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Trophic Relationships within Intertidal Communities of the Brittany Coasts: a Stable Carbon Isotope Analysis

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ABSTRACT

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More than 100 species belonging to plant and animal taxa that are commonly observed in the intertidal zone were collected on both rocky and soft bottom shores of Brittany, France, to be analysed for their $^{13}C/^{12}C$ ratio. Plant material displayed a wide range of $\delta^{13}C$ values (from −12 to −34‰), with relatively distinct values among producer groups (Chlorophyceæ, Fucales, Laminariales, Rhodophyceæ, seagrasses, plankton), and among strata of intertidal zonation. Animal $\delta^{13}C$ range was narrower (−15 to −22‰), and in general, values differed more between than within phyla or classes, according to the staple diet of organisms. A good correlation between the $\delta^{13}C$ values of food and consumers was noted, together with a slight ^{13}C-enrichment (≈1‰) with increasing trophic levels from suspension-feeders to predators.

ADDITIONAL INDEX WORDS: *Intertidal zone, food web, carbon, stable isotopes.*

INTRODUCTION

As they form the most accessible biotope in the marine environment, shorelines proved to be, from the beginning of the 19th century, an extraordinary field of investigation for marine biologists and ecologists. Since the pioneering works of STEPHENSON and STEPHENSON (1949, 1972) and of LEWIS (1961, 1964) who demonstrated the universal features of zonation, hundreds of papers have been published about different aspects of intertidal zone ecology. Excellent reviews can be found in PÉRÈS (1982), MOORE and SEED (1985), and, more recently, in MATHIESON and NIENHUIS (1991).

Associated with the environmental physical conditions, biological diversity in intertidal ecosystems is relatively low (at least in the supralittoral and eulittoral zones) when compared to the almost always submerged marine habitats (sublittoral zone). As both plant and animal species richness is low, and as most of the fauna has a reduced motility, many trophic relationships can easily be investigated by field observations. Intertidal food web schemes are relatively simple, with only two or three consumer levels (MATHIESON *et al.,* 1991). The ecosystem is also characterized by the prevalence of sessile animals, which feed on particulate material either as suspension- or as deposit-feeders. Ingested particles are mainly exogenous, brought into the zone by the high water flood. The particle origin, however, is not always obvious: to living or dead phyto- and zooplankton is added a bulk of detrital suspended organic matter either coming from coastal benthos and mobilized by resuspension processes (very active in shallow waters) or land-originated through river estuaries.

The present paper offers a data set on stable carbon isotope ratios obtained for various characteristic organisms from the intertidal zone—on both rocky and particulate shores—of the French Northern Brittany. The community structure of these shores has a long history of extensive study (DE BEAUCHAMP, 1914) and more recently by CRISP and SOUTHWARD (1958) or CASTRIC-FEY *et al.* (1973), and it is very similar to that of the coasts of the British Isles (CRISP and SOUTHWARD 1958; LEWIS, 1964) or the Northwest Atlantic shorelines (MATHIESON *et al.,* 1991). Stable carbon isotopes have proven to be a useful tool in delineating food webs, due to differential isotope fractionation by plants according to their photosynthetic pathway (BENDER, 1971) and the close relationships between diet and consumer stable isotopic ratios (DENIRO and EPSTEIN, 1978). Ratio analyses have been widely used by both terrestrial and marine ecologists to identify food sources and fluxes for ecosystems wherein different primary producers coexist (FRY and SHERR, 1989). Strangely, the stable isotope technique has not been applied to intertidal trophodynamic studies, with the noticeable exception of salt marshes (*e.g.,* HAINES, 1976; PETERSON *et al.,* 1986; PETERSON and HOWARTH, 1987) and mangrove swamps (*e.g.,* RODELLI *et al.,* 1984; NEWELL *et al.,* 1995).

As for Northeastern Atlantic intertidal communities, most trophic relationships are fairly well known from field or experimental investigations. We tried to see if a parallel existed between these understandings and informations supplied by the $^{13}C/^{12}C$ ratio analyses. Do both approaches match together, and are isotopic ratios providing additional data? Does fractionation occur between consecutive trophic levels and, if any, is it of the same order of magnitude than the one previously observed for other food webs? All these questions are hereafter approached, keeping in mind that a geographical

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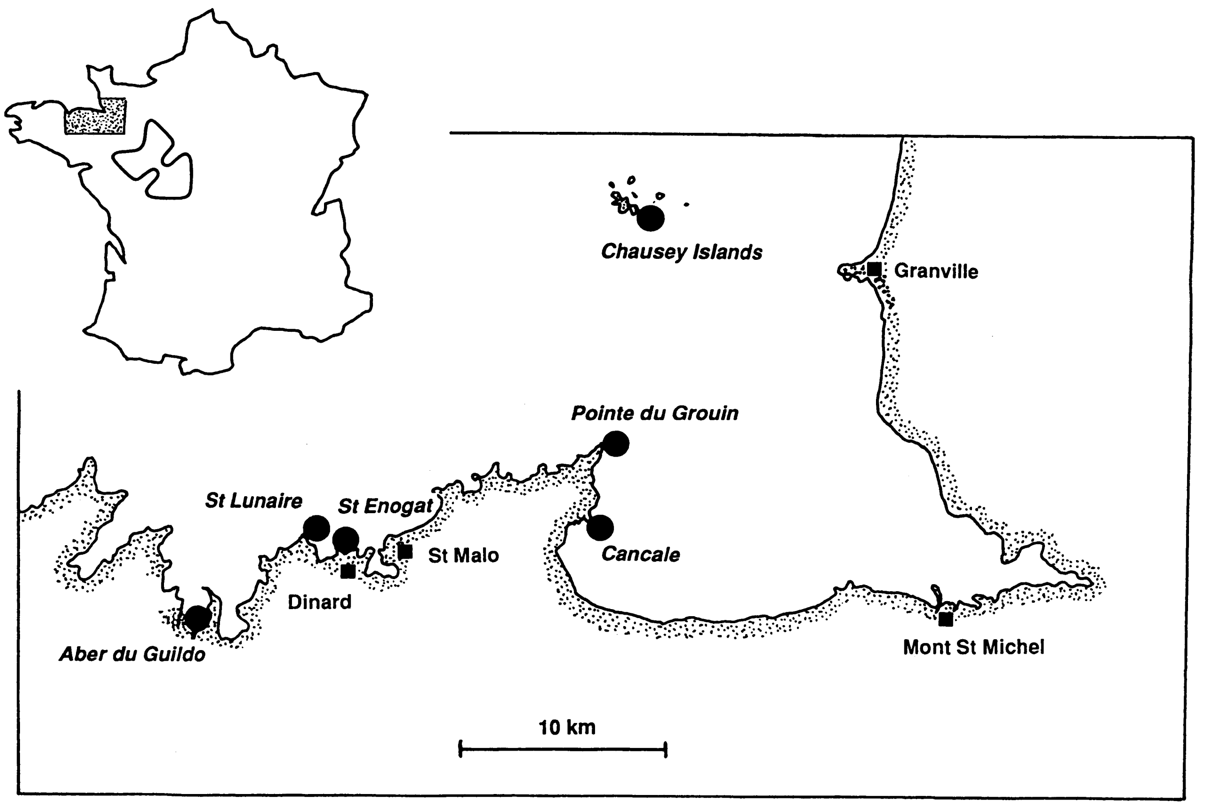

Figure 1. Location of the sampling sites (black spots) along the Northern Brittany coast.

variability could happen despite the narrowness of the prospected area.

MATERIAL AND METHODS

Sampling was performed during spring tides, at the vernal equinox (tidal range: about 8.5 m) in March 1989 and March 1992, on different shores in the area of Saint Malo (Northeastern French Brittany). Sampling sites (Figure 1) include rocky shores (*Pointe du Grouin, Saint Enogat*), muddy sand beaches (*Saint Lunaire, Cancale*), mixed biotopes (*Chausey Islands*), and a salt marsh (*Aber du Guildo*). A few samples were also collected on rocky breakwaters of the Belgian coast for comparisons. All these sampled shores are quite similar from the community structure point of view (with differences between rock- and sand-dominated ecosystems), and known to be stable in time as displayed from annual surveys since—at least—the beginning of the 1970's (Chardon, Demoulin and Vandewalle, *personnal communications*). As they are almost simultaneously washed by the same tidal current (SALOMON and BRETON, 1991), and owing to their close vicinity (longest distance between 2 neighboring sites: 15 km, if excepting the Belgian coast site), all the sampling shores can be considered as equivalent. Former ecological studies (CRISP and SOUTHWARD, 1958) have already shown the great homogeneity in the intertidal community structure of the English Channel western basin.

Samples were hand collected and kept in seawater until laboratory identification of specimens, then rinsed and immediately frozen. About 110 taxa, belonging to all the plant and animal divisions commonly found in the tidal zone, were gathered. Some sediment samples were also collected with a 10 cm high corer on muddy beaches in order to analyze their organic matter. For stable carbon isotope analysis, samples were first soaked in diluted hydrochloric acid to remove carbonates, then rinsed and oven-dried for several days at 50°C. Several individuals (up to 10, depending on organism size) of the same species—from the same site—were pooled and treated together whenever possible, in order to smooth eventual intraspecific variations. Different plant and animal single species, however, were tested in order to display such a possible interindividual variability (see further discussion). Dried samples were ground into fine powder and vacuum-sealed in glass tubes with copper oxide wire (SOFER, 1980); then they were combusted in a muffle furnace at 550°C for about 20 hours. Produced CO_2 was trapped cryogenically and analyzed with a Varian MAT CH5 IR-MS. Measurements, expressed in $\delta^{13}C_{V\text{-}PDB}$ notation, are accurate to within ± 0.35‰.

RESULTS

Plant Material

The measured $\delta^{13}C$ of lichens, green, brown and red algae, seagrasses, and some shoreline terrestrial plants are shown

Table 1. *$\delta^{13}C$ of plant material from the intertidal ecosystem, according to shore types and intertidal zones. Sampling sites are numbered from west to east (see Figure 1): (1) Aber; (2) St Lunaire; (3) St Enogat; (4) Pointe du Grouin; (5) Cancale; (6) Chausey Islands; (7) Belgian coast (not included on map).*

	Rocky Shores					Soft Bottoms				
	Species	Division	Site	Substratum	$\delta^{13}C$ (‰)	Species	Division	Site	Substratum	$\delta^{13}C$ (‰)
Land	*Cochlearia danica*	Spermatophyta	2		−27.9	*Beta maritima*	Spermatophyta	2	sand dune	−28.9
	Umbilicus rupestris	Spermatophyta	6		−28.5	*Lavaterra arborea*	Spermatophyta	6		−30.3
						Pinus pinaster	Spermatophyta	6		−26.3
Littoral fringe	Algal film (mixed sp.)		3	rocks	−17.9	*Aster tripolium*	Spermatophyta	1	schorre	−24.3
	Ramalina scopulorum	Ascomycetes	3	rocks	−18.8					
Eulittoral zone (upper)	*Lichina pygmea*	Ascomycetes	3	rocks	−13.0	*Halimione portulacoides*	Spermatophyta	1	schorre	−23.2
	Enteromorpha linza	Chlorophyceae	3	rocks	−18.4	*Salicornia* sp.	Spermatophyta	1	schorre	−23.9
	Enteromorpha intestinalis	Chlorophyceae	7	breakwater	−17.8					
	Enteromorpha compressa	Chlorophyceae	7	breakwater	−18.8					
	Porphyra umbilicalis	Rhodophyceae	7	breakwater	−19.9					
Eulittoral zone (mid)	*Codium tomentosum*	Chlorophycaae	3	rocks	−16.2					
	Ascophyllum nodosum	Phaeophyceae	6	rocks	−17.4					
	Birfurcaria bifurcata	Phaeophyceae	2	rocks	−16.1					
	Fucus serratus	Phaeophyceae	3	rocks	−20.7					
	Fucus vesiculosus	Phaeophyceae	6	rocks	−18.4					
	Sargassum muticum	Phaeophyceae	3	rocks	−19.6					
	Corallina officinalis	Rhodophyceae	3	tidepool	−20.8					
	Lomentaria articulata	Rhodophyceae	6	rocks	−20.8					
Eulittoral zone (lower)	*Colpomenia sinusa*	Phaeophyceae	3	rocks	−15.8					
	Scytosiphon lomentaria	Phaeophyceae	2	tidepool	−11.6					
	Ahnfeltia plicata	Rhodophyceae	2	tidepool	−18.5					
	Calliblepharis jubata	Rhodophyceae	3	rocks	−22.0					
	Chondrus crispus	Rhodophyceae	3	rocks	−18.7					
	Dilsea carnosa	Rhodophyceae	3	rocks	−16.5					
	Furcelaria furcelata	Rhodophyceae	2	tidepool	−19.2					
	Gigartina sp.	Rhodophyceae	2	tidepool	−20.7					
	Plocamium cartilagineum	Rhodophyceae	3	rocks	−33.7					
	Polyneura hilliae	Rhodophyceae	3	rocks	−31.8					
	Porphyra purpurea	Rhodophyceae	2	tidepool	−23.1					
Sublittoral zone	*Himanthalia lorea*	Phaeophyceae	7	breakwater	−12.3	*Zostera marina*	Spermatophyta	3	muddy sand	−12.1
	Laminaria digitata	Phaeophyceae	3	rocks	−15.5	*Zostera noltii*	Spermatophyta	2	muddy sand	−13.0
	Laminaria hyperborea	Phaeophyceae	3	rocks	−16.1					
	Laminaria saccharina	Phaeophyceae	3	rocks	−15.4					
	Saccorhiza polyschides	Phaeophyceae	2	rocks	−18.4					

in Table 1. $\delta^{13}C$ are listed by ecological zone within the intertidal area and by taxonomic divisions within each ecological zone.

Among algae, the Chlorophyceæ (especially the *Enteromorpha* species) appear to have very similar $\delta^{13}C$ values (mean ± SD: −17.8 ± 1.0‰). Phæophyceæ also represent a rather homogeneous group (−16.4 ± 2.6‰), with *Fucus* and *Laminaria* genera respectively the more and the less ^{13}C-depleted. Within Rhodophyceæ, $\delta^{13}C$ display a wide range of values (from −16.5 to −33.7‰) but are, on the average (−22.3 ± 5.0‰), significantly lower ($p < 0.01$ compared with both the other algal groups). Among higher plants, seagrasses, salt marsh species, and terrestrial species form three distinct groups with $\delta^{13}C$ means of −12.6, −23.8 and −28.4‰, respectively.

Sediment Organic Matter

In the *Zostera* seagrass meadow (*Saint Lunaire*), a small difference was observed between the $\delta^{13}C$ of the aerobic (−15.9‰) and the anoxic layer (−17.0‰). In the salt marsh (*Aber*), wherein the aerobic layer is quite thin (≤1 cm), $\delta^{13}C$ range from −18.0‰ for the tidal marsh level (slikke) to −20.7‰ for the subtidal marsh level (schorre) organic matter.

Animals

Animal $\delta^{13}C$ values are listed by ecological zone, and phylum (Table 2). They clearly display a narrower range of values than plants, varying from −15.1 to −22.5‰ with one exception of the sea-hare *Aplysia*. In general, values differ more among phyla than within.

The most ^{13}C-depleted group were tunicates, with quite constant $\delta^{13}C$ values: −21.2 ± 0.7‰. It was followed by sponges, the four analyzed species displayed values ranging from −21.8 to −17.2‰. The two sipunculids species also had similar $\delta^{13}C$ (average: −19.2‰).

At the opposite end of the $^{13}C/^{12}C$ scale, the starfishes displayed a mean value of −16.3‰ (± 1.2‰). Fishes also formed a homogeneous group, with relatively high and constant $\delta^{13}C$ (−17.4 ± 0.6‰). Polychætes and crustaceans represented intermediate but coherent groups, with values of −18.0 ± 1.2‰ and −18.2 ± 1.0‰, respectively.

Two phyla displayed a wider range of $\delta^{13}C$ values, cnidarians and molluscs. The former ranged over 5‰ (from −15.7 to −20.6) and the latter over 14‰ (from −15.9 for the topshell *Gibbula magus* to −29 for the sea-hare *Aplysia*).

DISCUSSION

The observed vertical distribution of the collected organisms (Tables 1 and 2) is quite standard and in good agreement with previously published zonation scenarios for similar shores, either natural (LEWIS, 1964; STEPHENSON and STEPHENSON, 1972; CASTRIC-FEY *et al.*, 1973; RUSSEL, 1991; MATHIESON *et al.*, 1991) or artificial (breakwaters: DARO, 1969, 1970; VAN DER BEN *et al.*, 1977). Abbreviations used afterwards for tidal levels are according to NIENHUIS and MATHIESON, 1991.

The relevance of $\delta^{13}C$ measurements to our intertidal food web study could be challenged as, for a number of plant or animal species, several specimens were pooled and analyzed together. One can argue that no statistical treatment of our isotopic ratios is possible since they represent values for 'averaged organisms' rather than means of replicate samples; variability in the diet of a given species, if any, could not thus be detected. In order to test the appositeness of such a remark, we have measured $\delta^{13}C$ of several individual specimens of two algae (7 *Fucus serratus* and 6 *Enteromorpha intestinalis*) and two animals (9 *Littorina littorea* and 7 *Mytilus edulis*) collected on the same rocky shore. Results (Figure 2) show that, despite variations (max.: 0.9‰ for *Fucus,* 0.4‰ SD), $\delta^{13}C$ ranges of analyzed species do not reveal important intraspecific variations. Similar small deviations were observed, *e.g.* for Georges Bank's coastal food web by FRY (1988) who noticed a maximal 0.6‰ SD for single species (with, however, a significant depth-related gradient). Such 'specific' $\delta^{13}C$ values are not quite surprising when taking into account that the stable isotope ratio is—for plants—a tracer of the CO_2-system speciation in local seawater and of the carbon uptake metabolism, and—for animals—a tracer of the 'mean' diet rather than of the instantaneous ingested food. Moreover, intertidal animals do not move long distances and thus, owing to seaweed zonation, do not graze on a large variety of foods. In other respects, even large ocean voyagers, such as seabirds, have been reported only to display slight intraspecific $\delta^{13}C$ variations though they visit extended geographical areas and feed on a variety of preys (HOBSON *et al.,* 1994).

Another criticism that could be put forward with regard to our intertidal food web isotopic study refers to the fact that samples were collected at different locations along the Brittany coast, as far apart as Dinard and the Chausey Islands (≈40 km, see Figure 1). One could assume the geographical variations in organism $\delta^{13}C$ to be larger than fractionation that occurs between two consecutive trophic levels (0.5 to 1.5‰, DENIRO and EPSTEIN, 1978; MCCONNAUGHEY and MCROY, 1979; RAU *et al.,* 1983; FRY and SHERR, 1989) which could hinder out the interpretation of the $^{13}C/^{12}C$ results. Samples of five species, which originated from different sites (including some from the Belgian coast, about 500 km northeasterly), were analyzed in the same way. Results (Figure 3) show that plant $\delta^{13}C$ can diverge from one site to another (even for two neighboring sites, such as Saint Lunaire and Saint Enogat). However, these differences are slight when taking into account the interindividual $\delta^{13}C$ variability within a given species from a given site (mean SD: 0.25‰) and the internal accuracy of the mass spectrometer (0.35‰). Nevertheless, site to site variations related to the $\delta^{13}C$ of the inorganic carbon source could exist, as suggested by strong differences in the dissolved CO_2-system speciation observed along the English Channel coasts (FRANKIGNOULLE *et al.,* 1996).

Geographical $\delta^{13}C$ variability in animals appears to depend upon the feeding mode; it seems larger for a herbivore such as *Littorina* (SD: 0.6‰) than for the filter-feeders *Crepidula* (SD: 0.2‰) and *Mytilus*. The high $\delta^{13}C$ measured for the Belgian periwinkle could be due to a difference in the species composition of the algal film upon which it feeds. On Belgian

Table 2. *$\delta^{13}C$ of animals from the intertidal ecosystem, according to shore types and intertidal zones. Site numbers:* cf. *Table 1. Abbreviations for diets: (D) detritus-feeder; (H) herbivore; (M) microphage; (O) omnivore-scavenger; (P) predator; (S) suspension-feeder.*

	Rocky Shores						Soft Bottoms					
	Species	Phylum	Site	Substrat.	Diet	$\delta^{13}C$ (‰)	Species	Phylum	Site	Substrat.	Diet	$\delta^{13}C$ (‰)
Littoral fringe	*Ligia oceanica*	Crustacea	2	rocks	O-D	−18.3	*Talitrus saltator*	Crustacea	6	muddy sand	O-D	−18.3
	Littorina saxatilis	Mollusca	3	rocks	M-H	−17.1						
Eulittoral zone (upper)	*Actinia equina*	Cnidaria	3	rocks	P	−18.4						
	Littorina littorea	Mollusca	6	rocks	M-H	−18.0						
	Monodonta lineata	Mollusca	3	rocks	M-D	−16.7						
Eulittoral zone (mid)	*Sagartia elegans*	Cnidaria	3	rocks	P	−16.6	*Owenia fusiformis*	Annelida	4	muddy sand	D-S	−18.1
	Carcinus moenas	Crustacea	3	rocks	O	−18.0						
	Galathea sp.	Crustacea	3	rocks	S	−18.4						
	Portunus puber	Crustacea	3	rocks	O	−19.9						
	Asterias rubens	Echinodermata	7	breakwater	P	−17.4						
	Acanthochites discrepans	Mollusca	3	rocks	H	−19.4						
	Crepidula fornicata	Mollusca	3	rocks	S	−18.8						
	Gibbula cineraria	Mollusca	3	rocks	M-D	−17.2						
	Mytilus edulis	Mollusca	3	rocks	S	−19.5						
	Nucella lapillus	Mollusca	3	rocks	P	−17.9						
	Patella vulgata	Mollusca	2	rocks	H	−17.9						
	Hymeniacidon sanguinea	Porifera	2	rocks	S	−19.7						
	Onos mustellus	Vertebrata	3	tidepool	P	−17.6						
Eulittoral zone (lower)	*Dynamena pumila*	Cnidaria	3	algae	S	−20.6	*Amphitrite rubra*	Annelida	4	seagrass bed	D-S	−18.3
	Tealia felina	Cnidaria	7	breakwater	P	−17.1	*Nephthys hombergi*	Annelida	6	seagrass bed	P	−15.2
	Balanus crenatus	Crustacea	2	rocks	S	−18.9	*Nereis* sp.	Annelida	6	seagrass bed	O	−18.1
	Chthamalus stellatus	Crustacea	2	rocks	S	−19.2	*Cerastoderma edule*	Mollusca	2	seagrass bed	S	−18.6
	Idothea balthica	Crustacea	3	tidepool	H	−16.6	*Crassostrea angulata*	Mollusca	5	oyster bed	S	−20.2
	Macropodia rostrata	Crustacea	3	rocks	O	−19.3	*Ensis siliqua*	Mollusca	2	seagrass bed	S	−19.6
	Palaemon sp.	Crustacea	4	tidepool	O	−16.4	*Gibbula magus*	Mollusca	2	seagrass bed	M-D	−15.9
	Pilumnus hirtellus	Crustacea	3	rocks	O	−19.0	*Mya arenaria*	Mollusca	6	seagrass bed	S	−19.9
	Asterina gibbosa	Echinodermata	3	rocks	O	−15.1	*Ostrea edulis*	Mollusca	5	oyster bed	S	−21.2
	Aplysia depilans	Mollusca	3	algae	H	−29.0	*Petunculus glycymeris*	Mollusca	2	seagrass bed	S	−20.2
	Calliostoma zizyphinum	Mollusca	3	rocks	M-D	−18.4	*Polynices catena*	Mollusca	2	seagrass bed	P	−19.8
	Crassostrea gigas	Mollusca	2	rocks	S	−21.2	*Spisula subtruncata*	Mollusca	2	seagrass bed	S	−19.8
	Nassarius reticulatus	Mollusca	3	rocks	P	−17.8	*Tapes decussatus*	Mollusca	6	seagrass bed	S	−21.4
	Grantia compressa	Porifera	2	overhang	S	−21.8	*Ammodytes lanceolatus*	Vertebrata	3	muddy sand	P	−17.1
	Polymastia mamillaris	Porifera	6	rocks	S	−17.2						
	Ascidia mentula	Tunicata	3	rocks	S	−21.2						
	Dendrodoa grossularia	Tunicata	2	overhang	S	−20.8						
	Distomus variolosus	Tunicata	3	rocks	S	−20.9						
	Botryllus schlosseri	Tunicata	3	algae	S	−20.4						
	Sidnyum turbinatum	Tunicata	2	overhang	S	−22.5						
	Styela clava	Tunicata	3	overhang	S	−21.2						
	Blennius gatorugine	Vertebrata	3	rocks	P	−18.4						
	Centronotus gunnellus	Vertebrata	3	rocks	P	−16.4						

Table 2. *Continued.*

	Rocky Shores						Soft Bottoms					
	Species	Phylum	Site	Substrat.	Diet	$\delta^{13}C$ (‰)	Species	Phylum	Site	Substrat.	Diet	$\delta^{13}C$ (‰)
Sublittoral zone	*Patina pellucida*	Mollusca	3	kelp	H	−16.3	*Lanice conchilega*	Annelida	2	seagrass bed	D	−18.7
	Gadus sp. (juv.)	Vertebrata	6	rocks	P	−17.5	*Sabella pavonina*	Annelida	2	seagrass bed	S	−19.2
	Labrus sp. (juv.)	Vertebrata	4	algae	P	−17.9	*Sabella pavonina* (tube)	Annelida	2	seagrass bed		−18.1
	Lepadogaster bimaculatus	Vertebrata	3	kelp	P	−17.0	*Sagartia troglodytes*	Cnidaria	2	seagrass bed	P	−15.7
							Callianassa subterranea	Crustacea	6	seagrass bed	S-D	−17.6
							Upogebia deltaura	Crustacea	6	seagrass bed	S-D	−17.3
							Aeolidium papillosum	Mollusca	6	seagrass bed	P	−16.1
							Buccinum undatum (eggs)	Mollusca	7	muddy sand	P	−15.7
							Tethya aurantium	Porifera	6	seagrass bed	S	−19.0
							Goldfingia vulgaris	Sipuncula	6	seagrass bed	D	−20.9
							Sipunculus nudus	Sipuncula	2	seagrass bed	D	−17.4

breakwaters, this film is largely dominated by Clorophyceæ (*Prasiola stipitata, Ulothrix flacca, U. pseudoflacca, U. subflaccida, Urospora wormskjoldii, Blidingia minima*) (VAN DER BEN *et al.*, 1977), while on the studied Brittany shores Cyanophyceæ (*Gleocapsa, Calothrix, Rivularia* and *Lyngbya* species) abound.

$\delta^{13}C$ of Rocky Shore Communities

The upper limit of both the littorinid snails and the *Verrucaria* lichens and the upper limit of the acorn barnacles (≈MHW, Mean High Water) roughly demarcate the upper and lower boundary, respectively, of the littoral fringe (LF). If we disregard lichens, on which apparently no marine animal feeds, the LF is rather poorly vegetated, except by inconspicuous algae that form an almost continuous felt on rocks. The algal film mainly consists of Cyanobacteria and minute green (*Endoderma, Blidingia*) and red (*Bangia*) algae. Large species are represented by *Porphyra* and Ulvaceæ. The most common consumer in the LF is *Littorina* of the *saxatilis-rudis* group. This rough periwinkle, with a mean $\delta^{13}C$ of −17.1‰, is isotopically similar to LF primary producers, especially the algal film it grazes upon. The slight ^{13}C-enrichment between *Littorina* and its diet agrees with similar observations on carbon isotope shift between food and consumer (DENIRO and EPSTEIN, 1978). Such a modest enrichment undergone by ^{13}C is the result of a slower specific respiration of this isotope with respect to ^{12}C (MOSORA *et al.*, 1971; MCCONNAUGHEY and MCROY, 1979). The sea slater *Ligia oceanica*, which also commonly occurs in the LF zone, has a $\delta^{13}C$ of −18.3‰, that is akin to other scavengers.

The eulittoral zone (EZ), the lower boundary of which lies approximately at MLWS (Mean Low Water of Spring tide), can be divided in three sub-zones (RUSSEL, 1991) according to the dominant algal community structure: upper, middle and lower levels (EZU, EZM, EZL). The brown Fucaceæ (*Fucus, Ascophyllum, Pelvetia*) form the bulk of algal biomass, with $\delta^{13}C$ ranging from −17.4 to −20.7‰; these values are slightly more negative than those of FAGANELI *et al.* (1986) for Adriatic *Fucus virsoides* populations (−16.1‰). Under this brown algal canopy species of Rhodophyceæ are found, with their number and abundance increasing progressively from EZU to EZL (Table 1). The floristically complex red turf shows a large range of $\delta^{13}C$ values, but is on the average significantly more ^{13}C-depleted than the fucoid overgrowth. Such a wide range of $\delta^{13}C$, with also relatively low values, has been reported as well in the review of KERBY and RAVEN (1985).

Eulittoral consumer community is richer in number than within the LF (with a positive diversity gradient from the upper to the lower boundary), and it is represented by organisms that feed on various food sources: suspension- and detritus-feeders, scavengers, herbivores and predators. Animals that obtain their food by removing particles and plankton from seawater include mainly barnacles (*Balanus, Chthamalus*), bivalves (*Mytilus, Crassostrea*), hydrozoans, and bryozoans (not sampled). Suspended particulate matter (SPM) has been sampled in surface waters of the whole English Channel and northern Biscay during 10 cruises of the R.V.

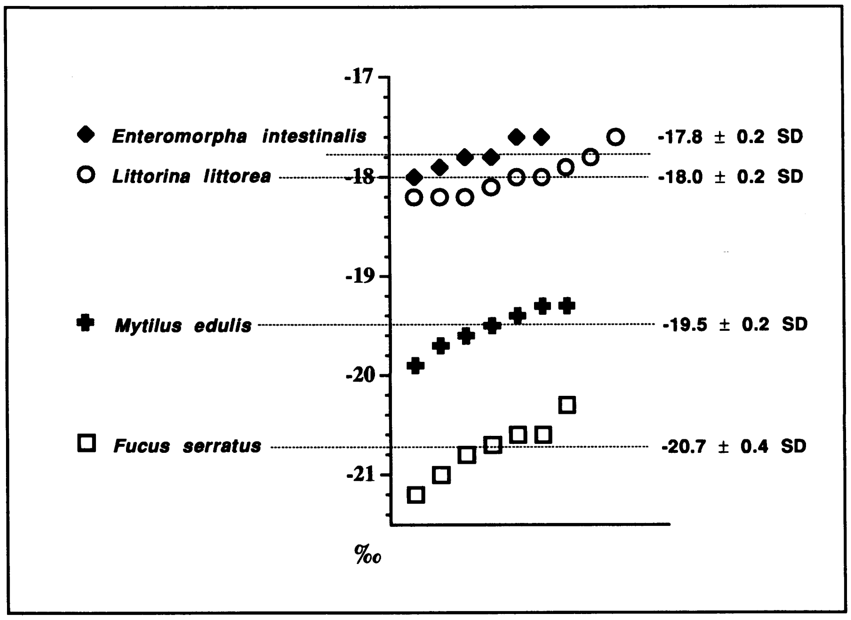

Figure 2. Interindividual variability of $\delta^{13}C$ values for four intertidal species.

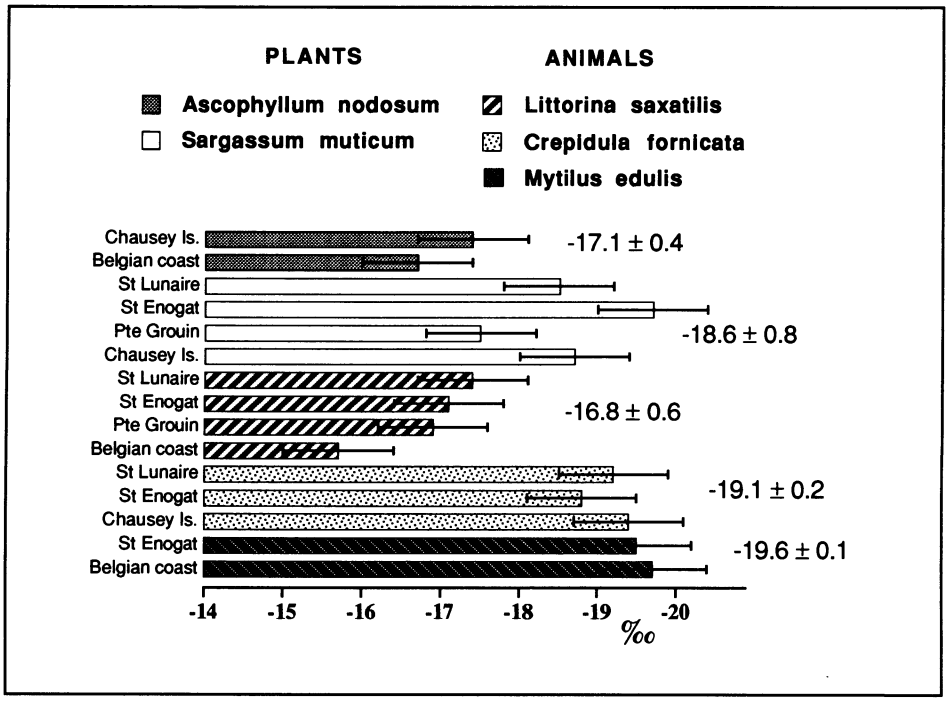

Figure 3. Geographical variability in the $\delta^{13}C$ of different common species. For each of them, bars are arranged from western to eastern sampling sites. Error lines refer to mass spectrometer accuracy.

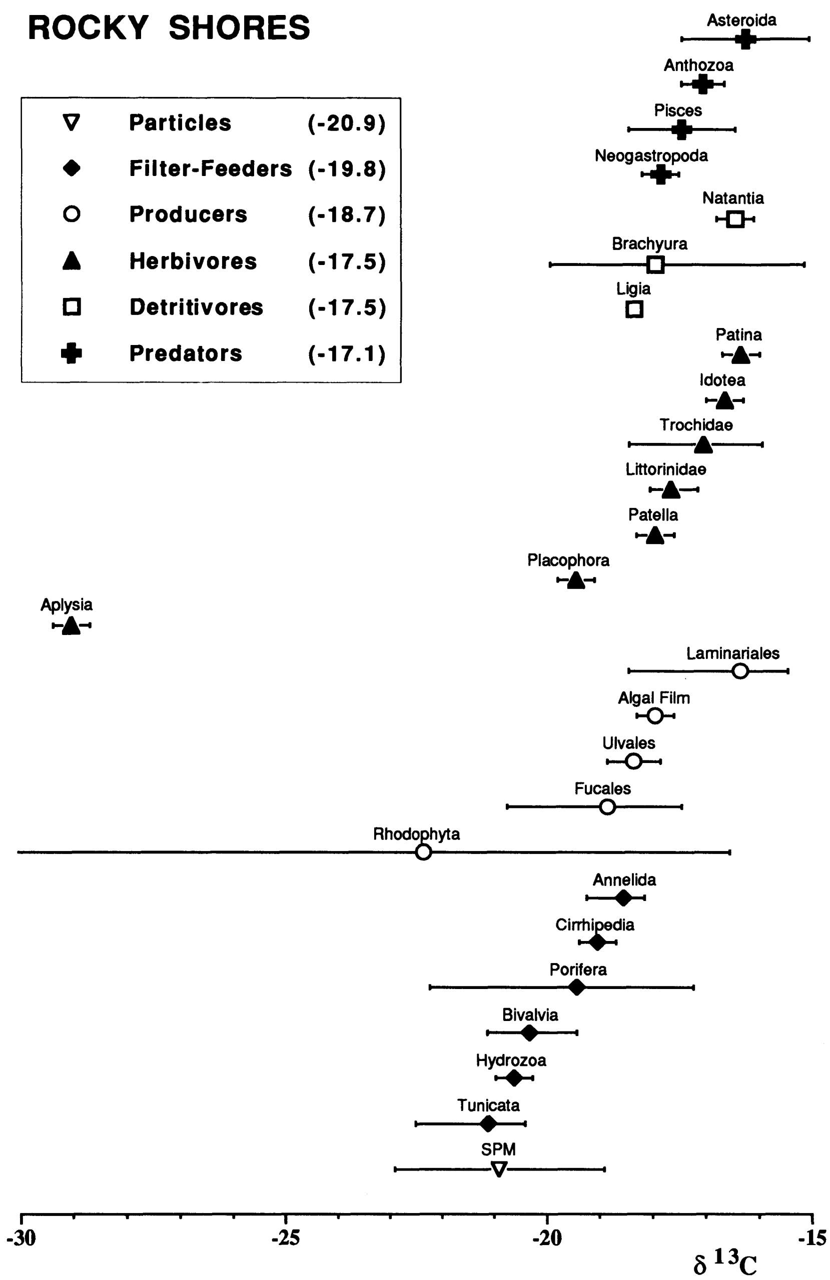

Figure 4. Distribution of δ13C values (means and absolute deviations) of the main systematic groups (according to trophic guild) encountered on rocky shores. SPM: suspended particulate matter. Overall values are given in the frame.

Belgica, performed at different periods of the year from 1989 to 1995. SPM has been analyzed with respect to its $\delta^{13}C$ (DAUBY *et al.*, 1992, 1994, and unpublished) which appeared only to vary slightly in the eastern Channel among cruises. As SPM $\delta^{13}C$ roughly ranges from −20 to −22‰, one should expect the isotopic ratio of the filter-feeders to be about −19 to −21‰, that effectively observed (Table 2).

The main EZ herbivores are gastropods, periwinkles (*Littorina littorea*) and limpets (*Patella*). Those genera feed on algal films covering the rocky substratum and have very similar $\delta^{13}C$ (~18.0‰), which is close to their diet. *L. littorea* also grazes on fucoids, and especially on *Fucus vesiculosus* (BARKER and CHAPMAN, 1990) whose $\delta^{13}C$ is −18.4‰. Other less conspicuous herbivores (chitons and the isopod *Idotea baltica*) are also common; the latter was reported to feed actively on fucoid algae (SALEMAA, 1987), and its $\delta^{13}C$ (−16.6‰) could reflect a mixed diet of *F. vesiculosus* and *Ascophyllum*. Finally, the sea hare *Aplysia* collected in the EZU displays by far the lowest $^{13}C/^{12}C$ ratio (−29‰) of the analyzed fauna. Such a ratio suggests that *Aplysia* might be grazing preferentially

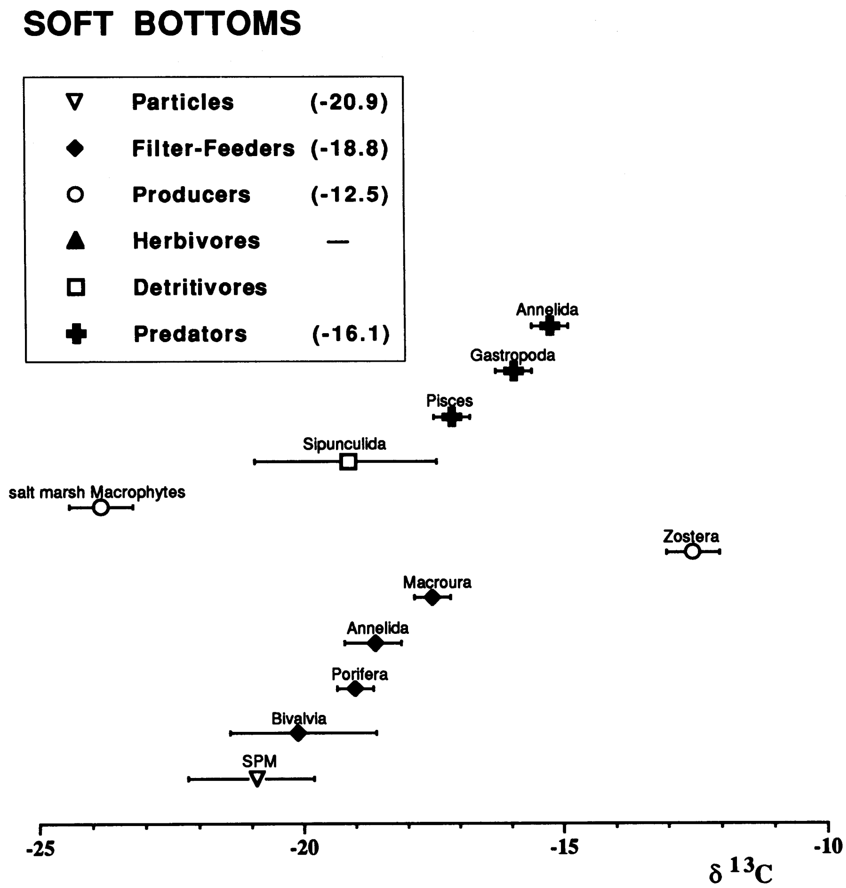

Figure 5. Distribution of $\delta^{13}C$ values (means and absolute deviations) of the main systematic groups (according to trophic guild) encountered on soft bottoms. Overall values are given in the frame.

on certain species of red algae (like *Plocamium* or *Polyneura*) that also has a very negative $\delta^{13}C$ (<-30‰). Low $\delta^{13}C$ values we did observe for a Mediterranean *Aplysia* species (-24.2‰) could corroborate this hypothesis.

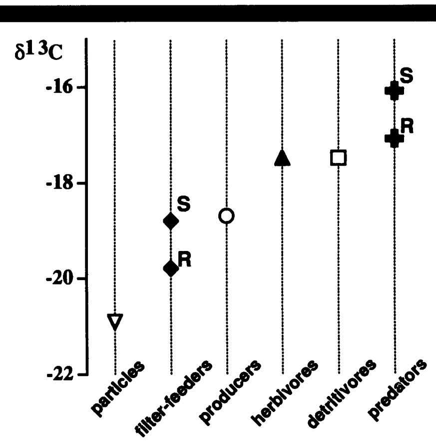

Figure 6. Summary of the mean $\delta^{13}C$ values observed for the different trophic levels from the intertidal zone. (R) rocky shores; (S) soft bottoms.

Trochid gastropods (*Gibbula, Monodonta, Calliostoma*) are also frequently observed in the EZ; they are known to have a mixed staple diet composed of microalgae and miscellaneous organic debris. Top-shells display a relatively wide range of $\delta^{13}C$ values (from -15.9 to -18.4‰), suggesting selectivity in food they ingest. Eulittoral omnivores-scavengers mainly include prawns (*Palaemon*) and crabs (*Carcinus, Pilumnus, Portunus, Macropodia*). The latter not only feed on animal remains but may also chip mussels or barnacles off rocks with their claws, and, as juveniles, do not scorn green algae. Accordingly they display relatively different isotopic ratios (from -16.4 to -19.9‰). Less negative values tend to suggest the importance of dead matter in the diet, while more negative ones could suggest the existence of a concurrent filter-feeding mode or the prevalence of plant food.

Eulittoral invertebrate predators include sea anemones, two gastropods (*Nucella* and *Nassarius*), and the starfish *Asterias rubens*. Both the latter and dog whelks feed directly on primary consumers (mussels and barnacles); they have very similar $\delta^{13}C$ values (-17.4 & -17.9‰) that reflect their position within the intertidal food chain. Anemones, on the other hand, are predators of a higher trophic level, as their staple diet also includes scavengers or even predators (crustaceans, small fishes). It is displayed by their relatively high $^{13}C/^{12}C$ ratio (−15.7 to −17.1‰), except for *Actinia equina* (−18.4‰) that probably also feed on large suspended particles.

The sublittoral zone (SZ) on Eastern Atlantic rocky shores extends downwards from the upper limit of Laminariales (LEWIS, 1964; STEPHENSON and STEPHENSON, 1972) and its uppermost boundary is only partially emerged at MLWS. As sampling was made at LLWS (Lower level of Low Water of Spring tide), different species living at the EZL-SZ frontier could be collected (Tables 1 and 2). The chief primary producers of this zone are kelps (*Laminaria* spp. and sister genera) that display relatively high $\delta^{13}C$ values (−15.4 to −16.1, with, a lower value for *Saccorhiza polyschides*).

The animal community of EZL-SZ is characterized by its richness and diversity, with the progressive emergence of new phyla, such as sponges or tunicates. With fewer fucoid algae and associated taxa, typical intertidal herbivores also decrease. The limpet-like gastropod *Patina (Helcion) pellucida* is the only permanent grazer observed within the zone; it lives and feeds on *Laminaria* stipes, which is confirmed by its $\delta^{13}C$ value (−16.3‰). The other herbivores reported as common in that zone (especially sea urchins) were not found in the sampling sites; this lack could be related to local powerful water movements which should cause sublittoral kelps to physically sweep large herbivores away (VELIMIROV and GRIFFITHS, 1979).

Suspension-feeders are the consumer group that occupies by far the wider surface in the upper SZ; it is especially represented by ascidians and sponges. The former show a characteristic range of $\delta^{13}C$ values (−20.4 to −22.5‰), which unambiguously denotes their planktonic food source and tends to suggest that these animals perform only a slight isotopic fractionation (perhaps because of a slow oxidative metabolism). Sponges also have low $^{13}C/^{12}C$ ratios, with an unexplained value for *Polymastia mamillaris* (−17.4‰). Collected sublittoral predators mainly consist of fishes, the $\delta^{13}C$ of which (measured for lateral muscle tissues) indicate a slight ^{13}C-enrichment with regard to lower trophic level.

$\delta^{13}C$ of Soft Bottom Communities

Because of the instability of sediments, soft bottom communities are almost devoid of macroalgae and associated epifauna. Zonation of organisms is inconspicuous and mainly governed by beach slope, which determines mean particle size, organic load and moisture retention capacity of sediments.

The LF is characterized by the tidal drift that piles up at about MHWS (Mean High Water of Spring tide) line. Drift is foraged by a number of scavengers, the most important of which are amphipods such as *Talitrus saltator* which has a $\delta^{13}C$ of −18.3‰, quite similar to those measured for the scavenging animals (*Ligia*, crabs) of rocky shores.

The upper half of the eulittoral zone (roughly the zone of drying and upper zone of retention) is almost uninhabited, especially by endomacrofauna. The latter mainly colonizes the lower EZ half (zone of resurgence, roughly corresponding to EZL) and includes burrowing bivalve molluscs (*Mya, Tapes, Ensis, Cerastoderma*) and tube-dwelling polychaetes. Nearly all these macroorganisms are suspension- or deposit-feeders, the $\delta^{13}C$ values of which are −19.8‰ and −18.8‰, respectively. The values reflect the $^{13}C/^{12}C$ ratio of their food sources, *i.e.,* SPM and a mixture of suspended and sedimentary organic matter, respectively. Eulittoral predators are mainly represented by catworms (*Nephtys*) which feed on different animal preys (meiofauna excepted; SCHEIBEL, 1981), and whose $\delta^{13}C$ values (−15.2‰) indicates their high rank in the intertidal food web.

The sublittoral zone in these areas lies about the upper limit of seagrasses, represented on Brittany coasts by the eelgrasses, *Zostera marina* and *Z. noltii.* The $\delta^{13}C$ values of these producers is −12 and −13‰, which is in good agreement with values published for other shorelines (MCMILLAN *et al.,* 1980). The influence of this ^{13}C-enriched seagrass matter, relative to that of benthic or planktonic producers, is noticeable in the *Zostera* bed sediment organic matter (−15.9‰). Such an enrichment could explain why thaliassinid crustaceans (*Upogebia, Callianassa*) that live in these meadows display slightly less negative $\delta^{13}C$ values than other filter-feeders at higher levels in the intertidal system.

In the Aber du Guildo salt marsh, producers have similar $\delta^{13}C$ values (from −23.2 to −23.4‰), and likely contribute for a significant part of their biomass to soil organic matter (−20.7‰ in the vegetated area), as suggested by HAINES (1976) for *Spartina* marshes.

Results from the carbon stable isotope technique confirm previously published observations about the food web structure on North Atlantic shores (LEWIS, 1964; STEPHENSON and STEPHENSON, 1972; HAWKINS and HARTNOLL, 1983; MATHIESON *et al.,* 1991). Intertidal food webs are outlined on Figures 3 and 4, wherein consumers are roughly ordered downwards by increasing $\delta^{13}C$. $^{13}C/^{12}C$ analyses performed on intertidal organisms also corroborate the ^{13}C-enrichment process between trophic levels, as has been previously shown for different freshwater and marine ecosystems (review in FRY and SHERR, 1989). This enrichment is roughly equal to 1‰ between two consecutive levels (Figure 6), value which is in good agreement with those presented in the literature.

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□ RÉSUMÉ □

Plus de 100 espèces, appartenant aux embranchements communément rencontrés dans la zone intertidale, ont été récoltés sur les côtes tant rocheuses que sablonneuses de Bretagne, France, en vue de l'analyse de leur rapport isotopique $^{13}C/^{12}C$. Le matériel végétal montre une large gamme de $\delta^{13}C$ (de −12 à −34‰), avec, toutefois, des valeurs relativement bien distinctes pour les différents groupes de producteurs (Chlorophyceæ, Fucales, Laminariales, Rhodophyceæ, phanérogames, plancton), et, par là, pour les différentes strates de la zonation intertidale. La plage de $\delta^{13}C$ des animaux est plus étroite (de −15 à −22‰), et, de façon générale, les valeurs diffèrent plus entre unités systématiques qu'au sein du même embranchement ou de la même classe, en relation avec le régime de base des organismes. Une bonne corrélation est observée entre le $\delta^{13}C$ de la nourriture et des consommateurs, ainsi qu'un léger bioenrichissement en ^{13}C (≈1‰) avec l'accroissement du niveau trophique, des suspensivores aux prédateurs.