

Deep cold-water coral ecosystems in the Brittany submarine canyons (Northeast Atlantic): Hydrodynamics, particle supply, respiration, and carbon cycling

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Abstract

The submarine canyons of the Brittany continental slope (Bay of Biscay–Northeast Atlantic) were studied to describe the conditions in which cold-water corals occur in these areas and their consequences for coral metabolism. Near-bottom current, oxygen, temperature, and particle flux, simultaneously measured for 2 yr at 850 m depth, revealed by spectral analysis the presence of several frequencies with a dominant semidiurnal tidal cycle and a current direction determined exclusively by the canyon topography. Sediment trap data also showed a seasonal input of material with a large peak of particles and carbon fluxes at the end of winter. Daily particle and carbon fluxes at 20 m above the bottom were $2.49 \text{ g m}^{-2} \text{ d}^{-1}$ and $20 \text{ mg C m}^{-2} \text{ d}^{-1}$, respectively. At the same area, in situ incubation of two cold-water coral species, *Lophelia pertusa* and *Madrepora oculata*, using the Calmar benthic chamber indicated a coral oxygen consumption rate of $7.3 \mu\text{mol O}_2 \text{ dry weight g}^{-1} \text{ d}^{-1}$, and a production rate of ΣCO_2 and NH_4^+ equal to $7.6 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ d}^{-1}$ and $0.18 \mu\text{mol NH}_4^+ \text{ g}^{-1} \text{ d}^{-1}$, respectively. The respiratory coefficient was equal to 1, indicating an omnivore food source. This conclusion was also confirmed by the O:N index. The coral energy requirement was equal to $2.1 \text{ mmol C m}^{-2} \text{ d}^{-1}$. Comparison between carbon input in terms of particle flux and carbon oxidation rate by corals indicates that the energy supply to the bottom seems not sufficient to sustain the development and growth of cold-water coral all year in the Brittany canyons. However, coral necessarily require another source of energy such as zooplankton, particularly in summer and autumn when particle flux is reduced. Overall, the presence of abundant cold-water coral in the Brittany submarine canyons indicates that this location is ideal for their development given appropriate hydrological condition, favorable hard substrate, and also food availability.

Cold-water coral reefs are biodiversity and biomass hotspots of the deep sea (Roberts et al. 2006; van Oevelen et al. 2009). Hosting a high variety of organisms and seabed habitat types, they provide shelter to abundant marine life including various species of commercial fishes (Rogers 1999; Fossa et al. 2002; Husebo et al. 2002). Their susceptibility to anthropogenic effects and their slow rates of recovery from disturbance (Gass and Roberts 2006) have led to an increasing realization that cold-water coral ecosystems deserve full protection and dedicated resource management policies. Indeed, climate change effects, most prominently rising seawater temperatures and aragonite saturation horizons, and subsequent calcification impediment, are projected to severely affect cold-water coral environments (Gattuso et al. 1995; Ramirez-Llodra et al. 2011). Bottom trawling, together with oil and gas exploration, further threaten the cold-water coral communities, pointing them out as one of the most vulnerable deep-sea ecosystems.

Cold-water corals occur in extreme conditions of low temperature, limited food supply (Roberts et al. 2003), in absence of light, and at depths $> 2000 \text{ m}$. Reefs can reach hundreds of meters in length and tens of meters high, and host a rich and complex ecosystem structure that can last some thousands of years (Roberts et al. 2009b). Cold-water corals depend on detrital particulate organic matter laterally advected by currents or sinking from the productive

euphotic zone (Duineveld et al. 2004), or by filter-feeding on zooplankton and small prey such as crustaceans and krill (Roberts et al. 2009a). Hence, cold-water corals live preferentially in turbulent hydrodynamic environments (Rogers 1999; Roberts et al. 2006). Indeed, strong currents may increase their food supply and prevent colonies from becoming buried in sediment (Duineveld et al. 2004; Thiem et al. 2006; Mienis et al. 2007). As net heterotrophic benthic communities are tightly coupled to surface primary productivity (Duineveld et al. 2004; Becker et al. 2009; Roberts et al. 2009b) and to the quality of organic matter reaching the seafloor (Duineveld et al. 2007; van Oevelen et al. 2009), the metabolism and development of cold-water corals are driven by local environmental parameters (currents, temperature, and substrate type). For example, cold-water coral respiration is known to be sensitive to short-term temperature changes (Dodds et al. 2007). However, the effects of several ecological drivers on coral metabolism and the interactions between cold-water coral ecosystems and regional benthic functioning are still poorly documented (van Oevelen et al. 2009).

Cold-water corals occur along the whole Northeast Atlantic continental margin, from Norway to Spain, and also in the head of the English Channel canyons (for review, see Réveillaud et al. 2008). Corals *Lophelia pertusa* and *Madrepora oculata* and associated fauna have been sampled on the continental margin of the Bay of Biscay in water depth from 150 to 1700 m (Le Danois 1948). However, these fragile ecosystems are poorly documented

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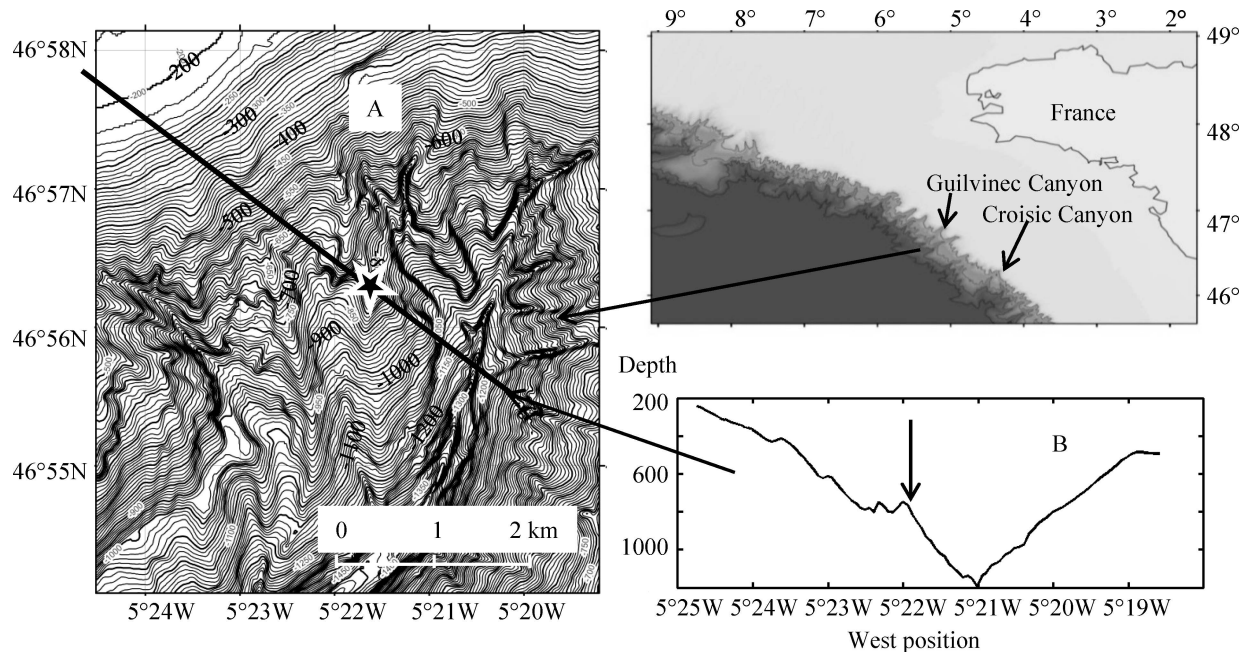


Fig. 1. (A) Map of the Guilvinec Canyon head where the Calmar benthic chamber and long-term moorings were deployed (white star). (B) Cross section of the canyon head corresponding to the white line on the map (the vertical arrow indicates the position of the moorings).

and little is known about their distribution or functioning in relation with local environmental conditions. Further information is therefore needed for a sustainable management of the area.

The aim of this study is to describe the habitat conditions of cold-water corals in deep submarine canyons on the Brittany continental slope (Bay of Biscay–Northeast Atlantic) by integrating information from the characteristics of the local coral habitat based on long-term measurements of current and organic carbon input and biomass and in situ coral metabolism. The proportion of organic carbon oxidized by the coral population is then analyzed to explore the energy budget needed for the development of cold-water coral reefs.

Methods

Study area—The canyons of Guilvinec and Croisic are located on the Armorican margin of the Bay of Biscay (Fig. 1), which extends between the basin of southern Britain and the north of the Bay of Biscay. This margin is cut by deep canyons and incisions. Canyon heads are particularly wide, and their complex morphology is controlled by the structural heritage of the margin and by past gravity events (Bourillet et al. 2003). The morphobathymetric map, recently drawn by J.-F. Bourillet (pers. comm.), shows slide scars, cliffs of several tens to hundreds of meters high generally found at the head of canyons.

Long-term measurements—Long-term moorings were deployed on the rocky outcrop located on the north wall of the head of Guilvinec Canyon (Fig. 1), at 850 m depth (46°56.25'N, 5°21.60'W). They were arrayed for nearly 2 yr from 23 October 2009 (BobGeo cruise) to 24 July 2010

(BobGeo2 cruise), and from 25 July 2010 to 13 September 2011 (BobEco cruise). The line was equipped with a Doppler Recording Current Meter (RCM 11, Aanderaa; range = 0–300 cm s⁻¹, accuracy = ± 0.15 cm s⁻¹) and an oxygen optode (model 3830, Aanderaa; response time = 30 s, accuracy = 8 μmol L⁻¹) fixed at 30 m above the bottom (mab) with a sampling interval of 1 h for both equipment, and a conical sediment trap (Pièges à Particules Séquentiels PPS 5-Technicap) with a sampling aperture of 1 m² at 20 mab. The sediment trap was covered with a honeycomb baffle with 10 cm deep cells, which were 1 cm in diameter and equipped with 24 sampling bottles. The duration of each sample sediment trap collection was 15 d. Before mooring, the sampling bottles of the sediment traps were filled with filtered seawater and sodium borate-buffered formalin to a final concentration of 3%. Once in the laboratory, the contents of each sampling bottle from the sediment traps were examined under a dissecting microscope to sort and count all the organisms. The remaining particles were then rinsed with Milli-Q purified water (pH ~ 7), freeze-dried, and weighed. The organic carbon concentration was measured with a Leco Carbon–Sulfur CS-125 elemental analyzer after removing carbonates with a 2 mol L⁻¹ HNO₃ solution for 12 h (Weliky et al. 1983). Inorganic carbon content was estimated as the difference between total and organic carbon. Nitrogen and total carbon were determined in duplicate using a Leco Carbon–Nitrogen–Sulfur CNS-2000 auto-analyzer.

A second mooring was deployed for 2 months (from 14 May 2010 to 24 July 2010) close to the position of the long-term mooring. It was equipped with a down-looking Acoustic Doppler Current Profiler (ADCP) 600 kHz (Teledyne RD Instruments; range = 0–500 cm s⁻¹, accuracy = ± 0.5 cm s⁻¹) and positioned at 25 mab. It recorded a current

vertical profile every 10 min. A vertical bin size of 0.8 m was used to provide horizontal and vertical current speed and direction at 23 elevations from 18 m down to 1 mab.

A third mooring was deployed for 15 d during the BobEco cruise at the same position as the ADCP. It was equipped with a SeaGuard current meter (Aanderaa; range = 0–300 cm s⁻¹, accuracy = ± 0.15 cm s⁻¹) with an oxygen optode (model 4330, Aanderaa; response time = 25 s, accuracy = 5 μmol L⁻¹), a conductivity sensor (range = 0–7.5 S m⁻¹, accuracy = ± 0.005 S m⁻¹), and a turbidity sensor (output signal = 0–5 V, noise < 1 mV). The SeaGuard was positioned at 25 m altitude. The recording interval was every 10 min.

The frequencies of fluctuation in current speed, temperature, pressure, and oxygen from these instruments were measured by power spectral density computations on data pre-filtered by a Hanning window.

Biomass and respiration rate—Coral beds were visually selected during the Remotely Operated Vehicle (ROV) *Victor* dives (BobEco cruise, September 2011) before sampling two coral species, *L. pertusa* or *M. oculata*, to ensure that they would be representative of the entire community. The distribution of coral at the Guilvinec station was not homogenous on the bottom, and the main density was calculated in two different ways. Coral density (branches m⁻²) of the two species was estimated using 10 h of video recordings to calculate the number of coral clumps on a surface of about 200 m², this surface area estimated from the ROV's movements as measured by acoustic positioning. A few dozen photos, taken during the Calmar deployments (Fig. 2, below), were also used to estimate coral branch density on smaller areas (~ 3 m²). In this case, Calmar was used as a scale. Videos and photos were recorded during two ROV dives. The wet weight of a clump was measured on the coral collected during the same dives. At the laboratory, wet weight, dry weight, and ash-free (AF) dry weight were determined. Dry weight was obtained after drying coral at 60°C for 24 h. Ash weight was measured after combustion for 12 h at 550°C. AF dry weight was determined after subtracting ash weight from dry weight. The conversion of dry organic matter to carbon is calculated based on the conversion factor of 51.8% (Salonen et al. 1976).

To assess the in situ coral respiration rate, the Calmar benthic chamber (Caprais et al. 2010) with its tank (Fig. 2) was deployed by the ROV *Victor* at both sites: Guilvinec Canyon (850 m depth) and Croisic Canyon (880 m depth). Calmar is a cylinder of 41 cm in diameter, open at one end. It is equipped with five sampling cells inside the chamber (100 mL each), an oxygen probe (model 3830, Aanderaa), and a stirrer to homogenize the water under the chamber. The position of cells under the chamber and their closure mechanism preclude any suction and infiltration of uncontrolled water movement (Caprais et al. 2010). At the beginning of the experiment, one or two coral branches were carefully sampled using the ROV arm and dropped into a cylindrical tank. Then the Calmar was placed over this tank, sealing the tank and immersing the coral in exactly 31 liters of bottom water. The incubation was then

started and lasted for 6 h in situ on the sediment. In the Guilvinec Canyon, two Calmar benthic chambers (Calmar B2 and A3) with accompanying tank were used, the first with 300 g wet weight of *L. pertusa* and the second with 400 g wet weight of *M. oculata*. In the Croisic Canyon, one Calmar (B1) was deployed with 450 g wet weight of *M. oculata*. Wet weight, dry weight, and AF dry weight were determined for the coral sampled in each Calmar chamber.

Values of oxygen concentration in the Calmar were obtained by the oxygen optode probe and by the Winkler titration method (Carritt and Carpenter 1966) on the sequential water samples (five sampling cells). Total dissolved inorganic carbon (ΣCO₂) was determined using a nondispersive infrared sensor gas analyzer Perichrom (Kaltin et al. 2005), and ammonium was measured using the fluorescence method (Holmes et al. 1999) on the water samples. The analytical methods are described in detail in Caprais et al. (2010).

Respiratory oxygen consumption was also measured ex situ on selected corals sampled in the B1 and B2 Calmar tanks 1 h after their recovery. About 20 g of wet coral was put inside a closed vial in a temperature-controlled shipboard room at 10°C (bottom-water temperature). An incubator vial of 1.8 liters was filled with water sampled in situ with the Calmar tank and it was equipped with a stirrer and an oxygen microprobe (Unisense). Changes of oxygen concentration over time were measured with the microprobe and recorded every 10 s. The oxygen probe was calibrated regularly using Winkler titrations.

Oxygen uptake, ΣCO₂ production, and NH₄⁺ excretion (in μmol dry weight g⁻¹ h⁻¹) were calculated using the following expression:

$$B^{-1} [VT^{-1}(C_2 - C_1)] \quad (1)$$

where B is the dry weight or carbon biomass of coral in tank or vial (g), C₁ and C₂ is gas or ammonium concentration in tank or vial with coral at time 1 and 2 (μmol L⁻¹), V is volume of tank or vial (liters), and T is time interval between measurements (h). The respiratory coefficient (RQ) was calculated as ΣCO₂/O₂ and the O:N index was calculated according to their atomic equivalents.

Results

Near-bottom hydrodynamics—Long-term sediment trap-current meter mooring, deployed for 2 yr at 30 mab, revealed an average current speed of 19.3 cm s⁻¹ (ranged from 0.3 to 74.8 cm s⁻¹) and the maxima were observed in March 2010 and March 2011. Mostly, temperatures, speeds, and oxygen concentrations were the highest when the current was oriented to the southwest (Fig. 3). The lowest values of temperature and the highest values of oxygen were observed in March in association with peaks in current speed. The average temperature was 10.25 ± 0.64°C, with a maximum of 11.47°C (January 2011) and a minimum of 7.55°C (March 2010). Oxygen concentration varied from 299 (March 2011) to 160 μmol L⁻¹ (July 2011).

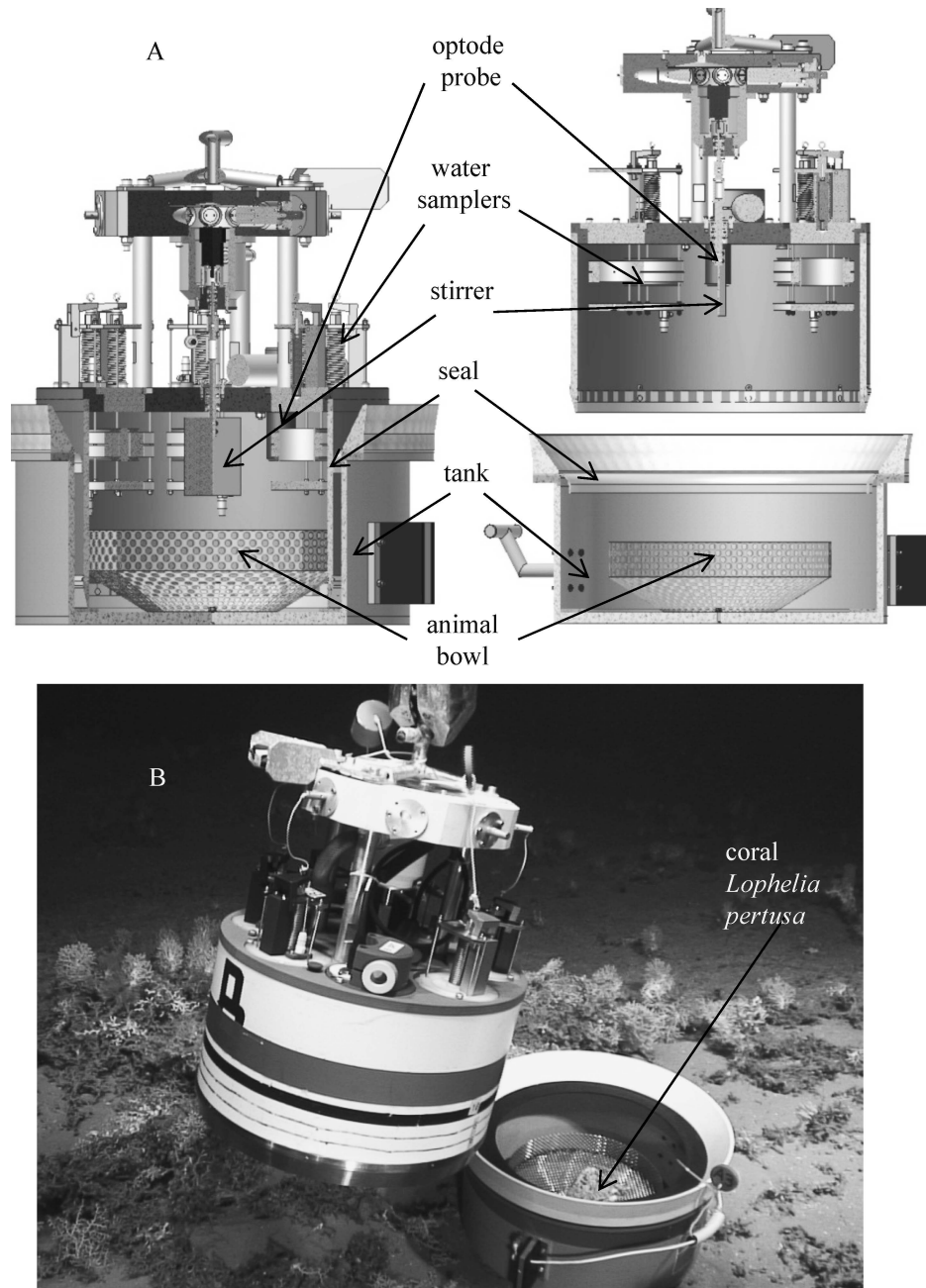


Fig. 2. (A) Scheme of the Calmar benthic chamber, with tank. (B) In situ picture of Calmar in the deep-water coral environment.

The progressive vector plots show the displacement of water (Fig. 4) and indicate the resultant of direction and magnitude of the current at the station where the mooring was deployed. Net displacement was exclusively governed by topography and was oriented in the general canyon direction with a residual current of 2.5 cm s^{-1} . A zoom of the progressive vector calculated from the ADCP records obtained for 2 months confirmed the general southwest orientation of the water mass, from the sea bottom to an elevation of 25 m (Fig. 4). The current characteristics recorded with the ADCP for 2 months did not present large variation at different altitudes in terms of speed and

direction from 0.8 m to 18.4 mab (Fig. 4). The speed was at its highest value very close to the sediment and decreased with elevation by about 2% per meter. The current was essentially oriented northeast–southwest, and no hydrodynamic vortex was observed during the measurements.

Current records at different time scales obtained with the ADCP, RCM 11, and SeaGuard current meters show different distinct oscillations (Fig. 5). Several well-marked frequencies were detected with the power spectrum density analysis with a distinct semidiurnal tidal cycle of 12.4 h and the harmonic. They were also observed in the data analysis of current speed, temperature, pressure, and oxygen (Fig. 5).

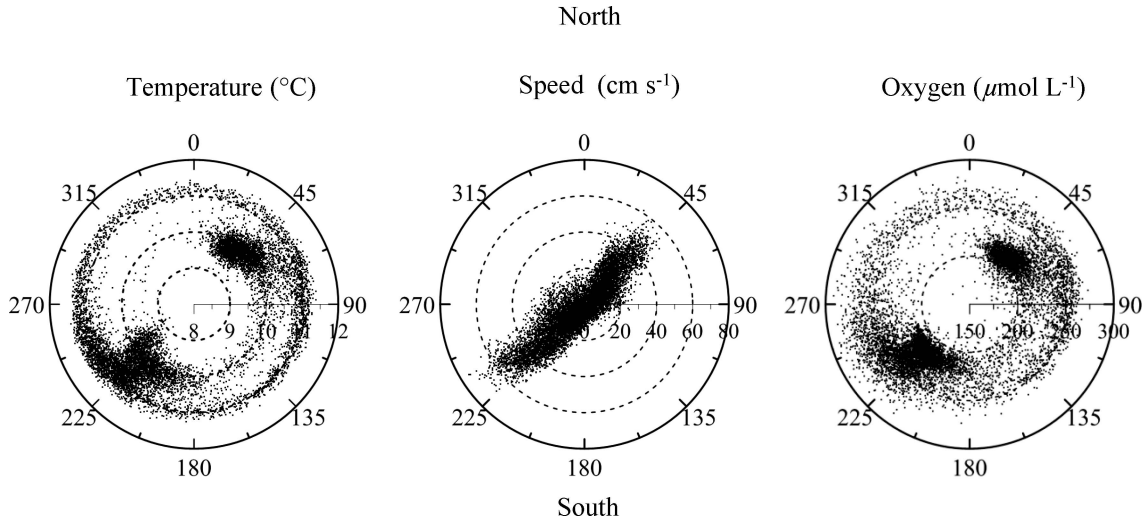


Fig. 3. Polar plots of the temperature, speed, and oxygen of the water mass flowing through the Guilvinec Canyon for 1 yr at 30 mab.

The other frequencies observed in the long-term current meter record were also associated with neap–spring tidal cycles with a cycle of 15 and 26 d for speed, temperature, and oxygen (Fig. 5).

The pattern of temporal variations in the bottom-water characteristics observed for 10 d with the SeaGuard current meter also indicated typical semidiurnal cycles (12.4 h) in temperature, oxygen, salinity, direction, and pressure (Fig. 6). The maximum daily ranges were 2.10°C for temperature, 70.5 μmol L⁻¹ for O₂ concentration, and 0.27 for salinity. When the current direction turned south–southwest, oxygen and temperature increased whereas salinity and pressure (low tide) decreased and vice versa when the current direction was north–northeast. Overtides of the principal lunar semidiurnal tide were also observed at periods of about 6.2 h and 4.1 h. The turbidity signal was not affected by tide or any other hydrological cycle (Fig. 6).

The particle material movements revealed by the vertical current measured with the ADCP current meter were downward when the current was to the northeast and upward when it was oriented to the southwest (Fig. 7).

Mass fluxes and particle composition—The efficiency of our sediment trap moorings in the high-speed environment in Guilvinec Canyon depended on current intensity. With a current speed of ≥ 15 cm s⁻¹, the mooring line took on a significant angle (Fig. 8). In this hydrodynamic context, we determined that the average particle mass flux measured over 690 d and at 20 mab was equal to 2.49 g m⁻² d⁻¹ (range 0.04–130 g m⁻² d⁻¹). These values are underestimated given that the mooring was tilted > 45% of the time, thus preventing sediment from properly entering the sediment trap. High temporal variation in the mass flux was observed during the 2 yr of the experiment, with a

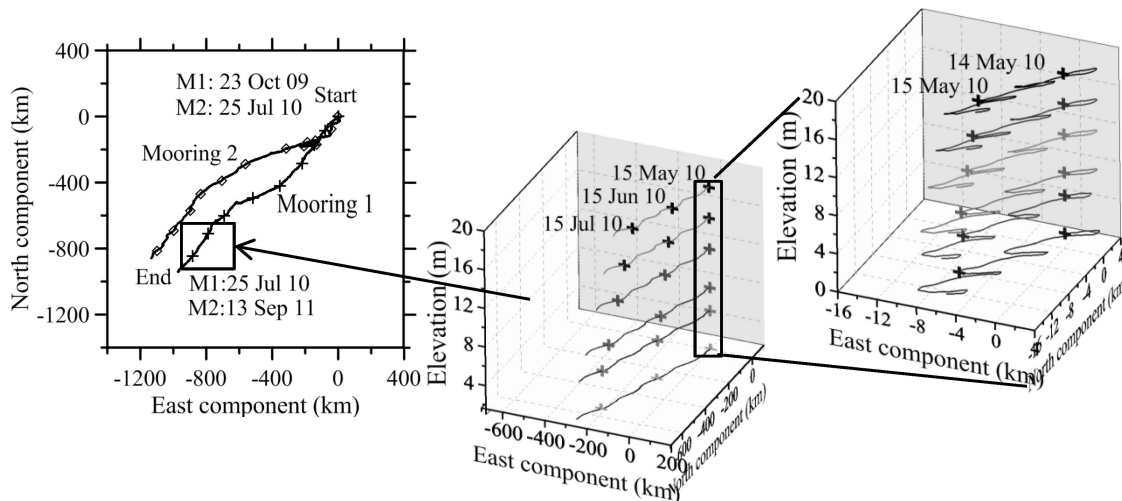


Fig. 4. Progressive vector plot of the current in the Guilvinec Canyon measured for 2 yr. The two insets show successive zooms of vector sections.

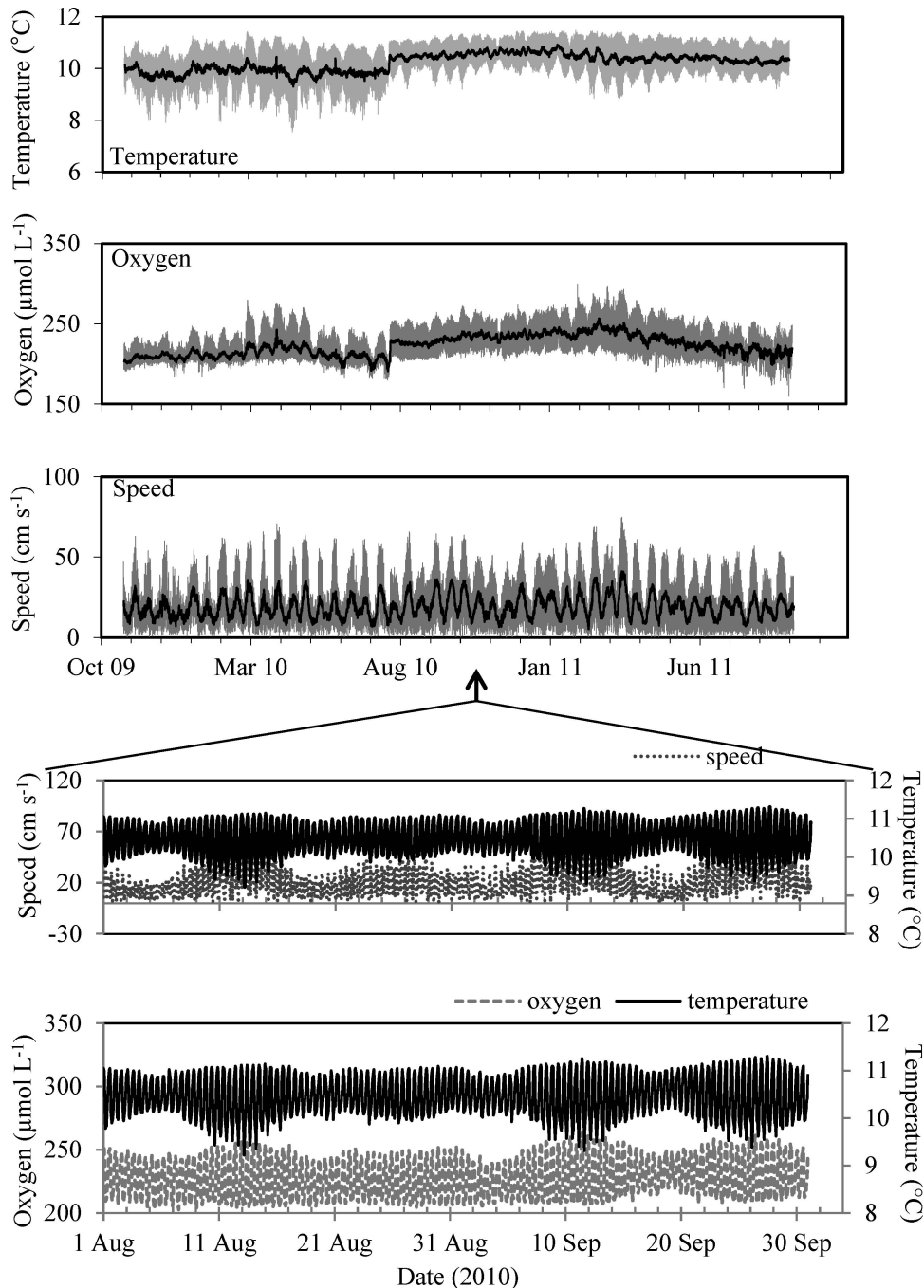


Fig. 5. (A) Two year records of temperature, oxygen, and current speed in the Guilvinec Canyon at 30 mab (black line shows the moving average in base 10). (B) Zoom of these records.

maximum in February–March 2010 and March 2011 and a minimum from April 2010 to January 2011 (Fig. 9).

The elemental composition of particles (Table 1) was characterized by organic carbon (OC) concentrations ranging from 0.25% to 4.2%. Maximum OC concentrations were measured in May–June 2010 when the particle flow was at its lowest. Inorganic carbon concentrations were always high (10%) and did not fluctuate throughout the year. The total OC flux was, on average, equal to $20 \text{ mg C m}^{-2} \text{ d}^{-1}$ ($1.7 \text{ mmol C m}^{-2} \text{ d}^{-1}$).

Biomass and respiration measurements—The mean density of coral, established using ROV *Victor* videos and photos, was three live coral branches m^{-2} on the bottom of the Guilvinec Canyon head. The mean weight for each branch was 350 g dry weight (or 10 g C). The density of living coral scleractinians (*L. pertusa* + *M. oculata*) was 1050 g m^{-2} or 30 g C m^{-2} .

At the two experiment sites, the oxygen concentration of the surrounding water was $230.8 \pm 0.2 \text{ } \mu\text{mol L}^{-1}$ at the beginning of the experiment. After 6 h of coral incubation

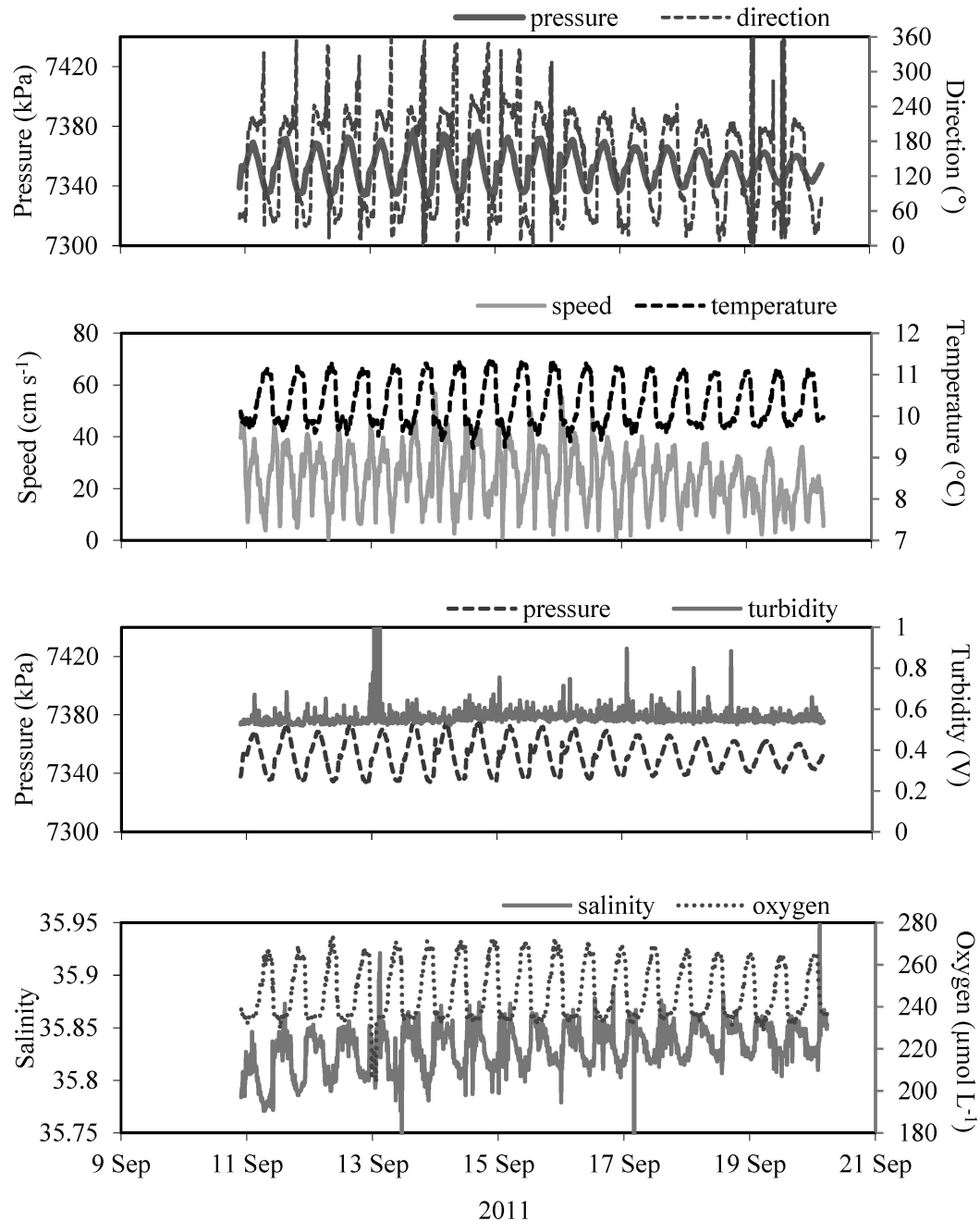


Fig. 6. High-frequency records of the water mass (pressure, direction, speed, temperature, turbidity, salinity, and oxygen) in Guilvinec Canyon at 30 mab, reflecting the neap and spring tidal cycles.

at 9.6°C to 10.2°C, the oxygen concentration was never lower than 190 $\mu\text{mol L}^{-1}$. The decrease of oxygen concentration was < 20% during the incubations. The mean coral oxygen respiration rate in the two canyons was equal to 7.3 $\mu\text{mol O}_2$ dry weight $\text{g}^{-1} \text{d}^{-1}$. No differences in respiratory metabolism were observed between *L. pertusa* and *M. oculata* or between the coral branches sampled in the Croisic and Guilvinec Canyons (Table 1). The O_2 consumption due to coral respiration was 7.7 $\text{mmol O}_2 \text{m}^{-2} \text{d}^{-1}$, using the conversion between dry weight and surface area calculated above.

The ex situ coral respiration, based on onboard incubation in the cold room at 10°C, was twice as high

(15.8 $\text{mmol O}_2 \text{g}^{-1} \text{d}^{-1}$) as the in situ experiments (Table 2).

The ΣCO_2 concentration at the sea bottom was, on average, $2086 \pm 56 \mu\text{mol L}^{-1}$. The mean ΣCO_2 respiration rate by the coral was equal to 7.6 $\mu\text{mol g}^{-1} \text{d}^{-1}$. The ΣCO_2 flux production by the coral was 7.9 $\text{mmol CO}_2 \text{m}^{-2} \text{d}^{-1}$. The general RQ was about 1.

The ammonium concentration in the surrounding water was $0.98 \pm 0.13 \mu\text{mol L}^{-1}$ at both sites. After 6 h of incubation, its concentration increased, indicating significant coral ammonium excretion. The ammonium rate produced by coral was 0.18 $\mu\text{mol NH}_4^+ \text{g}^{-1} \text{d}^{-1}$ and the

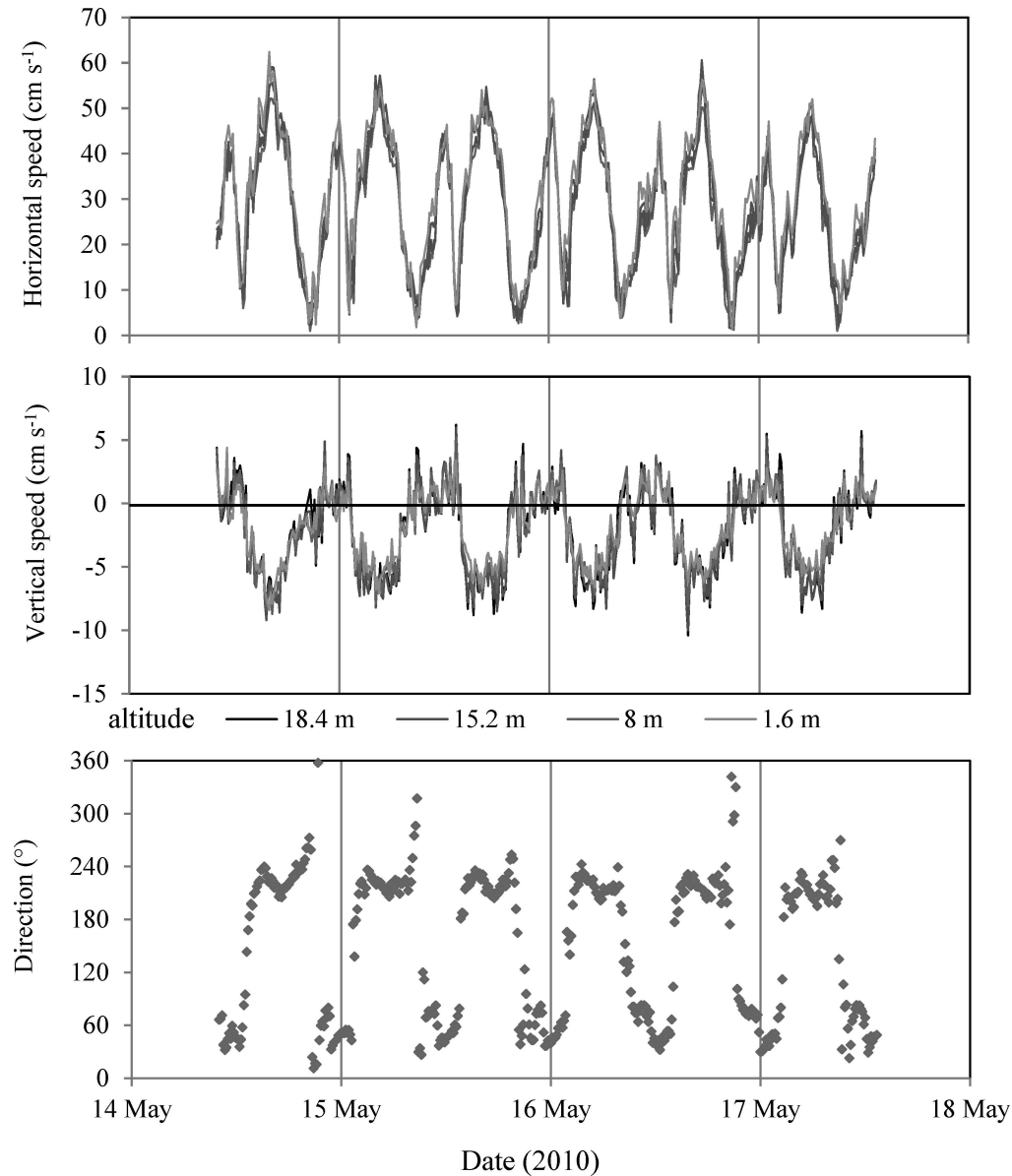


Fig. 7. Horizontal and vertical speed currents at four different altitudes, and current direction measured with ADCP current meter.

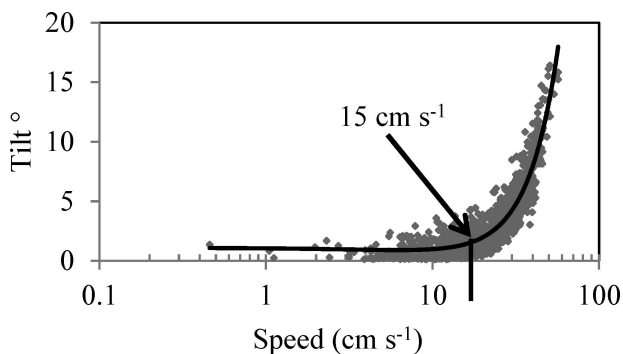


Fig. 8. Relationship between the tilt of the mooring and the current speed. The speed at 15 cm s^{-1} is the limit for proper functioning of the sediment trap.

flux was $189 \mu\text{mol NH}_4^+ \text{ m}^{-2} \text{ d}^{-1}$. The ratio between oxygen consumption and ammonium excretion rates (O : N index) was, on average, 44. These results are summarized in Tables 1 and 2.

Discussion

Abiotic environment—Hydrodynamic conditions are one of the essential factors influencing coral occurrence (Duineveld et al. 2007). Cold-water corals are also sensitive to short-term temperature changes (Dodds et al. 2007). They are generally restricted to water temperatures between 4°C and 12°C (see the review Roberts et al. 2006) and the temperatures measured in the Guilvinec Canyon ($8\text{--}11^\circ\text{C}$) fall in this range. In addition, the presence of hard substrate

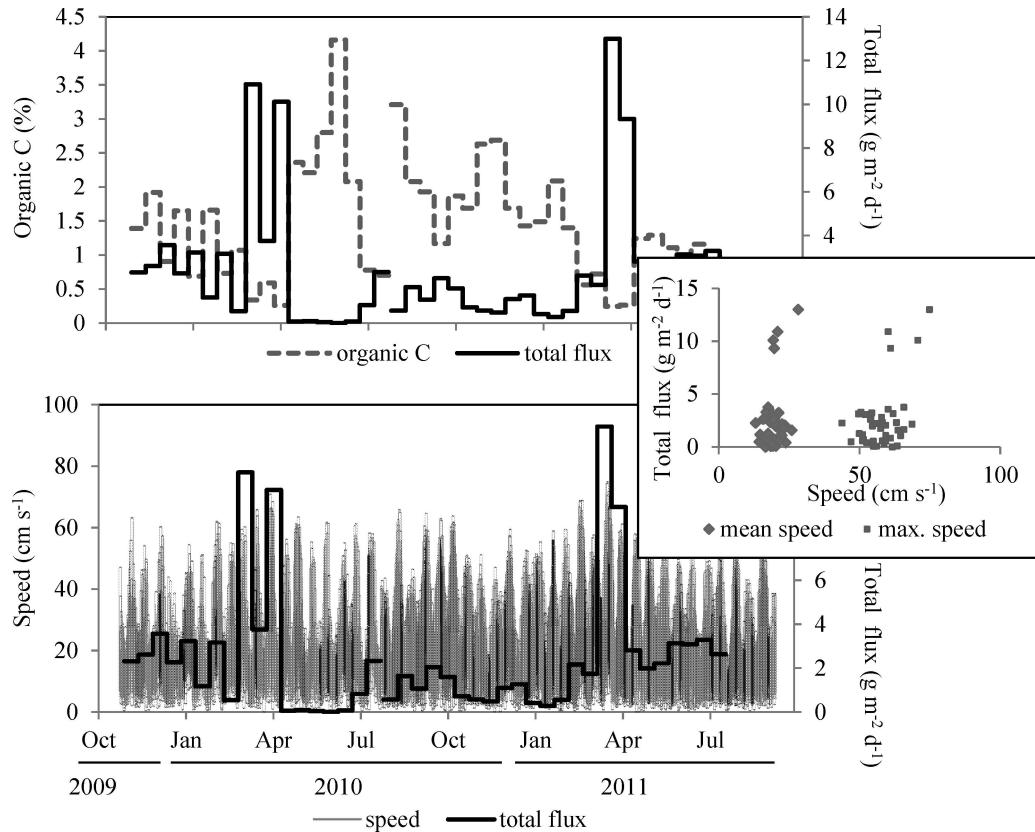


Fig. 9. Total particle flux, carbon concentration of particles (20 mab), and current speed (30 mab) during the 2 yr of measurement in the Guilvinec Canyon. In the inset, total flux vs. mean and maximum current speed.

plays a substantial role in cold-water coral development (but not exclusively, *see* Duineveld et al. 2004 for observation of cold-water corals on soft sediment).

In terms of current, large internal tides are generated at the head of the Guilvinec Canyon. The instantaneous bottom current leaves the upper slopes and propagates to the ocean along the local topography (the axis of the canyon) and the morphology of the mounds (Pingree and Le Cann 1989). The result is considerable daily variations in temperature, current velocity, salinity, and oxygen, allowing continual water-mass movements around the coral reefs with current speeds of up to 70 cm s⁻¹ at 30 mab and clear neap and spring tidal cycles (Fig. 5). These same conditions are commonly observed near the coral reefs found in the Atlantic (Duineveld et al. 2007; Mienis

et al. 2007; Roberts et al. 2009a). The daily variation in temperature, oxygen, and salinity are caused by the displacement of water masses from deep to shallow and vice versa twice per day along the topography of the canyon (Figs. 4, 6). The resulting internal waves have positive vertical speed when the current comes from the deep to the coast and negative vertical speed when the current flows down to the deep canyon. The elevated current speeds around the coral reefs facilitate oxygen flow around the coral and increase the amount of suspended material which is a potential food supply for the coral polyps. High current speed may also regularly remove any sediment that settles on the coral reef. In conclusion, expansion and growth of cold-water coral reefs in the Gulf of Biscay requires very specific and strong hydrodynamic

Table 1. In situ incubation of cold-water coral in the Calmar benthic chamber at 850 m depth.

Parameter	Site, Calmar No., and species			Mean
	Guilvinec, B2 (<i>Madrepora oculata</i>)	Guilvinec, A3 (<i>Lophelia pertusa</i>)	Croisic, B1 (<i>Madrepora oculata</i>)	
% organic matter	7.1	5.7	6.1	6.3
$\mu\text{mol O}_2 \text{ g}^{-1} \text{ d}^{-1}$	6.4	7.7	7.9	7.3
$\mu\text{mol CO}_2 \text{ g}^{-1} \text{ d}^{-1}$	7.5	8.5	6.75	7.6
CO ₂ :O ₂ respiratory quotient	1.2	1.1	0.85	1.05
$\mu\text{mol NH}_4^+ \text{ g}^{-1} \text{ d}^{-1}$	0.20	0.22	0.12	0.18
O:N	32	35	66	44

Table 2. Ex situ incubation results of cold-water coral obtained in the shipboard cold room (10°C).

Parameter	Site, Calmar No., and species	
	Guilvinec, B2 (<i>M. oculata</i>)	Croisic, B1 (<i>M. oculata</i>)
% organic matter	8.0	8.9
$\mu\text{mol O}_2 \text{ g}^{-1} \text{ d}^{-1}$	14.6	15.8

conditions that ensure regular water renewal. The absence of a relationship between the turbidity records and the current direction or speed contradicts the observations noted in Duineveld et al. (2007) in a similar situation. At the Guilvinec station, the hard substrate and the low sedimentation rates can explain the absence of notable particle resuspension whatever the current speed intensity. Although a high-energy hydrodynamic environment seems to be necessary for the coral colonization, likely limitations exist when coral larvae cannot settle in too high current speed. Moreover, high-energy conditions also hamper coral feeding by increasing the difficulty of catching particles (Purser et al. 2010). The question is: What are the mechanisms that ensure coral colonization on hard or soft substrates when the environment is characterized by very strong currents?

At the seasonal scale, changes were also observed on the Armorican shelf in early spring, with an increase of current speed and oxygen and a decrease in temperature (Fig. 5). These particular conditions may be a signal to synchronize the gamete emission. However, no primary production bloom was detected in the sediment trap during the 2 yr of the experiment. This primary production flux may be diluted by tidal movements when it settles to the bottom.

Particle supply—Food availability in terms of particle flux is also a major key factor influencing coral growth (Roberts et al. 2009a). The sediment trap that measures settling particle flux is used to quantify the energy supply that reaches the cold-water coral reefs (Duineveld et al. 2004; Mienis et al. 2009). The collection efficiency of sediment traps depends on flow velocity, trap shape, the tilt of the mooring, and the settling velocity of particles (Baker et al. 1988; White 1990; Gardner et al. 1997). Sediment traps in high-energy environments are generally not recommended since they are primarily designed to measure vertical particle fluxes and are disrupted when the mooring tilts due to strong currents. However, sediment traps in a canyon remain useful for a rough estimation of the amount of transported sediment by turbidity current, for example (Khripounoff et al. 2009, 2012; Xu et al. 2010). Compared to the measurements made on the Galicia Bank at 770 m depth ($0.9 \text{ g m}^{-2} \text{ d}^{-1}$; Duineveld et al. 2004) or in the Rockall Trough at 600–1000 m depth ($1.4 \text{ g m}^{-2} \text{ d}^{-1}$; Mienis et al. 2009), the near-bottom mass flux of $2.49 \text{ g m}^{-2} \text{ d}^{-1}$ in the Guilvinec Canyon is two times larger. The peculiarity of these fluxes observed in the Northeast Atlantic is that the most of the cumulated annual input from these fluxes (40% to 60%) is deposited in the winter over a short period of time (< 1 month; see

Fig. 9). This seasonality can be explained by possible resuspension from the seafloor due to strong currents (Duineveld et al. 2004) or internal waves, suggesting a common forcing mechanism (Mienis et al. 2009). In those previous studies, the strongest supporting evidence was the relationship between the average current speed and the mass flux. In our case, the origin of the peaks in particle flux observed in March 2010 and 2011 is not clear. There was no correlation between current speed and particle flux (Fig. 9). We discerned periods with high speed without increase in particulate material inside the sediment trap. In contrast, low particle fluxes were regularly obtained when currents were $> 60 \text{ cm s}^{-1}$ in autumn, for example (Fig. 7). The hypothesis that particle flux peaks originate from primary production blooms is not supported by the sea-surface satellite pictures taken during the same period. The maximum chlorophyll during the spring bloom was in April 2010 and April 2011, 1 month after the two particle peaks. Visual inspection did not reveal any differences in particle composition between the different periods of sampling. However, the elemental composition of sediment trap material indicated the lowest OC concentration when the particle flux was maximal. This result suggests that, during this period of high particle flux, the settling material had a sedimentary origin, poor in organic matter, rather than a primary production source. The hypothesis that the Guilvinec Canyon canalizes sediment material and transports it to the deep sea by sediment gravity flow cannot be excluded for some periods of the year. Nevertheless, the trigger for such an event is not known, and no distinctive storms were observed in February–March 2010 and 2011 along the coasts of Brittany.

Respiration and carbon cycle—We have found no literature reporting in situ O_2 respiration measurements of cold-water corals. However, Dodds et al. (2007) report a respiration rate of *L. pertusa* in aquaria of $5.3 \mu\text{mol O}_2 \text{ g}^{-1} \text{ d}^{-1}$ at 9°C and $7.7 \mu\text{mol O}_2 \text{ g}^{-1} \text{ d}^{-1}$ at 11°C. These values are similar to our results on respiration with an in situ rate at 10°C of $7.3 \mu\text{mol O}_2 \text{ g}^{-1} \text{ d}^{-1}$. The elevated respiration rate of *M. oculata* during our ex situ experiments ($15.8 \mu\text{mol O}_2 \text{ g}^{-1} \text{ d}^{-1}$) in the shipboard cold room was twice that observed in situ, also at 10°C, and can be tentatively attributed to fast decompression during sample recovery. On the other hand, a similar ex situ experiment on cold-water coral sampled at 800 m depth from the Rockall Bank indicates a much lower respiration rate ($1.7 \mu\text{mol O}_2 \text{ g}^{-1} \text{ d}^{-1}$; van Oevelen et al. 2009). The large difference in these two ex situ experiments may be a result of the increase in the respiration rate due to stress for the corals sampled in the canyons on the Brittany shelf, or bad sampling conditions or poor conservation of coral from Rockall Bank.

The in situ incubation method explored in this study provides a simultaneous measurement of ΣCO_2 production and O_2 consumption rate. We can calculate the RQ and give information on the catabolism and fuel energy of the cold-water corals. The RQ value changes for different organisms, and it is mainly determined by the elemental composition of the food source and the type of metabolism

(Hatcher 1989). The average value found in the literature for various marine invertebrate species is 0.75. For example, sponges feeding on algae have an RQ of 0.72 and a value of 0.85 when their food source is bacteria (Koopmans et al. 2010). A minimal RQ (0.7) is obtained when only fatty acids are consumed. RQ equal to 1.0 is obtained when sugars are the only food source. Since corals ingest a lot of algae and bacteria, an RQ value of 0.80 obtained during one incubation seems reasonable. RQ of 1.05, obtained during two other experiments, may be due to differential storage of respiratory gases. This kind of storage depends on intrinsic variation in individual animals. Protein-rich food sources have been observed directly in corals by Mortensen (2001), but stable-isotope analysis shows that cold-water corals are able to exploit a variety of organic matter such as phytoplankton, zooplankton, and particles (Duineveld et al. 2004; van Oevelen et al. 2009). This information is confirmed by our analysis of the O:N, which was between 30 to 66. This index indicates the proportion of protein relative to lipids or carbohydrates that is catabolized for the energy requirements of the metabolism. Thus, a high protein-based metabolism, observed in carnivorous–omnivorous organisms, is expressed by a low O:N index compared to diets high in lipids or carbohydrates (Babarro et al. 2000).

The average daily organic carbon flux on the Guilvinec Canyon calculated over 2 yr was $1.7 \text{ mmol C m}^{-2} \text{ d}^{-1}$. This value is very similar to the organic C flux obtained for the coral reef in the Galicia Bank ($1.4 \text{ mmol C m}^{-2} \text{ d}^{-1}$; Duineveld et al. 2004), and higher than in the Rockall Bank ($0.77 \text{ mmol C m}^{-2} \text{ d}^{-1}$; Mienis et al. 2009). The average calculated carbon oxidation rate due to coral metabolism was $7.9 \text{ mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ ($2.1 \text{ mmol C m}^{-2} \text{ d}^{-1}$). Cold-water corals consume energy provided by bottom particle carbon flux, as indicated in the observations of Duineveld et al. (2004) on the Galicia Bank. About half of the yearly carbon input settles on the bottom in the Guilvinec Canyon in less than a month during winter. Its origin is unknown but could conceivably come from a sediment landslide at the top of the canyon. Apart from this short winter period, organic carbon flux is very weak, and the food supply in terms of settling particles is low during the rest of the year for the entire benthic ecosystem. On what food source do cold-water corals rely for > 10 months of the year? Sediment traps sample only passive particles and cannot estimate the density of live plankton, which is known to contribute in situ the coral diet (Duineveld et al. 2004). Large clouds of Euphausiacea krill were observed during several ROV dives in the Brittany canyons (B. Guillaumont pers. comm.). Cold-water corals have an opportunistic behavior and are able to exploit a variety of food sources (van Oevelen 2009), which certainly varies throughout the year.

The presence of living coral indicates that the Guilvinec and Croisic Canyons are ideal locations for their growth and development, given their food availability, appropriate hydrological condition, and favorable hard substrate. The hydrodynamic conditions close the sediment, along with tidal currents are sufficient to transport water masses with particles and oxygen all year. High current speed also

prevents sediment from settling on the organisms. Input of material is well marked by a large seasonal peak in particle flux at the end of winter. The origin of this large pulse is unknown and it cannot be explained only by current dynamics. The respiratory metabolism of cold-water corals is characteristic of a carnivorous–omnivorous diet with an RQ value from 0.8 to 1. The transfer of carbon through the cold-water coral ecosystem in the Brittany canyons shows that the energy supply by particle flux is certainly not sufficient during summer and autumn. Coral development and growth necessarily require another source of energy such as zooplankton.

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