Stable isotope variations in benthic filter feeders across a large depth gradient on the continental shelf

Caroline Nerot [a], Anne Lorrain [a,*], Jacques Grall [b], David P. Gillikin [c], Jean-Marie Munaron [a], Hervé Le Bris [d], Yves-Marie Paulet [a]

[a] LEMAR, UMR CNRS/UBO/IRD 6539, Institut Universitaire Européen de la Mer, Place Nicolas Copernic, 29280 Plouzané, France
[b] Observatoire des Sciences de l'Univers, UMS 3113, Institut Universitaire Européen de la Mer, Place Nicolas Copernic, 29280 Plouzané, France
[c] Department of Geology, Union College, 807 Union St., Schenectady, NY 12308, USA
[d] Université Européenne de Bretagne, UMR 985 Agrocampus Ouest, Inra « Ecologie & Santé des Ecosystèmes », Ecologie halieutique, Agrocampus Rennes, 65 rue de St Brieuc, CS 84215, 35042 Rennes, France

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ABSTRACT

Spatial variations in carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) of benthic filter feeders were investigated on an inshore-offshore gradient (0–250 km) along the continental shelf of the northern Bay of Biscay (NE Atlantic Ocean). $\delta^{13}C$ and $\delta^{15}N$ values were measured in muscle tissues of four filter-feeding mollusc species (epifaunal: *Pecten maximus*, *Aequipecten opercularis*; infaunal: *Glycymeris glycymeris*, *Venus casina*) and in benthic particulate organic matter along a corresponding water-depth gradient from 6 to 220 m. All four species showed a decreasing pattern of muscle $\delta^{13}C$ and $\delta^{15}N$ values with increasing depth. At the Ushant front ($\sim$130 m water depth), where there is a decrease in both bottom water chlorophyll *a* and suspended particulate matter, muscle $\delta^{13}C$ and $\delta^{15}N$ values decreased in all species. Although $\delta^{13}C$ values of infaunal clams initially decreased at 30 m depth, $\delta^{13}C$ values of epifaunal scallops decreased around 120 m depth, far below the expected depth reduction in microphytobenthic production suggesting that carbon isotopes might not simply track microphytobenthic utilization. The difference between infaunal and epifaunal bivalve stable isotope values may reflect differences in feeding strategies. Muscle $\delta^{15}N$ values at the deepest stations ($\sim$2‰) were lower than expected considering the typical trophic enrichment value of 3–4‰ between prey and consumers. These low $\delta^{15}N$ values may result from low metabolic rates and suggest the classic trophic enrichment may not hold true in species inhabiting deep waters. Stable isotopes in benthic filter feeders can reveal much information regarding their ecology and environment, but are not straightforward recorders of stable isotope baseline variations as is often assumed.

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1. Introduction

Numerous studies in marine isotope ecology have demonstrated the suitability of carbon ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$) in benthic filter feeders for revealing trophic and ecosystem functioning (e.g. Riera and Richard, 1996; Fry, 1999; Grall et al., 2006; Mintenbeck et al., 2007; Lefebvre et al., 2009). Filter feeders are assumed to be good candidates to delineate long-term processes and changes in ecosystem trophic functioning because of their sedentary nature and the relatively long turnover time (usually several months or more) of C and N isotopes in their tissues (Lorrain et al., 2002; Jennings and Warr, 2003). Stable carbon isotopes are a powerful tool to differentiate energy fluxes from benthic or pelagic production; typically benthic producers are enriched in ^{13}C when compared to pelagic producers by an average of $\sim$7‰ (France, 1995). For example, Riera and Richard (1996) used carbon isotopes to reveal that microphytobenthos and not phytoplankton were the main food source of estuarine oysters. In addition, nitrogen stable isotopes can indicate watershed influences on downstream production (Fry, 2002) as anthropogenic wastewaters usually elevate $\delta^{15}N$ of dissolved inorganic nitrogen, which then propagates throughout the food web (Cabana and Rasmussen, 1996).

Continental shelves are an interesting but underutilized environment to test pelagic benthic coupling and anthropogenic nutrient inputs because they offer both depth and land-sea gradients. Indeed, large depth gradients are present where

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* Corresponding author.
  E-mail address: anne.lorrain@ird.fr (A. Lorrain).

microphytobenthos production ranges from high in shallow waters to zero in deep waters (MacIntyre et al., 1996). Stable carbon isotopes in benthic filter feeders can be used to check the assumption that microphytobenthos have an important role in the diet of coastal filter feeders by sampling the same species along this depth gradient. Moreover, the land-sea gradient along the continental shelf should lead to a dilution of anthropogenic nitrogen loading, resulting in a decrease in the filter feeder $\delta^{15}N$ values going offshore. Finally, differences in water mass structures (e.g., stratified or mixed) can lead to differences in phytoplankton $\delta^{13}C$ and $\delta^{15}N$ values (Fontugne and Duplessy, 1978; Mauna et al., 2010), which can be recorded in filter feeder tissue (Fry, 1988; Iken et al., 2010). If filter feeders do record these environmental structures, then their carbon and nitrogen stable isotope values can be used to provide environmental information, which is limited on continental shelves.

In this study, we investigated spatial variations in the C and N stable isotope ratios of adductor muscle of four filter-feeding bivalves (two epifaunal and two infaunal) along a depth gradient from 6 to 220 m on the French continental shelf. We aimed to test the hypotheses that (1) a reduction in microphytobenthos utilization with depth is reflected in decreasing muscle $\delta^{13}C$ values; (2) a difference in microphytobenthos utilization between species related to their different modes of life (e.g., epi- or infaunal; cf. Grall et al., 2006) will be indicated by different $\delta^{13}C$ values between species; (3) physical and hydrological structures of the ecosystem (water masses, currents, fronts) lead to differences in muscle C and N stable isotope values, and (4) anthropogenic nitrogen loading decreases with distance from land and result in decreasing muscle $\delta^{15}N$ values with depth.

2. Material and methods

Sampling followed a nearshore-offshore water depth gradient (Fig. 1), from station 1 (6 m depth, 4°26′ W, 48°22′ N) to station 14 at the edge of the continental shelf in the northern Bay of Biscay (up to 220 m depth, 8°15′ W, 48°12′ N), a distance of 250 km. Over this part of the continental shelf, the tidal wave from the open Atlantic is largely amplified and is responsible for the vertical mixing of the water column and the creation of different water masses (Koutsikopoulos and LeCann, 1996; Lazure et al., 2009). The Iroise front and Ushant front are two hydrological structures created by this tidal mixing (Le Boyer et al., 2009). From the coast to the Iroise front (see Fig. 1), the water mass is shallow and well mixed. Between the Iroise and Ushant fronts, the water column is also well mixed but is considerably deeper. After the Ushant front, in the deepest area of the shelf, the water column is stratified, and there is limited exchange between the surface mixed layer and deep waters. At the shelf break, the slope currents are responsible for strong vertical mixing and nutrient input, creating suitable conditions for primary production (Pingree et al., 1982).

Samples were collected during two scientific cruises in May and September 2008. Previous work on Pecten maximus muscles at site 3 showed very small inter-annual variability (<1‰) in both $\delta^{13}C$ and $\delta^{15}N$ values (Lorrain et al., 2002), therefore we did not expect large differences between May and September sampling dates. When possible, P. maximus, Aequipecten opercularis, Glycymeris glycymeris, and Venus casina were collected at each station by dredging (scallop dredge, 50 mm). The epifaunal P. maximus is usually recessed in the sediment with the upper (left) valve level with the substrate (see Brand et al., 2006) and A. opercularis is a more mobile species which lies on top of the substratum (Chapman et al., 1979), but can also be attached with a byssus (Brand et al., 2006). The two infaunal species G. glycymeris and V. casina both bury shallow in the sediment and filter water from the overlying water column. (Ansell, 1962; Ansell and Trueman, 1967). Muscle tissues of bivalves were dissected and stored frozen. Muscle tissues were chosen due to the relatively long
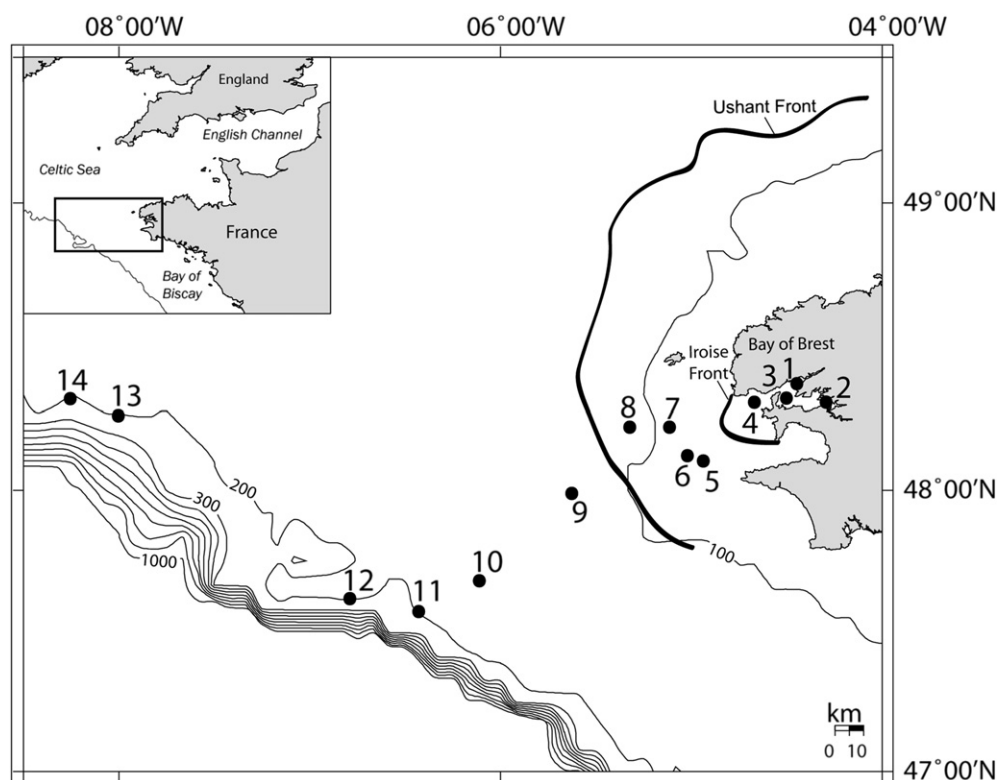

Fig. 1. Map of the study area in northern Bay of Biscay showing bathymetry, position of sample stations (black circles, 1–14), and the position of the Iroise and Ushant fronts.

metabolic turn over time of this tissue (Lorrain et al., 2002; Paulet et al., 2006; Hill and McQuaid, 2009). Muscles were then freeze-dried, ground into powder, and weighed in tin cups for isotopic analysis (about 250 µg in 4 × 6 mm tin cups). $\delta^{13}C$ and $\delta^{15}N$ were measured at the University of New Brunswick (Canada) using a Costech 4010 elemental analyzer coupled to either a Finnigan Delta Plus or a Finnigan Delta Plus XP mass spectrometer.

Seawater was sampled at the same stations, 1 m above the sediment using a Niskin bottle to collect particulate organic matter (POM) for determination of suspended particulate matter concentration (SPM), chlorophyll *a* concentration (Chl *a*), C/N ratios and C and N stable isotope analysis. For SPM, seawater was filtered through pre-combusted and pre-weighed GF/F Whatman filters (47 mm); filters were rinsed with distilled water to dissolve sea-salt and were stored frozen. SPM filters where then oven-dried (60 °C, 48 h) and weighed again; SPM was only sampled during the September cruise. For Chl *a* concentration, seawater was filtered through GF/F Whatman filters (47 mm), rinsed with filtered seawater and stored frozen. Chl *a* was extracted with acetone (4 °C, overnight, rotating mixing) and measured with a fluorometer (10-AU Turner Design). POM samples were processed following Lorrain et al. (2003), and $\delta^{13}C$ and $\delta^{15}N$ values of POM were measured in the LIENSs laboratory (La Rochelle, France) using a Thermo Scientific

Delta V Advantage mass spectrometer and a Thermo Scientific Flash EA1112 elemental analyzer. $\delta^{13}C$ of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) was also sampled in May and analyzed at the Vrije Universiteit Brussel following Gillikin and Bouillon (2007). Results are expressed in standard δ notation based on international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the equation: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$ (in ‰), where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Analytical precision based on repeated analysis of acetanilide (Thermo Scientific) was <0.15‰ for both carbon and nitrogen.

All data were log-transformed to match normality and variance homogeneity. Rank of $\delta^{13}C$ and $\delta^{15}N$ values of the four species were tested at each site with a Kruskall–Wallis test on species ranks.

3. Results

All bivalves showed the same pattern of decreasing isotopic values with water depth from the coast to the shelf break (Fig. 2). Average $\delta^{13}C$ values ranged from -15.9 ± 0.2‰ at station 1 to -19.0 ± 0.2‰ at the deepest stations (a 3.5‰ decrease), and $\delta^{15}N$ values varied from 9.4 ± 0.3‰ to 2.8 ± 0.4‰, representing a decline of 6.6‰ (Fig. 2). The pattern of muscle $\delta^{13}C$ and $\delta^{15}N$ values with
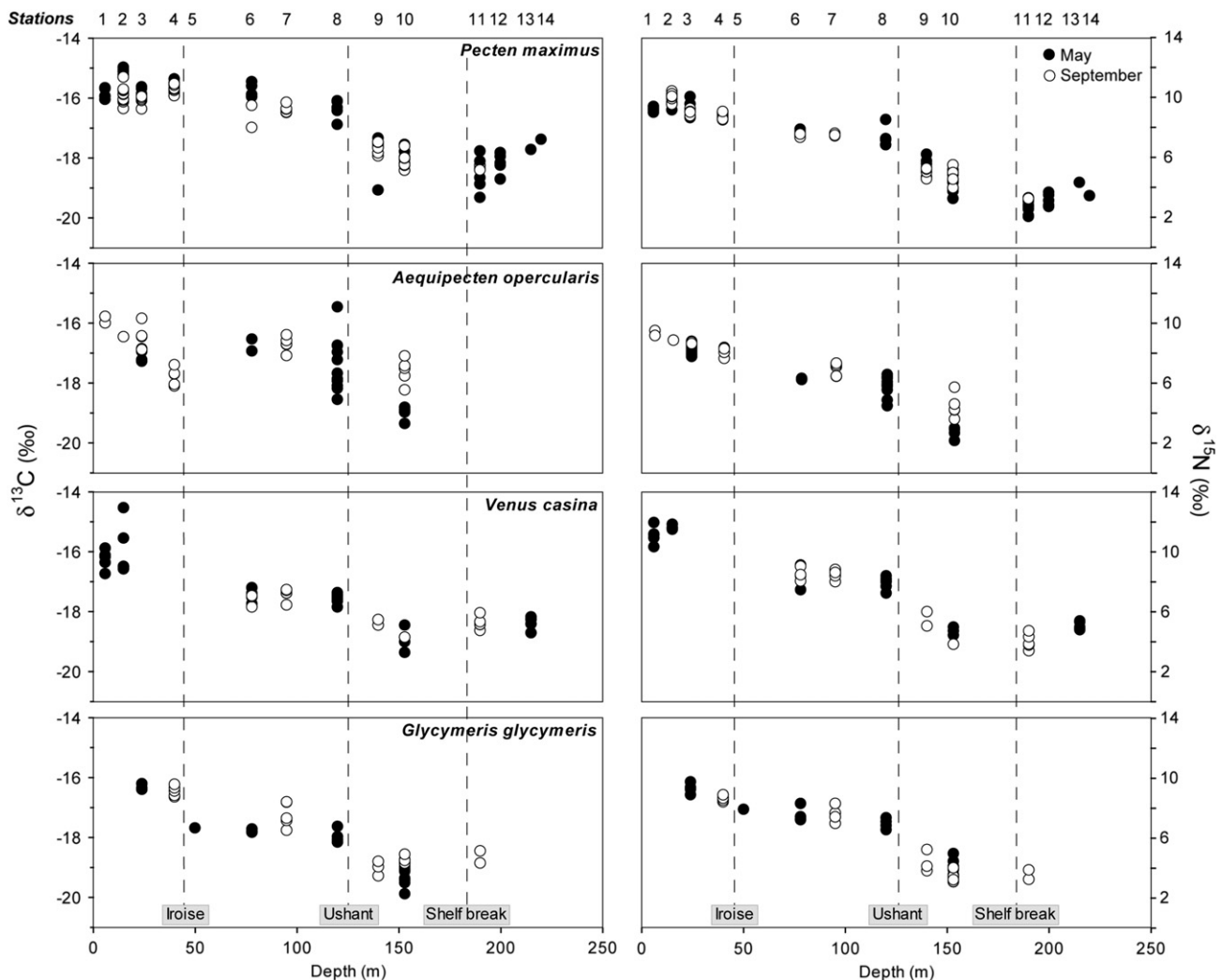

Fig. 2. Muscle $\delta^{13}C$ (left) and $\delta^{15}N$ (right) values along the water depth gradient for both cruises (May and September 2008). Stations 1 to 3 are within the Bay of Brest, and stations 4 to 14 ranged from 7 to 250 Km off shore (see Fig. 1). Dashed lines represent the approximate position of the fronts.

water depth showed a strong decrease between station 6 and station 7, at a ~120 m water depth.

Across the depth gradient, we observed a significant ranking of species $\delta^{13}C$ values from station 3 to 10 (Kruskal−Wallis test on species ranks: $p < 0.03$; Fig. 3): *Pecten maximus* had higher $\delta^{13}C$ values than the other species, and at deep water stations, *Aequipecten opercularis* had higher $\delta^{13}C$ values than *Glycymeris glycymeris* and *Venus casina*. *G. glycymeris* and *V. casina* had variable $\delta^{13}C$ rank positions. There was also a significant rank in $\delta^{15}N$ values for the four species from station 1 to 8 and at station 11 (Kruskal−Wallis test on species ranks: $p < 0.016$): *V. casina* had the highest $\delta^{15}N$ values (up to $8.5 \pm 0.3\text{‰}$), followed by *P. maximus* and/ or *G. glycymeris*, with *A. opercularis* having the lowest values.

The isotopic values of bottom water POM were variable and did not show a clear trend with water depth (Fig. 4). The overall $\delta^{13}C$ values ranged from −18.2‰ to −24.5‰ while $\delta^{15}N$ values ranged between 4.7‰ and 8.5‰. C/N ratios of POM showed an increase from 4.6 to 7.2 with increasing water depth (Fig. 5A). Chl *a* concentrations decreased with water depth, from 2.9 µg L^{-1} to below detection limit (Fig. 5A). SPM concentrations in bottom water in September (Fig. 5B) also showed a decrease from 148.0 to 10.3 mg L^{-1} with

water depth. $\delta^{13}C_{DIC}$ values were not significantly different between sites and averaged $0.96 \pm 0.15\text{‰}$ (data not shown).

4. Discussion

In the shallow well-mixed waters of the Bay of Brest, the euphotic zone extends to the bottom, allowing microphytobenthos primary production, which accounts for 12−20% of total primary production (Longphuirt et al., 2007) and has been suggested to be a major food source for benthic bivalves (Lorrain et al., 2002; Grall et al., 2006). Microphytobenthos typically have a $\delta^{13}C$ value of −16‰ (France, 1995; Kang et al., 1999; Riera et al., 1999; Kharlamenko et al., 2008), while phytoplankton is often assumed to be approximately 18−22‰ lighter than $\delta^{13}C_{DIC}$ (e.g. Cai et al., 1988; Fry, 2002). Therefore, we were expecting a shift in the filter feeder $\delta^{13}C$ values (from high to low values) beyond the light extinction zone situated here at about 30 m depth (Le Boyer et al., 2009).

Our results show a consistent pattern of decreasing $\delta^{13}C$ values with increasing depth for the four species considered. However, although *Venus casina* and *Glycymeris glycymeris* $\delta^{13}C$ values followed the expected trend (decreasing at 30 m), *Pecten maximus* and
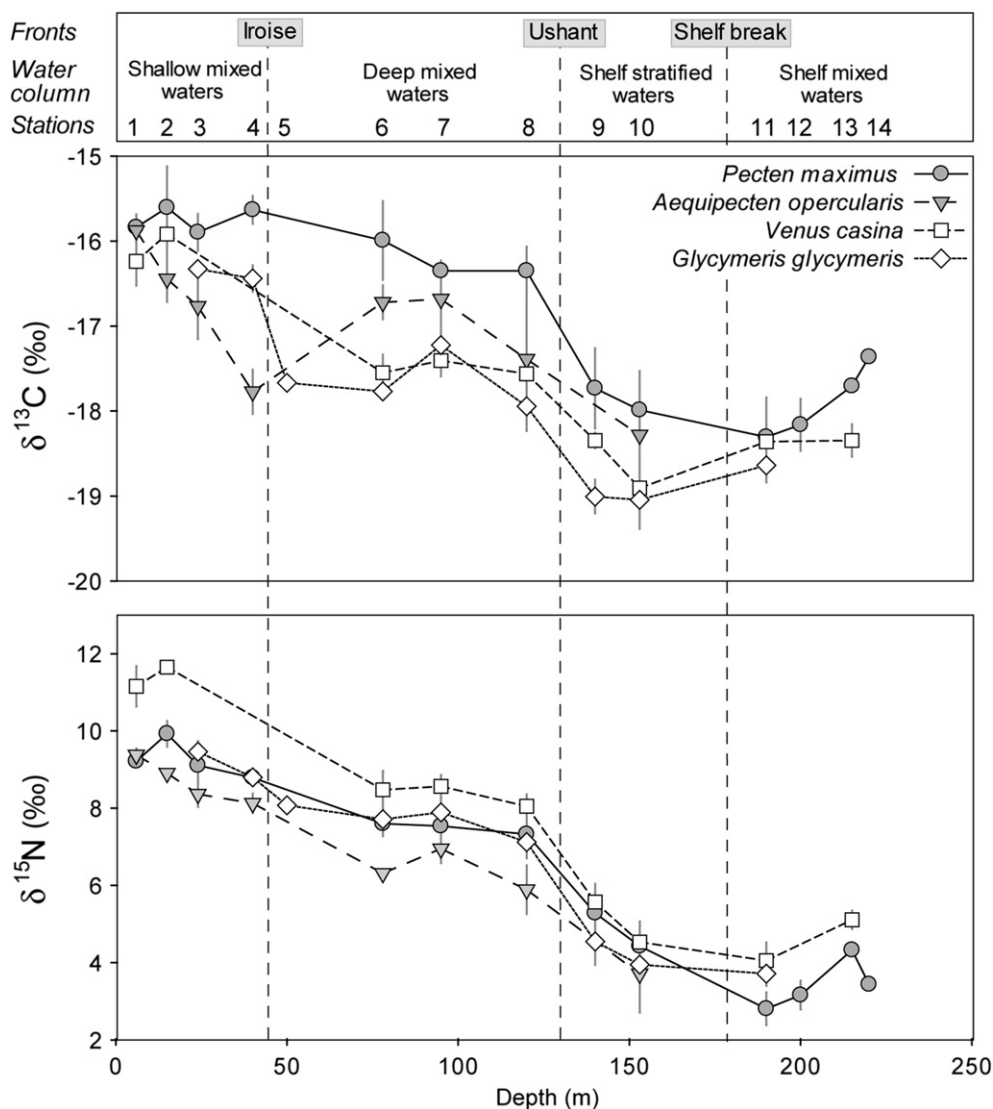

Fig. 3. Average muscle $\delta^{13}C$ and $\delta^{15}N$ values (±SE) along the water depth gradient illustrating the ranking of the species at each station (see Fig. 1 for location of stations). Dashed lines represent the approximate position of the fronts.
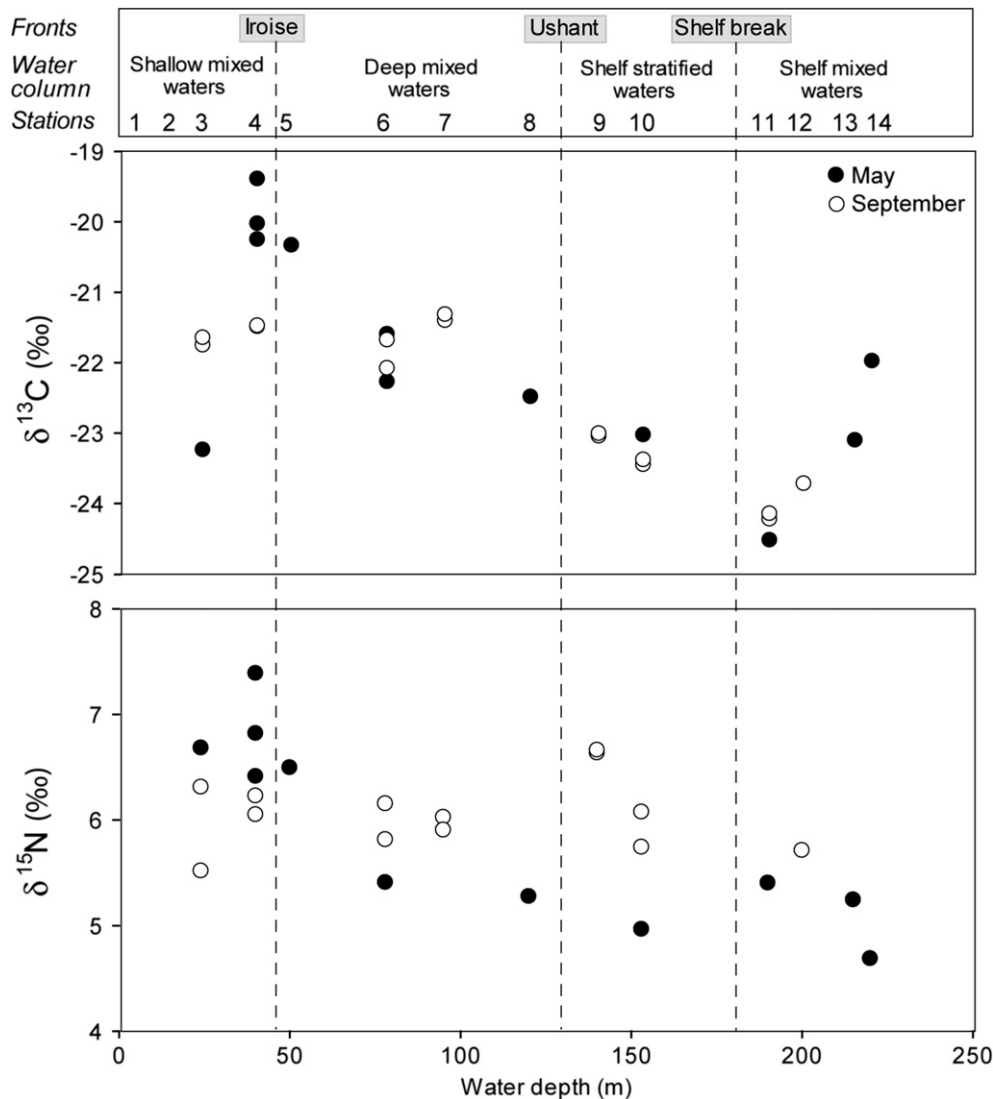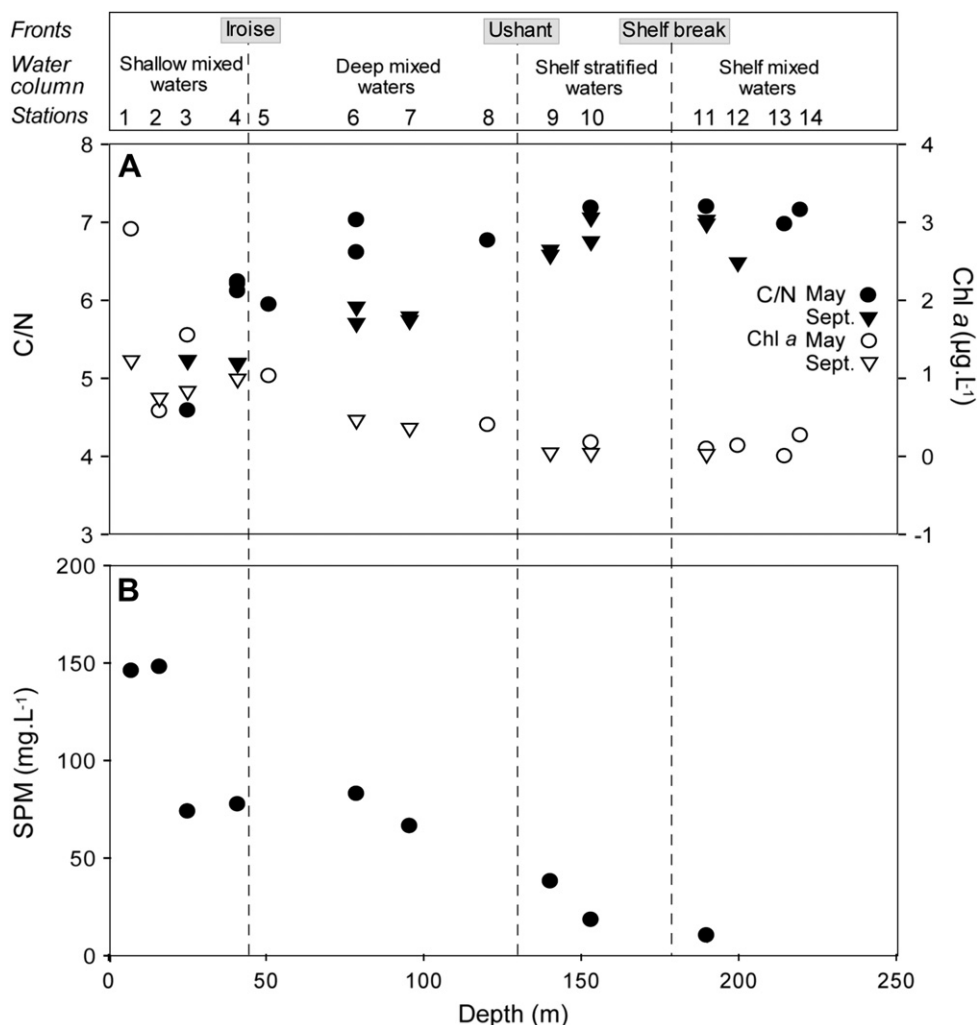
Fig. 4. Particulate organic matter (POM) $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values along the water depth gradient for both cruises in 2008 (May and September). Samples were collected one meter above the seafloor. Dashed lines represent the approximate position of the fronts.

Aequipecten opercularis $\delta^{13}C$ values decreased around 120 m (Fig. 2), far below the expected depth reduction in microphytobenthic production (MacIntyre et al., 1996). Therefore, high $\delta^{13}C$ values of shallow consumers may not simply be attributable to microphytobenthos consumption. Similarly, Nadon and Himmelman (2006) urged caution in interpreting $\delta^{13}C$ values to reflect microphytobenthic sources. In a similar study, Fry (1988) recorded a depth-related decrease of 1.2‰ in scallop (*Placopecten magellanicus*) $\delta^{13}C$ values (−16.8 to −18‰) on the Georges Bank (0–160 m), and hypothesized that it reflected a landward gradient in phytoplankton productivity; with high productivity in shallow waters drawing down ^{12}C and enriching DIC, and thus phytoplankton, in ^{13}C. If differences in productivity were causing the difference in $\delta^{13}C$ values in our bivalves then the DIC would also have showed this difference, but $\delta^{13}C_{DIC}$ over the entire depth gradient was constant (0.96 ± 0.15‰) and has been shown to vary only ∼1‰ throughout the year in the Bay of Brest (Lorrain et al., 2004). Moreover, we found a much larger decrease in $\delta^{13}C$ values for both *G. glycymeris* and *P. maximus* (up to 2.7‰) than would be expected from a productivity signal. This provides strong evidence that differences in productivity are not what is driving the changes in bivalve $\delta^{13}C$ values along this depth gradient.

Further evidence that $\delta^{13}C$ values do not simply record microphytobenthos utilization can be seen in the ranking of $\delta^{13}C$ values between species (Fig. 3). For example, considering that *Glycymeris glycymeris* is showing the expected pattern with a $\delta^{13}C$ decrease after 40 m depth (and possibly *Venus casina*, but we do not have data for this species between 15 and 78 m), it could be argued that this is the only of these species feeding on microphytobenthos. If this were the case, *G. glycymeris* should have the highest $\delta^{13}C$ values at shallow water sites compared to the other species. However, *Pecten maximus* had the highest $\delta^{13}C$ values and not *G. glycymeris*, which is contradictory to $\delta^{13}C$ values reflecting microphytobenthos utilization. Moreover, this same ranking is also observed at deep stations, below the euphotic zone. We expected the muscle isotopic values of the four bivalve species to become more similar offshore, as microphytobenthos growth is inhibited in aphotic deep water and the available food source is presumably limited to sinking pelagic phytoplankton. Because this $\delta^{13}C$ ranking was maintained across the depth gradient, it might arguably reflect a similar diet with different muscle $\delta^{13}C$ enrichment factors (Post, 2002; Vanderklift and Ponsard, 2003), or different metabolic tissue turnover times among species (Paulet et al., 2006). Studying only one species, such as *G. glycymeris*, would have incorrectly

Fig. 5. (A) Chlorophyll *a* and POM C/N ratios from both cruises (May and September 2008), (B) Suspended particulate matter (SPM) collected in September 2008. Samples were collected one meter above the seafloor. Dashed lines represent the approximate position of the fronts.

confirmed the power of carbon isotopes to detect micro-phytobenthic contribution to bivalve diets. This study therefore illustrates the necessity for multi-species studies to reveal large scale trophic functioning.

Explaining the differences in $\delta^{13}C$ values between stations and between species is not straightforward. POM $\delta^{13}C$ values do approximately show a decreasing $\delta^{13}C$ pattern with depth (Fig. 4), which could be interpreted as the driver of the decreasing tissue $\delta^{13}C$ pattern (Fig. 3). POM, however, is a mixture of different sources of carbon and it is well known that bivalves select specific components of this carbon pool (Ward and Shumway, 2004). For example, Fry (2002) was able to match $\delta^{13}C_{DIC}$ and bivalve tissue $\delta^{13}C$ values and Gillikin et al. (2006) found a 1:1 relationship between $\delta^{13}C_{DIC}$ and bivalve tissue $\delta^{13}C$ values, but not between POM $\delta^{13}C$ values and bivalve tissue $\delta^{13}C$ values. Therefore POM does not equate to what the bivalves are assimilating.

Chl *a*, SPM and C/N ratios can provide an indication of food abundance and quality. As Chl *a* is a proxy of phytoplankton biomass, it is a good proxy of quality food availability (e.g. Bacon et al., 1998). SPM on the other hand can include various other low quality particles and even inorganic sediments. The C/N ratio can also provide insight to the quality of the available particles, with phytoplankton having a theoretical C/N ratio of 5.7 (Redfield et al., 1963). The C/N ratio in our deeper stations is around 7, which could

imply lower quality particles, but phytoplankton can have variable C/N ratios (e.g. Burkhardt et al., 1999), so this value is not neces-sarily evidence of poor food quality. Nevertheless, the higher SPM (see Fig. 4B) and Chl *a* (0.41 ± 0.05 vs. 0.10 ± 0.09 µg/L; $p = 0.01$) at stations 6 to 8 compared to deeper stations could explain the differences we see between $\delta^{13}C$ values in epifaunal scallops and infaunal clams. Several authors have noted differences in selectivity between infaunal and epifaunal filter feeding bivalves (e.g. Bacon et al., 1998; Hawkins et al., 1998). Perhaps the infaunal clams are better at selecting phytoplankton from the SPM pool (cf. Bacon et al., 1998), which results in their tissues reflecting the expected $\delta^{13}C$ value of pelagic phytoplankton (roughly −19‰), while scallops rely more on lower quality organic matter derived from the coastal zone. This lower quality organic matter is likely to be out-welled macroalgae detritus (macrophyte-derived particulate organic matter). Macroalgae constitutes a large component of primary production in this area (e.g., Arzel, 1998; Schaal et al., 2010; Golléty et al., 2011), can be a significant part of bivalve diets (see Arambalza et al., 2010 for review), and has ^{13}C enriched isotope values (e.g., Schaal et al., 2010), which could explain the enriched ^{13}C values in scallops between the Iroise and Ushant fronts. Macroalgae detritus has been suggested to be an important food source for intertidal mussels (Hill et al., 2006, 2008), but we hypothesize that it can also contribute to bivalve diets as far as 50 km offshore in 120 m water

depth. After the Ushant Front, when both SPM and Chl *a* values are low (Fig. 5), $\delta^{13}C$ values of both epifaunal and infaunal bivalves drop to the expected values, but still maintain the same ranking, with scallops being the most ^{13}C enriched (Fig. 3). On the other hand, $\delta^{15}N$ values suggest that the infaunal clams are feeding on degraded ^{15}N enriched organic matter (see Mintenbeck et al., 2007; Trull et al., 2008) or are including microzooplankton in their diet resulting in a ^{15}N trophic enrichment (see Bode et al., 2006). Little is known about the feeding selectivity or diets of these species, but our results suggest they could be complex.

We found a clear decrease in muscle $\delta^{15}N$ values from inshore to offshore stations (Fig. 2), probably reflecting a decreasing anthropogenic input. Although the Bay of Brest is not defined as truly eutrophic because its strong tidal currents dilute the increasing terrestrial inputs of anthropogenic origin (Chauvaud et al., 2000), major signs of benthic eutrophication have been reported (Grall and Glémarec, 1997), and eutrophication is generally associated with high $\delta^{15}N$ values for organic matter (Cabana and Rasmussen, 1996; McClelland et al., 1997). Indeed, we observe elevated $\delta^{15}N$ values in bivalve muscles from inshore stations (from ~9 to 12‰; Fig. 2), similar to reported values in other urbanized coastal areas (Jennings and Warr, 2003; Nadon and Himmelman, 2010). However, the bivalves in the deepest waters had unusually low $\delta^{15}N$ values. Most large scale studies report a decrease of $\delta^{15}N$ muscle values when going offshore, with values in deepest sites of ~5‰ (105 m, Jennings and Warr, 2003; 143 m, Le Loc'h et al., 2008), while offshore values in our study are surprisingly much lower (2.8‰ at 190 m depth). Considering the typical 3 to 4‰ trophic ^{15}N enrichment between prey and consumers (DeNiro and Epstein, 1981; Vander Zanden and Rasmussen, 1999), the low $\delta^{15}N$ values in our study would imply a trophic source with a $\delta^{15}N$ value that was close to 0‰ or even negative, which is typical of diazotrophic producers in oligotrophic areas (Lourey et al., 2003), while the Bay of Biscay continental shelf is a highly productive area (Varela et al., 2006). Physical parameters such as the cold and constant temperature of bottom water (~12 °C in the Bay of Biscay) and the low food quantity may be responsible for major metabolic changes in deep water organisms, such as reduced growth rate (Turekian et al., 1975; Buick and Ivany, 2004), respiration (Smith and Teal, 1973), and reproduction (Peck et al., 2007). These metabolic changes could modify classical trophic isotope enrichment factors between food sources and the muscles of bivalves at the deepest stations (depth > 120 m). It is possible that the slow metabolism at depth could result in low N excretion and little to no isotopic fractionation (see Fry, 2006 for a discussion on N excretion and fractionation). This hypothesis should be further explored because it calls into question the use of bivalves as integrators of temporal variations of isotopic values of primary producers (isotopic baseline), as several authors have proposed (Post, 2002; Jennings and Warr, 2003).

Finally, there has been a recent interest to use stable isotope values in consumer tissues to differentiate water masses. For example, Iken et al. (2010) found significant differences in benthic food web stable isotope values between water masses in the southern Chucksi Sea. Similarly, Mauna et al. (2010) reported different $\delta^{13}C$ values in the Patagonian scallop (*Zygochlamys patagonica*) according to the position on the Argentine shelf break front. Our study showed four discrete water masses are present (Koutsikopoulos and LeCann, 1996; Reffray et al., 2008; Muller et al., 2009), but are not all marked by significant differences in bivalve stable isotope values (Fig. 3). The most evident isotopic shift is observed at the Ushant front (~120 m depth) which separates mixed and stratified water and where there is a large change in SPM and Chl *a* (Fig. 5). All four species exhibit an abrupt change in both carbon and nitrogen isotope values whereas the other water mass boundaries show little or no isotopic shift (Figs. 2 and 3).

5. Conclusions

Four species sampled over a large depth gradient all show a decrease in muscle $\delta^{13}C$ and $\delta^{15}N$ values with depth, but only some show this change where microphytobenthos abundance should decrease. Therefore, $\delta^{13}C$ values do not reflect microphytobenthos utilization alone. There were however similarities in $\delta^{13}C$ values among epifaunal and infaunal species, with epifaunal species following the expected trend of benthic vs. pelagic consumption. Moreover epifaunal species typically had the most ^{13}C enriched and the most ^{15}N depleted tissues indicating different diets or particle selectivity. However, despite four discrete water masses, only one major shift was observable in the tissue stable isotopes, indicating that delimiting water masses using stable isotopes in filter feeder tissues is not straightforward. The decrease in $\delta^{15}N$ values with distance from land is likely a result of the dilution of anthropogenic N inputs from land, but the deepest $\delta^{15}N$ values were much lower than expected. These low $\delta^{15}N$ values suggest the classic 3 to 4‰ trophic enrichment may not hold true in species inhabiting deep waters.

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