generally, the morphology of canyons flanks is relatively irregular and no significant cover of draping sediments is observed. This zone is most likely subject to constant reworking by downslope (turbiditic) or alongslope (contouritic) current processes (Arzola et al., 2008; Bourillet et al., 2006; Cunningham et al., 2005; Huthnance, 1995; Pingree and Le Cann, 1989; Toucanne et al., 2009). Within the depth window corresponding to the ROV observations, seismic profiles show single, high-amplitude reflections or diffraction hyperbolae that might indicate the presence of lithified calcarenite or calcilutites banks (Figs. 3, 10) which possibly belong to the Miocene Jones or Cockburn Formations (Bourillet et al., 2003; Paquet et al., 2010). Within

canyons and gullies, predominantly downslope erosion has gradually exposed these consolidated carbonate-like sedimentary sequences, which have been shaped into step-like banks or escarpments. This process is more intensive towards the centre (thalweg) of the canyon or gully, providing a higher availability of suitable substrates for epibenthos colonization (Fig. 10). Evidently, this will also affect the communities of the sessile organisms that colonize these substrates. If they are too exposed, the epifauna may be removed by the episodic downslope currents. The overhanging banks and the vertical escarpments may provide a sufficiently sheltered habitat for the deep-water oysters, which are capable to settle on such surfaces. However, this particular habitat does not allow plenty of co-occurring species such as cold-water corals which necessitate the current exposure. Along the steeper slopes of the La Chapelle continental slope, relatively more suitable substrates with large deep-water oyster communities were observed, compared to the Guilvinec area. Moreover, almost no observations were made of cold-water corals, while they are abundantly present on the gentler Guilvinec slope (Figs. 4 and 6).

Additionally, the asymmetry of the Guilvinec Canyon clearly demonstrates a second factor influencing the location of the deep-water oyster habitats. Both morphologically and stratigraphically the (north-) western slope of the Guilvinec Canyon shows more evidence of erosion than the eastern slope, which is characterized by depositional features (Figs. 1c and 3). ROV observations have shown the presence of seabed ripples on different parts of this slope between 300 and 950 m (Figs. 6 and 8), suggesting the presence of an E-W bottom current with velocities between 20 and 40 cm/s (Stow *et al.*, 2009). These observations fit the cyclonic flow circulation and observed depth of the

MOW in the Bay of Biscay (Fig. 2). The (north-)western slope of the canyon(s) could act as an obstacle which might intensify the easterly bottom currents through isopycnal doming, leading to erosion (Hernández-Molina et al., 2003; Iorga and Lozier, 1999; Van Rooij et al., submitted). A similar process was also observed on the upper part of the Portimao Canyon (Marches et al., 2007). As such, this effect is not present on the eastern slope, leading to preferential deposition on this side of the canyon, making it nearly devoid of banks and escarpments. This example also proves that a combined influence of turbiditic and contouritic currents may shape the canyon morphology and hence determine the location of preferential habitats of (hidden) deep-water ecosystems. Both the banks as the cliffs will not easily be subject to sediment burial and provide a suitable hard substrate for this type of filter feeders. As such, there is not much competition between the deep-water oysters and cold-water corals, since they seem to have slightly different physical habitat requirements.

5.3 Oceanographic drivers for deep-water oyster occurrence

Next to the necessary settling grounds, a successful oyster habitat needs the suitable oceanographic environment and sufficient nutrients. During some of the ROV dives, an intense marine snow was present in the area where the oyster community was discovered (Figs. 5a, 7c-d and 9c). This aggregated particulate matter composed of phytodetritus and pellets, sinking from the upper water layers, constitutes an important aspect in the trophic input of this community. Oysters are filter feeders, commonly located in low salinity coastal shallow water and feeding on phytoplankton. The occurrence of oysters at these depths is at least remarkable given the higher salinities and generally lower input of phytodetritus. On the other hand, a relatively high surface

primary production is present along this part of the margin (Joint et al., 2001; Pingree and Le Cann, 1990). Moreover, according to the available hydrographic data, the depth range in which *Neopycnodonte zibrowii* is observed lies just beneath the physical boundary between the upper Eastern North Atlantic Water and the intermediate saline Mediterranean Outflow Water (Fig. 2). The lower limit of the oyster's occurrence coincides with a local salinity and temperature maximum of respectively 35.75 and 10°C, which might indicate a certain amount mixing of both water masses. Within this zone of upper MOW, seabed features indicate a locally vigorous hydrodynamic environment near the gully shoulders (Figs. 4, 6 and 8). The observations of straight sand ripples during dive B06-02 indicate the presence of strong bottom currents between 10 and 40 cm/s (Stow et al., 2009). Apart from the flow velocity of the MOW, the bottom currents may be enhanced by strong internal tides (White, 2007) and funnelled along the canyon axis, as observed in the Portimao Canyon (Marches et al., 2007). This is consistent with previous measurements along the Armorican margin (Pingree and Le Cann, 1989, 1990), where a strongest bottom current near the 500 m contour was observed in the downslope direction with a maximum instantaneous velocity of 95 cm/s. Intersected with canyons, these tidally induced transports may be channelled and result in regions of locally increased flow, resuspension and local circulations (Pingree and Le Cann, 1990). A dominant effect caused by internal tides from the upper slope is proposed to explain the entrapment and downward transport of the enhanced levels of surface phytoplankton abundance (Holligan et al., 1985; Pingree et al., 1982) as recently inferred above the Nazaré Canyon (Arzola et al., 2008) and above giant carbonate mound provinces colonised by reef-forming cold-water corals (Mienis et al., 2007; White, 2007) . The significance of submarine canyons as coral and

oyster habitats (Mortensen and Buhl-Mortensen, 2005) may be due to their capacity to accumulate organic debris (Canals et al., 2006), which may directly benefit filter-feeders, such as scleractinians (Roberts et al., 2006). It is highly likely that this water-mixing above the seabed results in enhanced suspended material and favours concentration of filter/suspension feeders (de Stigter et al., 2007).

Moreover, the oyster banks occur in a potential density envelope of 27.4 – 27.7 kg/m^3 (Fig. 2), overlapping the range of values which are considered to be a prerequisite for the development, growth and distribution of cold-water coral reefs along the Celtic and Nordic European margin (Dullo et al., 2008) and within the Guilvinec area (De Mol et al., accepted). This control through potential density may be linked to the formation of intermediate nepheloid layers, which increase nutrient supply and resuspension (de Stigter et al., 2007; Mienis et al., 2007). As such, in contrast to the shallow marine oyster occurrences, the dynamic oceanography within deep-sea canyons can provide a stable ecosystem which enables a theoretical co-habitation with sponges, hydrozoans, gorgonians and scleractinians (De Mol et al., accepted).

6. Conclusions

In this paper, the occurrence and the environmental drivers of a hidden deep-water habitat (540-846 m), inhabited by *Neopycnodonte zibrowii* oysters along the French Atlantic continental margin, is described. The present observations indicate that canyons and steep slopes may provide the most suitable physical environment for these oysters, which are predominantly observed underneath overhanging banks or on escarpments. Turbiditic and contouritic processes are responsible for (1) the erosion which exposes

consolidated carbonate-like sedimentary sequences, shaping them into step-like banks, and (2) the delivery and resuspension of nutrients in association with funnelling of internal tides into canyons. Although these deep-water oysters occur in a similar oceanographic setting as cold-water corals, their very specific physical habitat requirements do not seem to be fully compatible with most of the other sessile organisms. Once these rather strict and sparsely distributed environments are encountered, *Neopycnodonte zibrowii* can be observed in relatively high number up to 100 individuals per m².

This little-known population located in an inaccessible environment sheds light on the richness of canyon systems in terms of filter feeder species. Because of the verticality of this habitat, acoustic hull-mounted systems and bottom sampling with conventional towed devices will be unsuitable for a fine description of this population. As such, further in situ observations and habitat mapping from ROV's should be performed to estimate the oyster coverage along the Bay of Biscay and other Atlantic canyons. They may represent an overlooked deep-water community, being part of a still vastly underestimated biodiversity of bathyal benthic communities, especially within canyons.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at...

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Tables

Table 1: Metadata of the ROV Genesis dive tracks

Dive name & Date	**Location**	**Start**		**End**		**Oyster depth**
		Coordinates	**Time & Depth**	**Coordinates**	**Time & Depth**	
B06-02 17 June 2006	East flank Ostrea Spur	47°33.34'N 7°20.69'W	08:31 587 m	47°34.07'N 7°19.44'W	15:25 557 m	540 – 680 m

B08-02 1 June 2008	North-western flank Guilvinec Canyon	46°56.27'N 5°22.89'W	11:24 712 m	46°55.72'N 5°22.90'W	15:46 900 m	720 – 846 m
B08-05 3 June 2008	Western flank Guilvinec Canyon	46°55.68'N 5°28.52'W	11:17 305 m	46°55.16'N 5°29.00'W	14:27 737 m	737 - 740 m

Table 2: Metadata of the CTD casts

Name	**Date**	**Location**	**Latitude**	**Longitude**	**Depth**
Station 3 cast B	1 June 2006	La Chapelle slope	47°25.00'N	7°16.00' W	1396 m
B0813-CTD-4	4 June 2008	Guilvinec canyon	46°54.53'N	5°21.26'W	1404 m

Figure captions

Figure 1: (a). Location of the study areas along the French Atlantic continental margin (GEBCO bathymetry, contour lines every 250 m), with indication of the CTD locations (Table 2) and of the historical *Massifs Coralliens* mapped by Le Danois (1948); MCBC: *Massif Corallien du Banc de la Chapelle*; MBP; *Massif Corallien du Sud Ouest de Penmarc'h*; MCGV; *Massif Corallien de la Grande Vasière*. (b). Detail of the Ostrea Spur area with EM1002 bathymetry (contour spacing 25 m) and the location of ROV dive B06-02 (white). (c). Detail of the Guilvinec Canyon area with EM1002 bathymetry (contour spacing 25 m), with the location of seismic profiles (red) and ROV dives B08-02 and B08-05 (white).

Figure 2: Hydrographic data of the two study areas. (a). Temperature/salinity plot for both CTD casts (Table 2), with indication of the boundary (dashed grey line) between the Eastern North Atlantic Water (ENAW) and the Mediterranean Outflow Water (MOW). The red and blue dashed envelopes refer to the occurrence of cold-water coral (CWC) reefs in respectively the Porcupine Seabight (Dullo et al., 2008) and within the Guilvinec canyon (De Mol et al., accepted). The estimated occurrence envelope of deep-water oysters in the Bay of Biscay is based on the ROV observations (Table 1), plotted on the CTD data of respectively (b) cast "Station 3 cast B" and (c) cast "B0813-CTD-4" in full grey. Here, the black vertical bars indicate the corresponding depth range of ROV observations.

Figure 3: Seismic profiles Ga080605 (A) and Ga080604 (B), illustrating the seismic stratigraphy and thickness of the sedimentary cover across the Guilvinec Canyon (Fig. 1c). Note the asymmetry of canyon morphology and the difference between the sedimentary processes on both flanks. The white dashed lines indicated additional unconformities within the main sequences. These figures have a 10 times vertical exaggeration.

Figure 4: ROV dive B06-02 track superimposed on the R/V Belgica EM1002 bathymetry (contour lines every 50 m) with indication of the recognized lithologies, seabed features and the location of the imagery shown in Fig. 5. The black trackline represents a featureless, sandy bioturbated seabed.

Figure 5: Video-derived images of oyster assemblages and facies recognized during dive B06-02 (Fig. 4). Each image bears depth information and orientation. (a) NW-SE straight sand ripples, (b) carbonate knolls with *Hexadella* sp. sponge, (c) carbonate banks in a series of steps, (d) overhanging carbonate bank with (low-density) oyster community attached below the bank, in association with a dead cold-water coral, (e) close-up of a probably living (high density) deep-water oyster community, (f) steep oyster cliff, note the altitude of the ROV (5.3 m above sea floor).

Figure 6: ROV dive B08-02 track superimposed on the R/V Belgica EM1002 bathymetry (contour lines every 50 m) with indication of the recognized lithologies, seabed features and the location of the stills imagery shown in Fig. 7. The black trackline represents a featureless, silt-sandy bioturbated seabed.

Figure 7: Stills images of oyster assemblages and facies recognized during dive B08-02 (Fig. 6); (a) E-W escarpment (± 3 m high) with frequent oyster colonization, (b), S-N oriented escarpment with a mixed solitary oyster and cold-water coral community (*Lophelia pertusa*, black corals (*Parantipathes* sp., *Stichopathes* sp., *Trissopathes* sp.), (c) undulatory S-N oriented sand ripples with sparse live solitary *Madrepora oculata*, (d) leeward side of a W-E outcropping and overhanging rock (± 1 m high), colonized by deep-water oysters.

Figure 8: ROV dive B08-05 track superimposed on the R/V Belgica EM1002 bathymetry (contour lines every 50 m) with indication of the recognized lithologies,

seabed features and the location of the stills imagery shown in Fig. 9. The black trackline represents a featureless, silty-sandy bioturbated seabed.

Figure 9: Stills images of oyster assemblages and facies recognized during dive B08-05 (Fig. 8); (a) undulatory SSE-NNW oriented sand ripple field and the fish *Chimera monstrosa* and *Helicolenus dactylopterus dactylopterus*, (b) overhanging cliff with a thriving mixed oyster and *Madrepora oculata* colony, (c) distant view of a S-N colonized overhanging cliff, (d) detailed view of the densely packed deep-water oyster community.

Figure 10: Conceptual sketch of the deep-water oyster environment, based on ROV dive B06-02 on the La Chapelle continental slope. The main oyster communities are located at the gully axis, fed by cascading currents enabling a suitable nutrient supply. The banks upon which the oysters are seated probably are Miocene carbonate banks (calcarenites).

Figure 01

Click here to download high resolution image

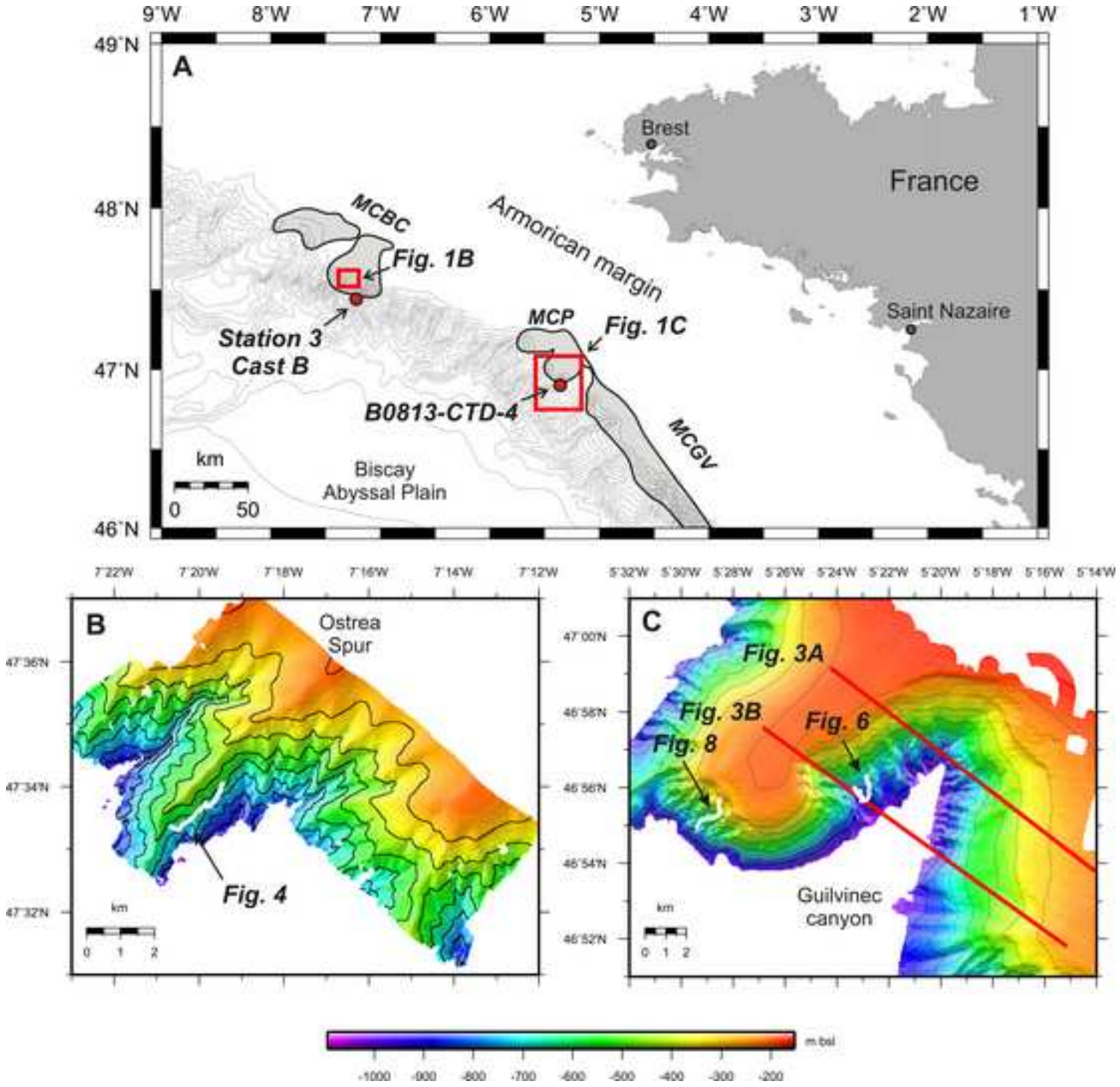

Figure 02

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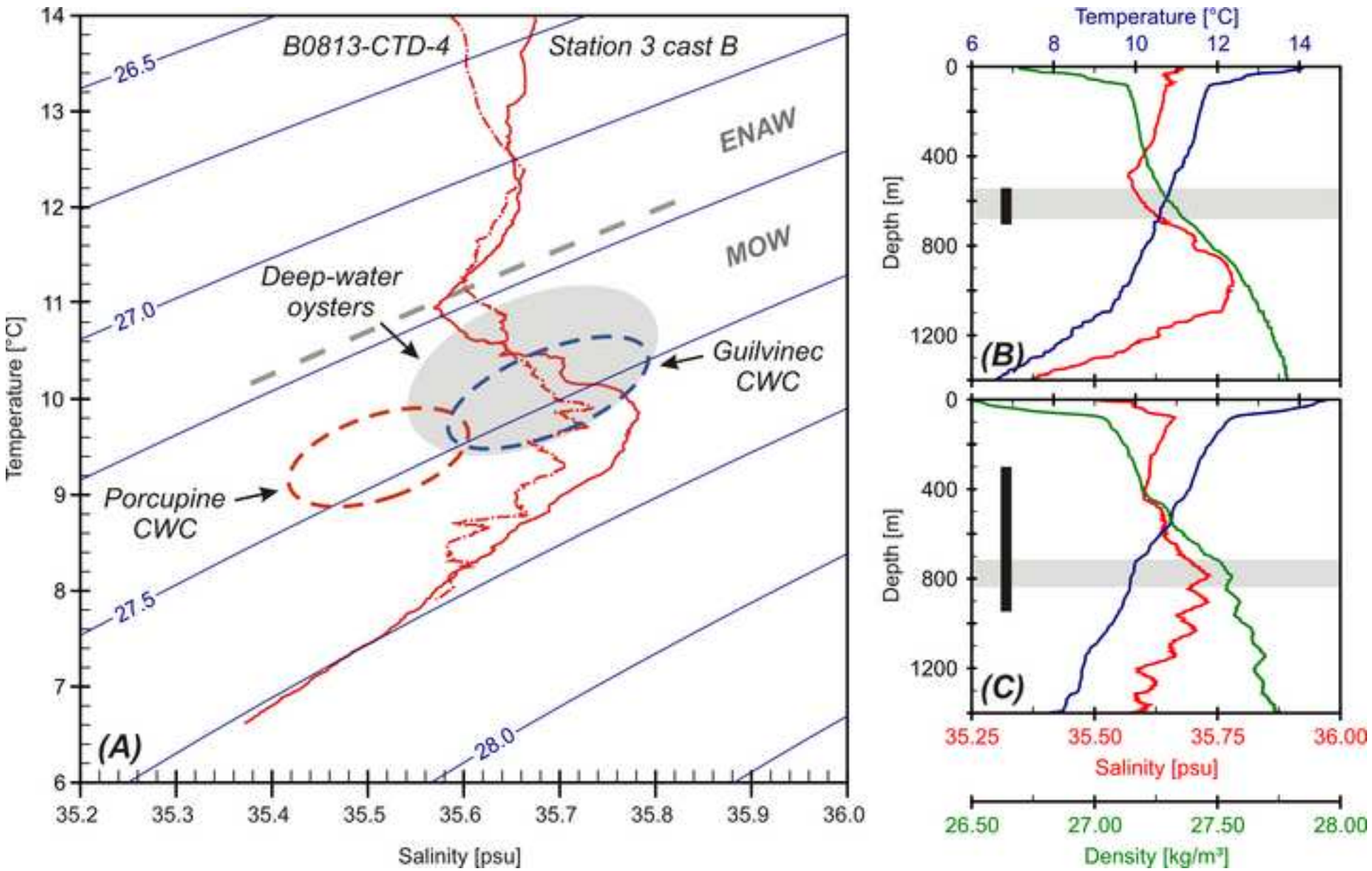

Figure 03

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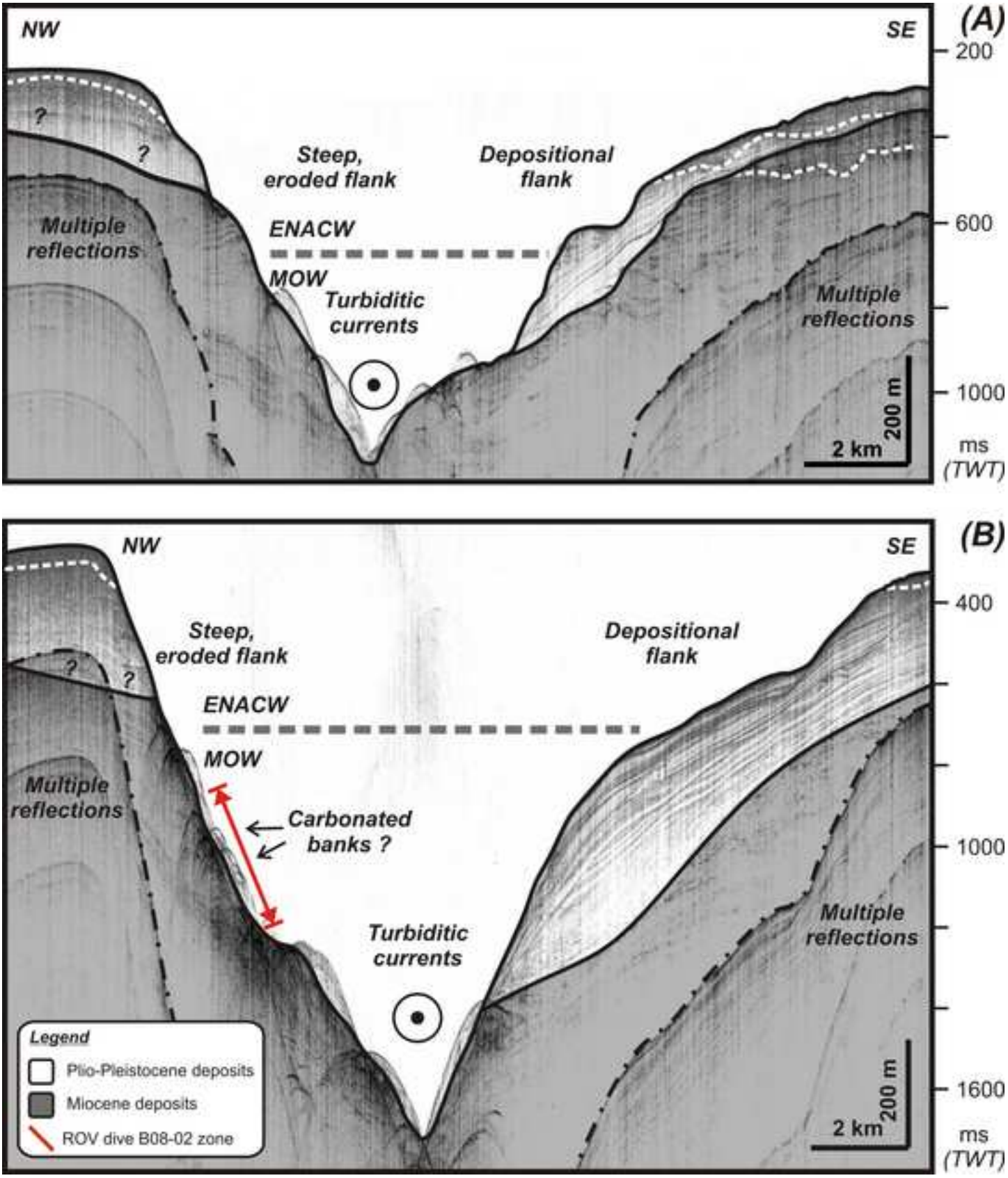

Figure 04

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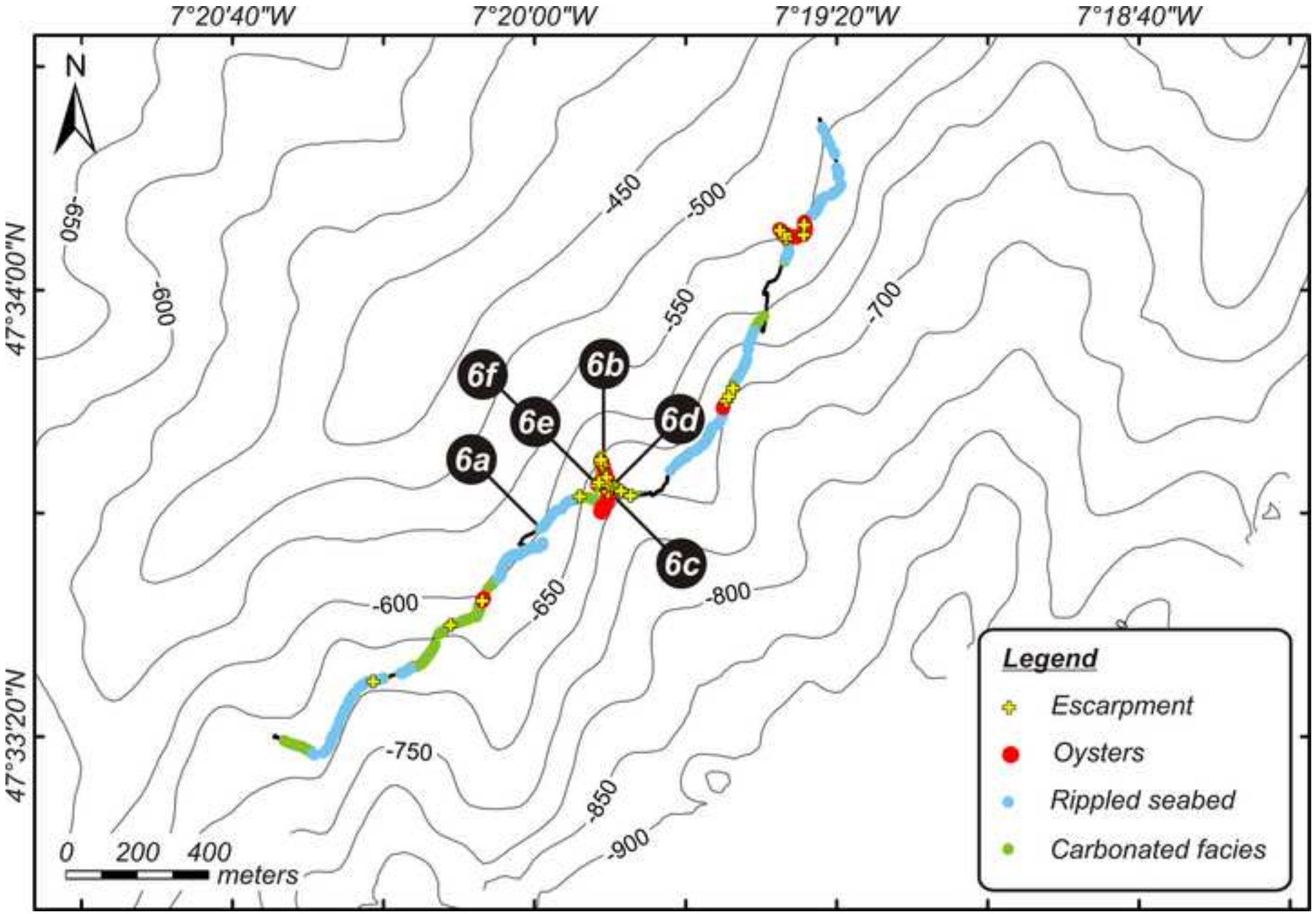

Figure 05

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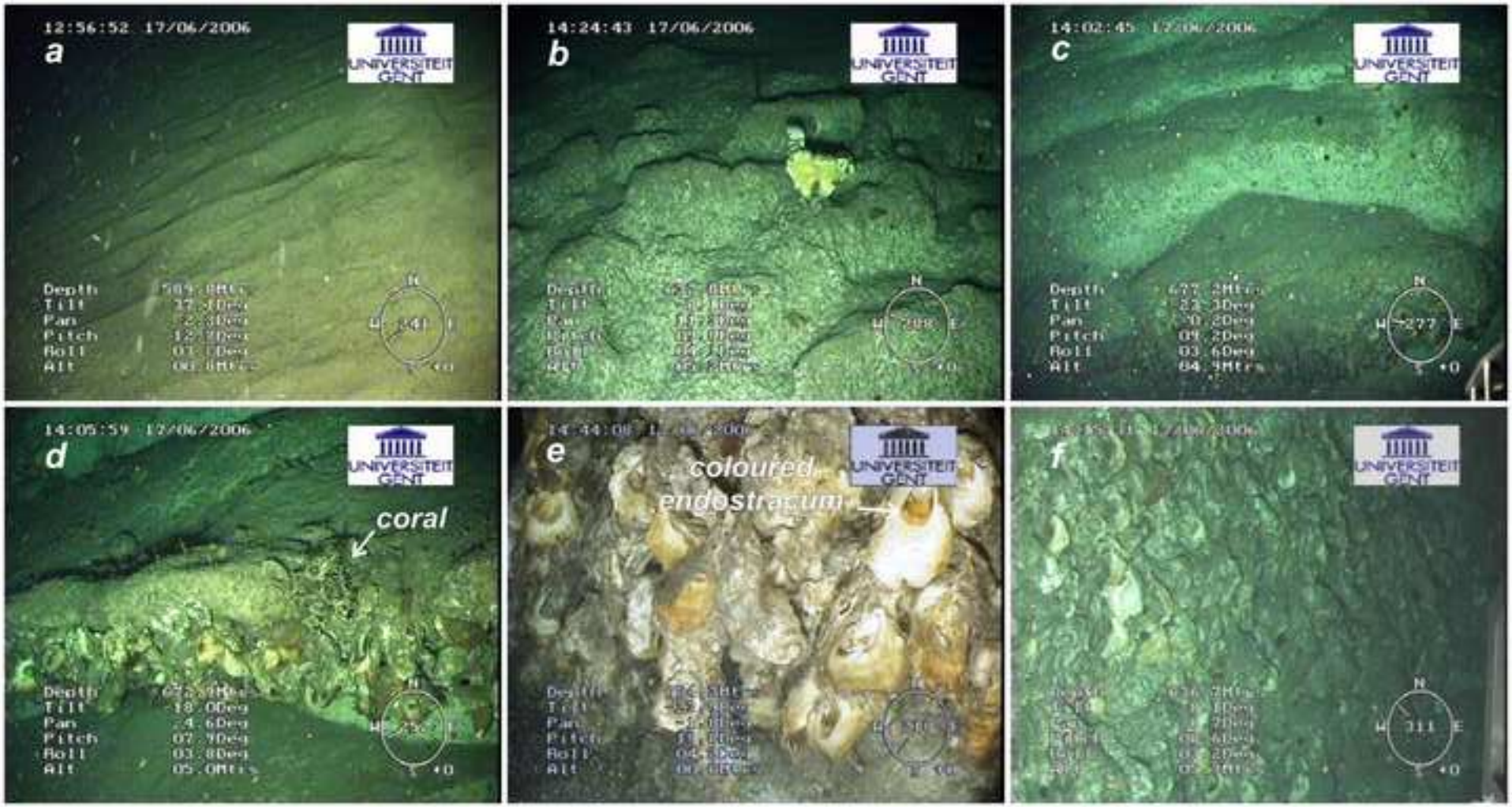

Figure 06

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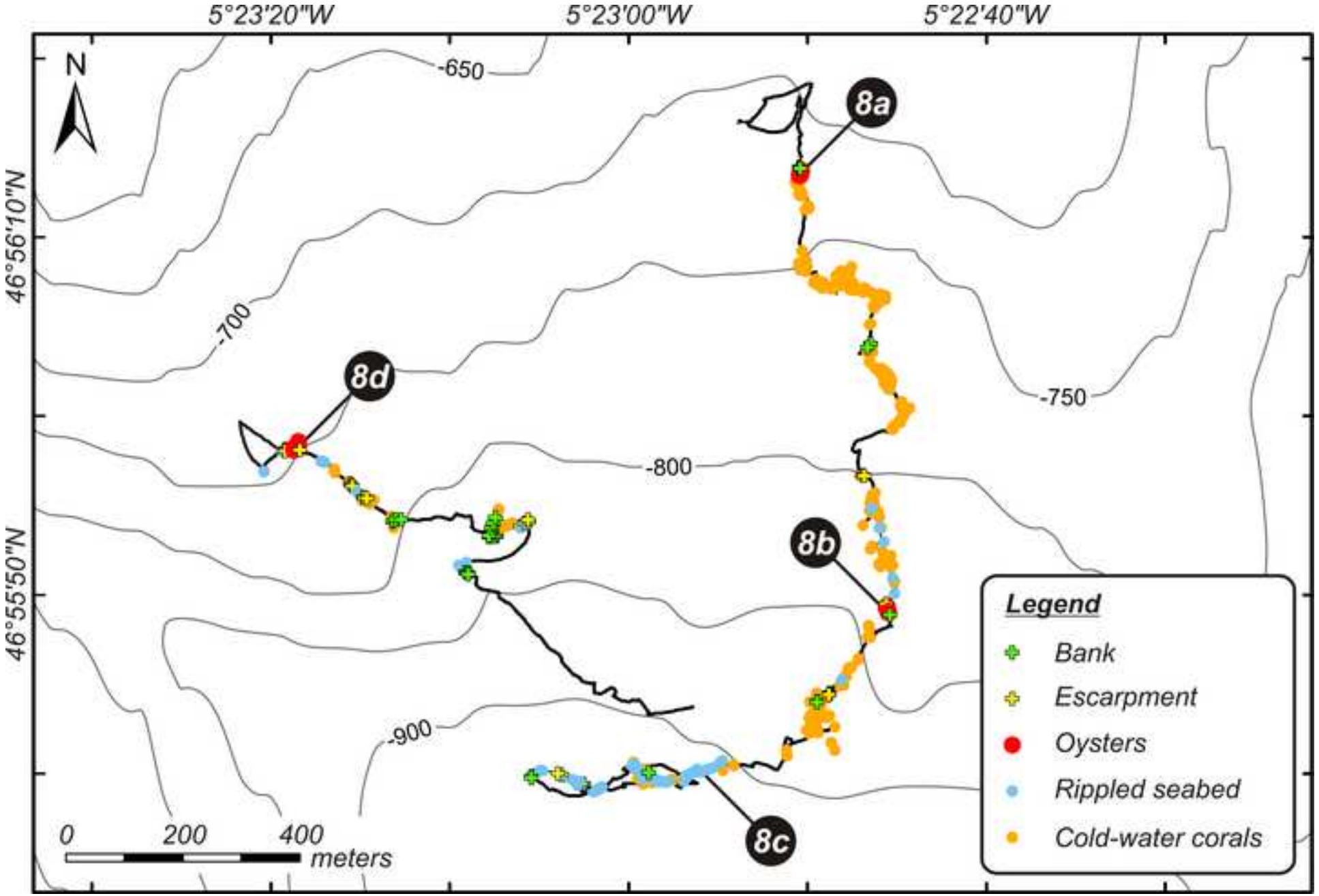

Figure 07

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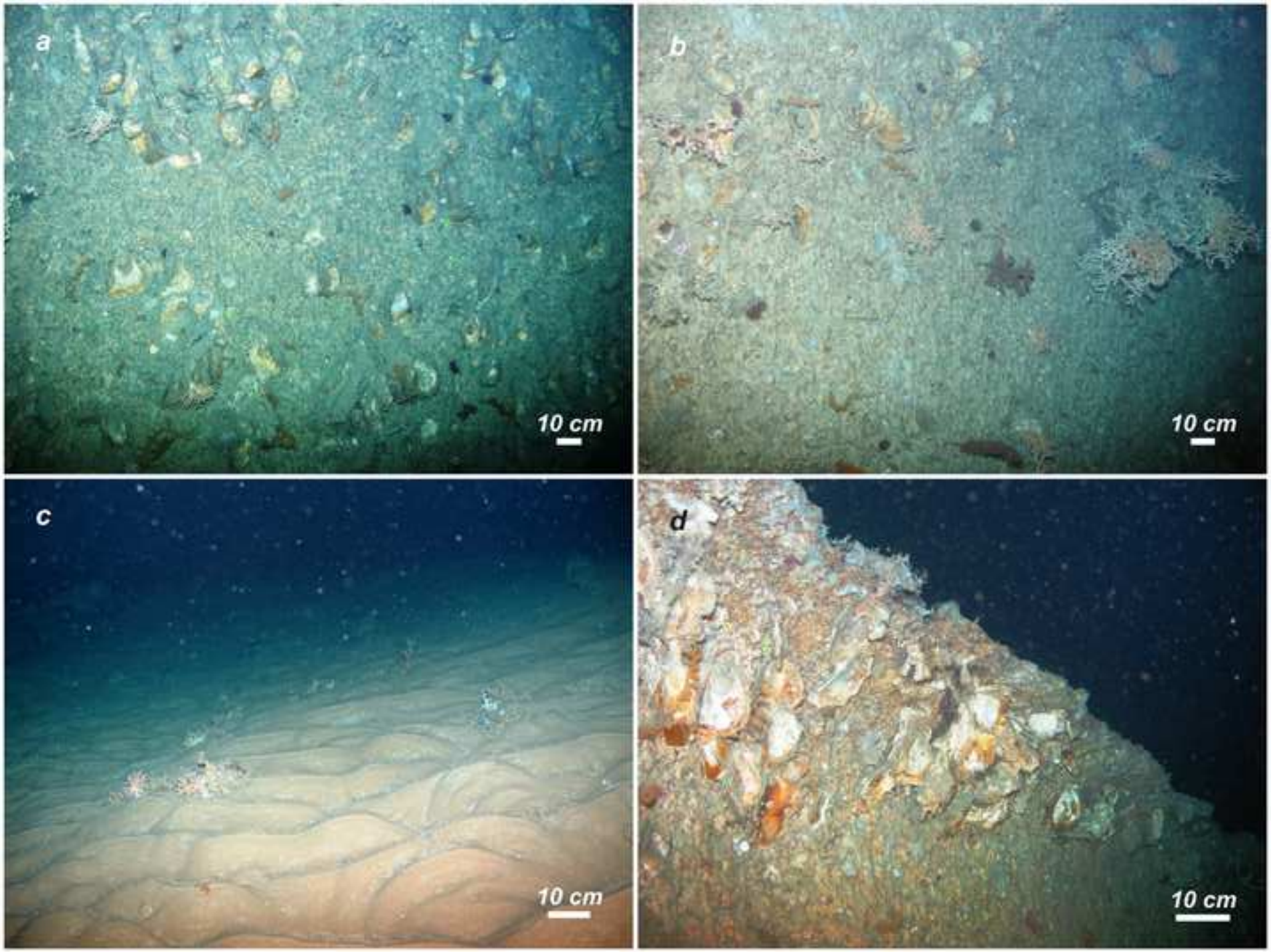

Figure 08

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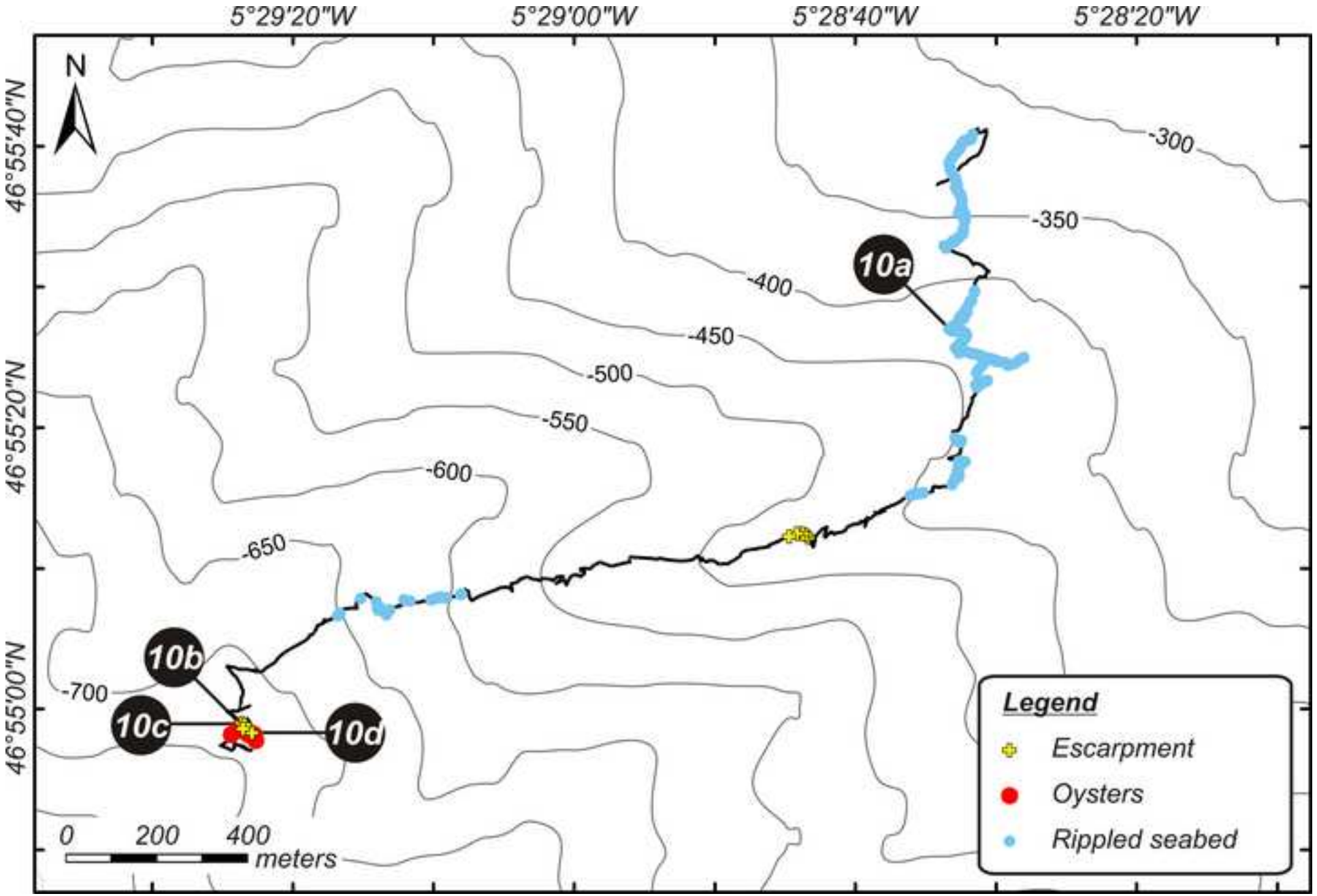

Figure 09
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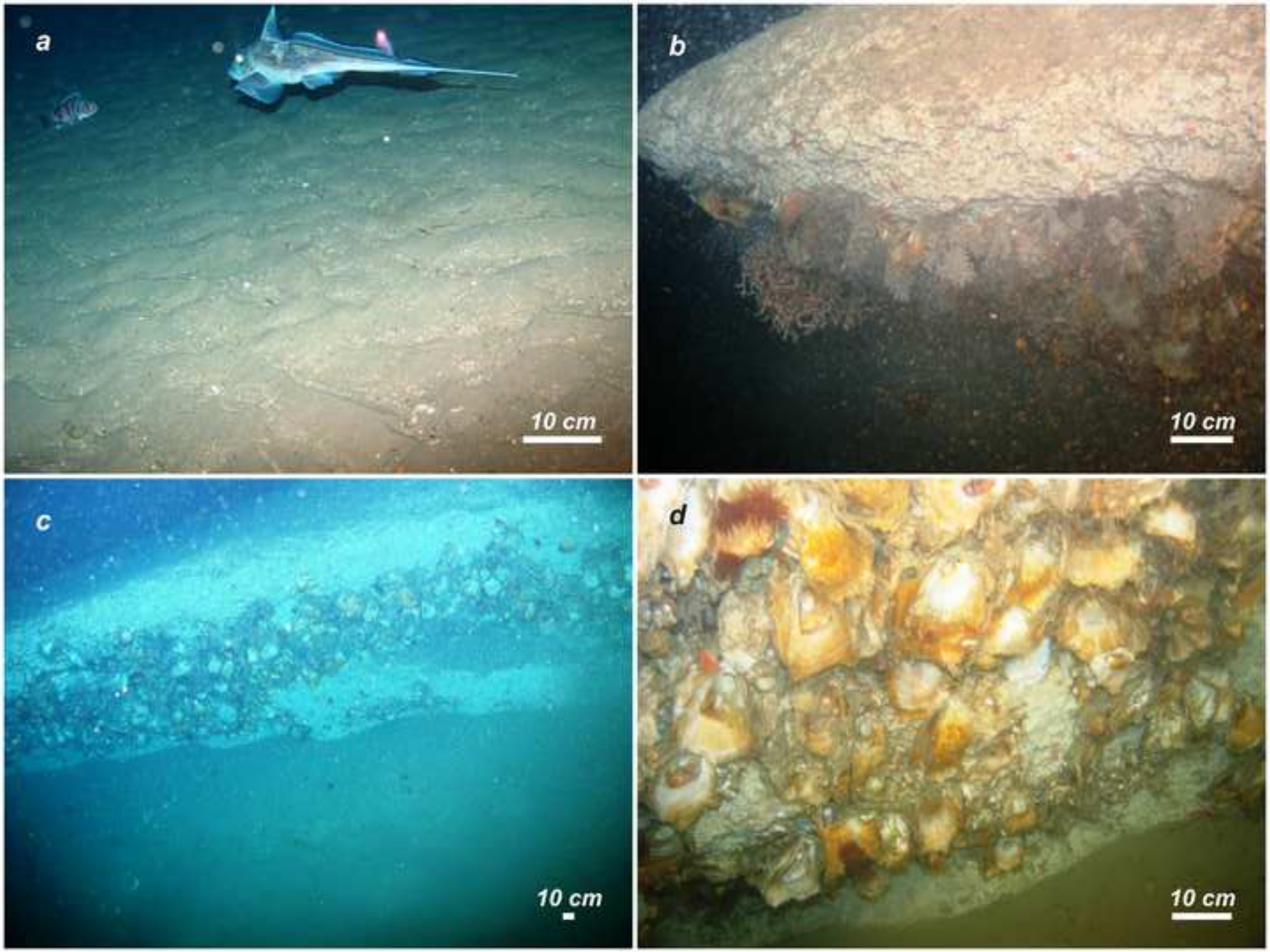

Figure 10

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