

The stable carbon isotope ratios in benthic food webs of the Gulf of Calvi, Corsica

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Abstract—The Gulf of Calvi, Corsica, presents a wide diversity of biocoenoses, amongst which the seagrass *Posidonia* meadow is prevalent. More than 100 plant, animal and sediment samples from various biotopes were analysed for their stable carbon isotope ratios, to assess carbon flows within the food chains. Marine plants display a wide range of $\delta^{13}\text{C}$ values, from -6 to -32‰ but with three relatively well distinct peaks for *Posidonia*, brown algae and phytoplankton (-9 , -19 and -23‰ , respectively), which are the main carbon sources. The range of isotopic values of animals is narrower, from -14 to -24‰ , suggesting that they feed mainly on algae and plankton. Computations based on simple equations show the proportion of each carbon source in the diet of the animals. *Posidonia*, notwithstanding their important biomass, appear to be a minor food source; this is possibly because of the transfer of their dead leaves, towards the shorelines, in winter.

INTRODUCTION

SINCE the discovery of differences in the stable carbon isotopes fractionation by higher plants according to their photosynthetic carbon metabolism (SMITH and EPSTEIN, 1971; BENDER, 1971), and of the close relationships in the $^{13}\text{C}/^{12}\text{C}$ contents of food and consumers (MOSORA *et al.*, 1971; DE NIRO and EPSTEIN, 1976, 1978), stable carbon isotope ratio analyses have proved to be a useful tool in the delineation of carbon flows in many food webs. Such an approach has been used successfully in terrestrial ecosystems, varying from grasslands (FRY *et al.*, 1978a; BOUTTON *et al.*, 1980), through sand dunes (FRY *et al.*, 1978b) and savannah (TIESZEN *et al.*, 1979), to lakes (RAU, 1980; RAU and ADNERSON, 1981). The most convincing results provided, however, by $^{13}\text{C}/^{12}\text{C}$ analyses were obtained for coastal marine ecosystems, especially those where terrestrial and marine vegetation carbon sources (algae, phytoplankton, macrophytes) coexist, i.e. salt marshes (HAINES, 1976; PETERSON *et al.*, 1980), estuaries (HAINES and MONTAGUE, 1979; GEARING *et al.*, 1984; PETERSON *et al.*, 1985), and seagrass beds (THAYER *et al.*, 1978; FRY and PARKER, 1979; MCCONNAUGHEY and McROY, 1979a; FRY *et al.*, 1982, 1983). For such areas, $\delta^{13}\text{C}$ of the different primary producers (phytoplankton -23‰ ; benthic algae -17‰ ; seagrasses -10‰ ; marsh *Spartina* -13‰) have been compared with the $\delta^{13}\text{C}$ values of different invertebrates from the first trophic levels, or even of larger animals at the top of food chains: thus, investigators could determine precisely which kind of plant food was selected by consumers, or the relative share of each primary producer biomass in the total amount of detrital organic matter ingested (e.g. by suspension feeders).

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In the Gulf of Calvi, a complex ecosystem is observed, containing a large *Posidonia oceanica* meadow (10.7 km²) and a fringe of rocks covered by algae, low phytoplanktonic production (900 tons C y⁻¹) and intermittent inputs of terrestrial material. The purpose of the present study is to clarify the origin of detrital material consumed by the main deposit and suspension feeders, and to trace the fate of that carbon throughout the benthic food webs.

STUDY AREA

Sampling was carried out from STARESO, the oceanographic station of the University of Liège, Belgium, which is on Revellata Head, on the western side of the Gulf of Calvi, northwestern Corsica (8°45'E, 42°35'N). The site is open to the northwest and has a total area of about 2200 ha. Water depths increase here progressively (slope: 2%) from south to northwest, reaching down to 100 m (Fig. 1). The annual pattern of surface water temperatures has a summer maximum (about 26°C in August) and a winter maximum (13°C in March). The water column is stratified, with a seasonal thermocline, from May to September.

Further information concerning the sedimentology, hydrology, physical and chemical properties of the gulf waters has been given by BURHENNE (1981), BAY (1984), DAUBY (1985a) and FRANKIGNOULLE (1986). Five different biocoenoses cover the gulf bottom:

(1) On rocky substrates, in water depths from 0 to 5–8 m, there is a dense algal community ["Biocoenose à algues photophiles"—"AP", in the system proposed by PERES and PICARD (1964) for benthic bionomy in western Mediterranean]. The dominant algae species in the community are the rhodophyta *Corallina mediterranea* and *Jania rubens*, the chlorophyta *Halimeda tuna*, *Codium bursa* and *Udotea petiolata*, and the pheophyta *Halopteris* spp., *Padina pavonica* and *Cystoseira* spp. The dominant invertebrates are mainly small crustaceans, molluscs, and annelids; fishes are principally from the families Scorpaenidae, Gobiidae and Labridae.

(2) A large *Posidonia oceanica* meadow ("Biocoenose de l'herbier de Posidonies"—"HP") covers 48% of the gulf area; it occurs in water depths from about 5 to 38 m. The mean density of the vegetation shoots varies from about 400 m⁻², at 10 m, to 66 m⁻² at 38 m depth (BAY, 1984). The typical fauna associated with such seagrass beds has been studied extensively (HARMELIN, 1964; LEDOYER, 1966); the main epiphytic algae are the two Pheophyta *Myrionema orbiculare* and *Giraudya sphacelarioides*, and the calcareous *Melobesia* spp. (MESUREUR, 1981).

(3) A smaller seagrass bed, containing *Cymodocea nodosa*, covers a few areas of mud ("Biocoenose des stables vaseux superficiels en mode calme"—"SVMC"), especially within the sheltered part of the gulf, near to the town of Calvi. This community occurs in shallow waters, down to 18 m, and covers 12% of the total area.

(4) Seated area of between 40 and 60 m are covered with detrital coarse sand ("Biocoenose des fonds détritiques côtiers"—"DC"). The coverage becomes progressively more scarce in deeper waters, with mainly red algae, tunicates and echinoderms.

(5) Beneath 60 m, the bottom is covered with terrigenous muds ("Biocoenose des vases terrigènes côtières"—"VTC").

(6) Other limited biocoenoses are also observed in the gulf, such as the "Biocoenose coralligène" ("C"), located on the rocky walls at the extremity of Revallata peninsula, with a high diverse fauna.

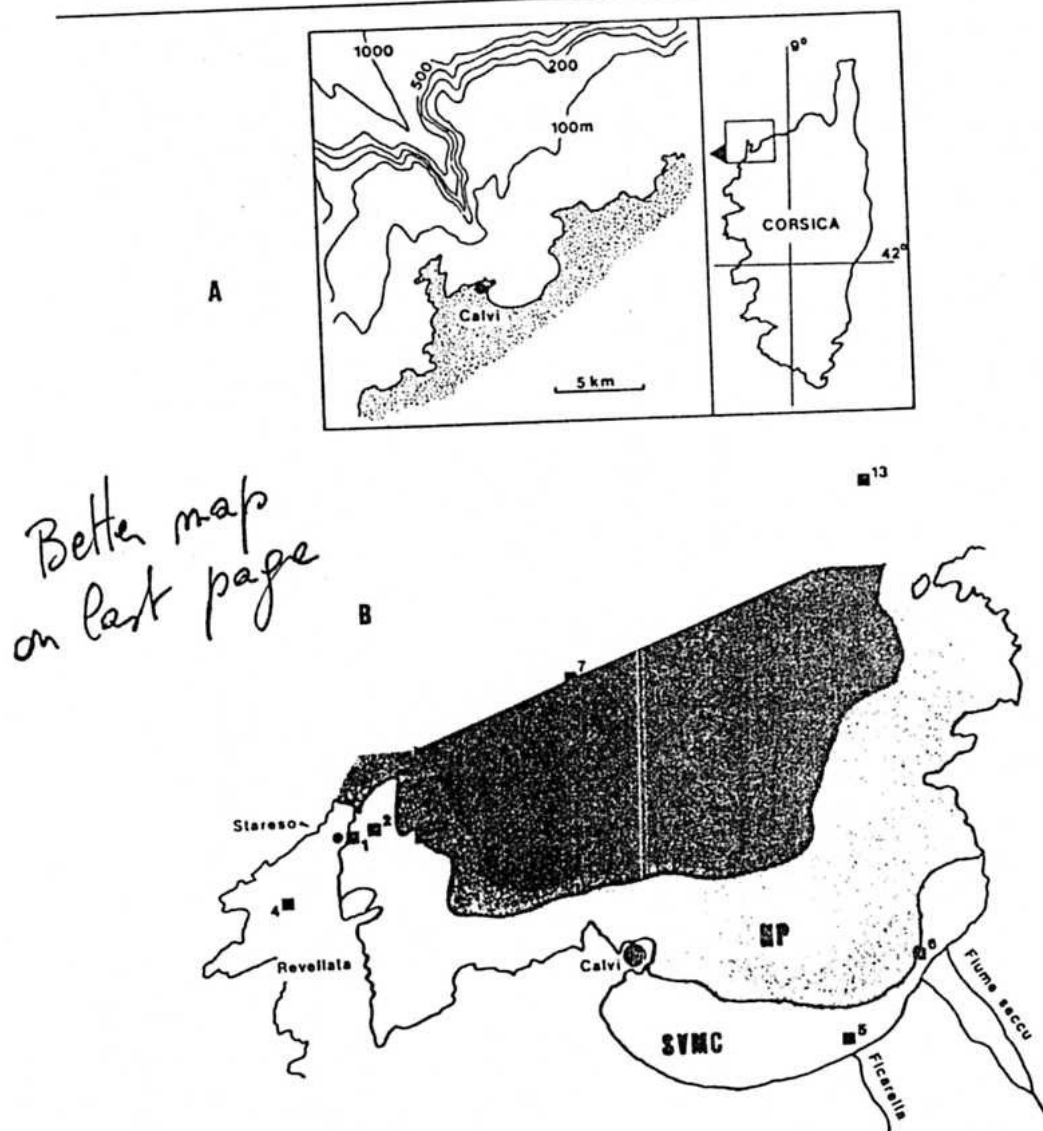


Fig. 1. (A) Diagram of the Calvi area, showing bathymetry (in metres). (B) Distribution of the different biocoenoses inside the Gulf (for explanation of symbols, see the "Study Area" section). Squares indicate sampling locations of the sediment cores.

MATERIALS AND METHODS

All the samples were collected during the summer and autumn, 1985. Phytoplankton samples were obtained by filtering about 20 l of surface seawater on GF/C glassfibre filter paper. Zooplankton were trapped using an assemblage of three WP2 standard nets (mesh sizes: 50, 180 and 470 μm) from the R.V. *Recteur Dubuisson*. Benthic organisms were collected alive, by SCUBA diving, at different locations in the gulf, from surface waters to those of 40 m depth. Cores of sediments were taken either by diving, or, in deeper waters (down to 120 m), using a Van Veen grab.

Samples were acidified with 2 M phosphoric acid to remove carbonates; they were rinsed, and then oven dried at 60°C for several days. Samples were then ground into fine powder, and combusted in a furnace under an oxygen atmosphere; then CO₂ was collected using a liquid nitrogen gas-trapping apparatus. As far as possible, several specimens were combined and were treated together to reduce individual variability. Determinations of δ¹³C values were performed with a Varian Mat CH5 mass spectrometer. All values are reported relative to the international Pee Dee Belemnite (CRAIG, 1957) as

$$\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000,$$

where R is the ¹³C/¹²C ratio. Routine measurements are accurate to within ±0.25‰.

RESULTS

Carbon isotopic ratios in the organic matter producers

Within the gulf ecosystem studied, at least four sources of photosynthetically fixed carbon are available to the animal consumers: phytoplankton in the water column, the two seagrass species, algae living either as epiphytes or attached to the bottom, and detritus from land producers streaming down to the sea via two seasonal rivers (Fig. 1).

Both the seagrass species blades show a rather constant δ¹³C value: -9.3‰ for *Cymodocea nodosa*, and -8.2‰ (±0.8) for *Posidonia oceanica*. These data, obtained for living blades, compare fairly well with the ones obtained for the same seagrasses from the Straits of Gibraltar (*Cymodocea*: -9.3‰) and the Marseilles area (*Posidonia*: -8.3‰) (McMILLAN *et al.*, 1980). *Posidonia* roots gave more negative values (-12.7‰) than their blades, which can be attributed to the high degree of encrustation on these underground organs. In the same way, old and dead *Posidonia* leaves show more depleted values (-13.3 ± 0.4‰) than young and green ones, suggesting a non-negligible influence of the epibiotic community on the isotopic composition of the entire plant.

This epibiotic community consists of bacteria, diatoms, encrusting red algae (*Melobesia*), brown algae (*Myrionema*, *Geraudya*), hydrozoans, bryozoans (*Electra*), and in the lower part, foraminifera, serpulid worms and invertebrate larvae (MESUREUR, 1981). No attempt was made to measure the isotopic composition of each component of the community; gross values were obtained however, for several blades, ranging from -13.9 to -19.6‰ (with a mean of -17.1‰). As was noted by THAYER *et al.* (1978), these values are much less negative relative to the δ¹³C of phytoplankton; these authors suggest that dissolved organic carbon released by seagrass leaves could be a potential carbon source for the epibiotic community.

Macroalgae undoubtedly display the wider range of δ¹³C values (Table 1), from -10.1‰ for *Padina pavonica* to -30.8‰ for *Udotea petiolata*, with a mean of -19.1‰. Such a wide scale of isotopic ratios has been reported by several authors [see e.g. KERBY and RAVEN (1985) for a synthesis] and has not yet received a complete and satisfactory explanation. These macroalgae are essentially concentrated on the "AP"-substrate, between surface and about 8 m depth. The main part of their biomass is formed by the brown algae (mean δ¹³C: -18.4‰).

Phytoplankton from the area had a quite constant isotopic ratio, between -21 and -23‰ (mean -22.4‰). During the sampling period (summer), it comprised equal parts of diatoms and dinoflagellates. The yearly phytoplankton production is 40 g C m⁻², and,

Table 1. Habitats, sampling depths and $\delta^{13}\text{C}$ values of various organic carbon producers of the Gulf of Calvi. See "Study Area" section for explanation of habitats abbreviations

Species	Biota	Depth (m)	Remarks	$\delta^{13}\text{C}$
Phytoplankton				-21 to -23
Blue-green algae				
<i>Phormidium frigidum</i>	AP	1.5	From culture	-5.8
Green algae				
<i>Acetabularia acetabulum</i>	AP	4		-10.5
<i>Udotea petiolata</i>	AP	5		-30.8
<i>Codium bursa</i>	AP	5		-14.8
<i>Colpomenia sinuosa</i>	AP	3		-13.8
<i>Halimeda tuna</i>	AP	5		-17.8
<i>Cladophora prolifera</i>	AP	1		-18.2
<i>Blidingia chadefaudii</i>	Intertidal			-20.1
Red algae				
<i>Rissoella verruculosa</i>	Intertidal			-23.1
<i>Jania rubens</i>	AP	10		-12.8
<i>Pseudolithophyllum</i> sp.	C	30	Inorganic C	-2.6
<i>Ceramium rubrum</i>	AP	5		-30.0
<i>Corallina mediterranea</i>	C	30		-16.9
Brown and yellow algae				
<i>Tribonema</i> sp.	HP	15		-24.6
<i>Halopteris scoparia</i>	AP	5		-19.1
<i>Cystoseira spinosa</i>	C	35		-22.4
<i>Cystoseira spinosa</i>	C	35	+ Epiphytes	-19.6
<i>Cystoseira barbata</i>	AP	5		-15.9
<i>Cystoseira balearica</i>	C	35		-23.2
<i>Padina pavonica</i>	AP	3		-10.1
Higher plants				
<i>Cymodocea nodosa</i>	SVMC	15		-9.3
<i>Posidonia oceanica</i>	HP	15		-8.2
<i>Posidonia oceanica</i>	HP	15	Roots	-12.7
<i>Posidonia oceanica</i>	HP	15	Dead leaves	-13.2
<i>Posidonia oceanica</i>	HP	15	+ Epiphytes	-13.5
<i>Calicotome</i> sp.	Terrestrial			-24.9
<i>Brachypodium retusum</i>	Terrestrial			-27.8
<i>Myrtus communis</i>	Terrestrial			-25.6
<i>Lavandula stoechas</i>	Terrestrial			-27.2
<i>Erica arborea</i>	Terrestrial			-27.2

for the whole gulf, about 900 tons C y^{-1} (DAUBY, 1985b). By comparison, *Posidonia* meadows produce 2000 tons C y^{-1} (BAY, 1984).

Terrestrial plants which were analysed as part of the study were typical species of the surrounding Corsican bush (or "margins"). All of them are C_3 (Calvin cycle) plants, with $\delta^{13}\text{C}$ ranging from -24.9 to -27.8‰ (with a mean of -26.5‰). The humic substances ($\delta^{13}\text{C}$: -25.8‰) reflect well this prevalence of the C_3 plants. Assessment of the amount of terrestrial organic matter streaming down to the sea either through the small rivers, or from rain, is quite impossible to determine. All that can be said is that this flux is at a maximum in winter, because of the frequent storms; it is negligible during the warmer months. Moreover, the similarity between the isotopic ratios of this terrestrial POC and of phytoplankton makes the differentiation between these two carbon sources difficult.

Table 2. Locations and $\delta^{13}\text{C}$ values of the organic matter from different sediments of the Gulf of Calvi (see also Fig. 1)

Sediments	Biota	Depth (m)	$\delta^{13}\text{C}$
1. STARESO harbour	–	5	–22.4
2. <i>Posidonia</i> meadow	HP	15	–18.0
3. Revellata tip	DC	35	–21.0
4. Humus	Terrestrial		–25.8
5. Ficarella mouth	SVMC	12	–17.3
6. Fiume Secco mouth	SVMC	10	–17.8
7. Canyon	VTC	120	–20.4
13. Espano	DC	40	–21.8
15. Off Calvi town	DC	50	–20.9
16. <i>Posidonia</i> inf. limit	HP	38	–18.1

Isotopic ratios in sediments

Organic matter collected in sediments located alongside the *Posidonia* meadows (Table 2, points 3, 7, 13, 15) displays $\delta^{13}\text{C}$ values close to those observed for the planktonic system (–20.4 to –21.8‰), which suggests that the source of sedimentary carbon within the system is phytoplankton. These values suggest also that the horizontal transport of organic matter originating from *Posidonia* beds is low and can be neglected in the overall balance. Hydrodynamical measurements within the bottom water layer have shown already that the mean current speed was low, at only a few cm s^{-1} (S. DJENIDI, personal communication).

Sediments sampled from within the *Posidonia* meadow (points 2 and 16) have isotopic ratios (–18‰) which are less negative than previous ones, but are about 10‰ lower than *Posidonia* blades. Such intermediate $\delta^{13}\text{C}$ values, between those of the phytoplankton and seagrasses, have been observed also by THAYER *et al.* (1978) for sediments from a North Carolina *Zostera* bed, by HAINES (1976) for soils of a *Spartina* salt marsh in Georgia, and by FRY *et al.* (1983) for various seagrass beds in Queensland, Australia. These intermediate $\delta^{13}\text{C}$ values can result either from a close mixture of organic matter originating from *Posidonia*, phytoplankton and epiphytes, or from bacterial isotopic fractionation of *Posidonia* carbon; alternatively, from a combination of both processes. Microscopic examinations of sedimentary organic matter from the seagrass beds revealed a mixing of algal fragments, *Posidonia* fibres and dead zooplankton, which can explain the relatively low isotopic ratios of these sediments.

At the mouths of both small rivers, Ficarella and Fiume Secco (points 5 and 6, Figure 2), the sediments display much the same $\delta^{13}\text{C}$ levels: –17.3 to –17.8‰. These values are intermediate between those of phytoplankton and *Cymodocea* carbon; they suggest that inputs of terrestrial materials are of little importance, at least during summer; complementary sampling should be performed during the winter season to corroborate this hypothesis.

Samples collected from STARESO harbour (point 1, –22.4‰) have values similar to those for phytoplankton, but must be regarded cautiously as sewage, organic pollution and oil may have contaminated these samples.

Carbon isotopic ratios in the consumers

Some 50 species belonging to all the common marine animal phyla, representative of all the feeding modes and living in the different biocoenoses of the gulf, were sampled

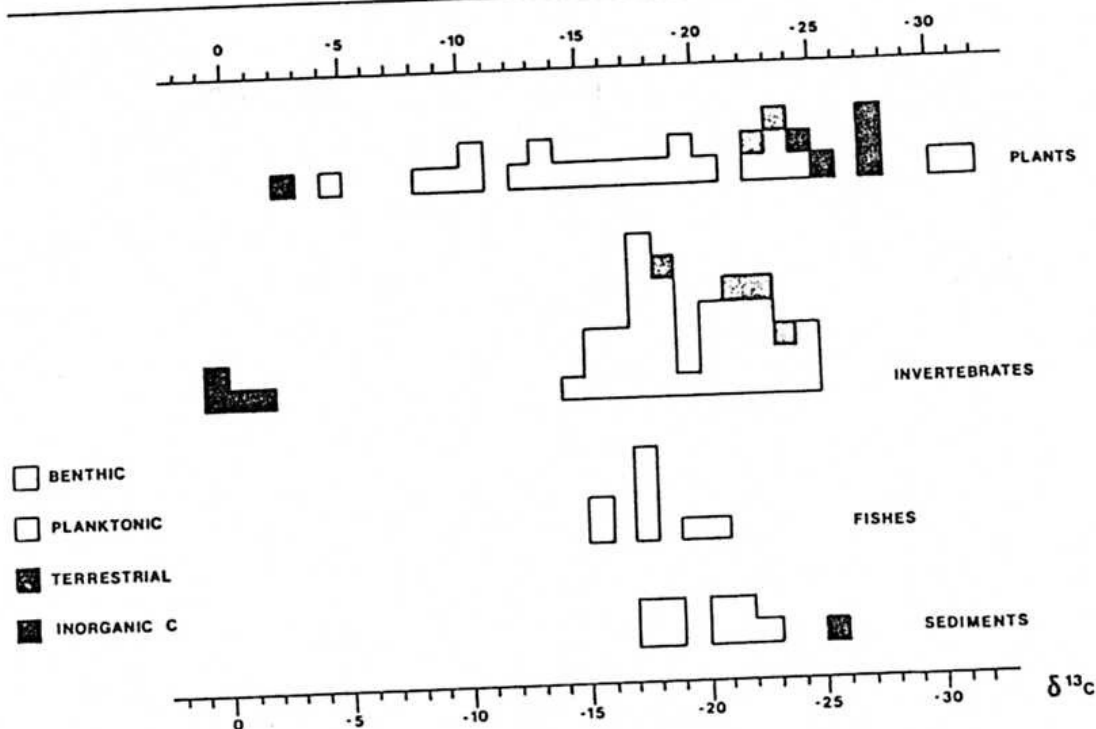


Fig. 2. Histograms of $\delta^{13}\text{C}$ values for plants, invertebrates, fishes and sediments.

and analysed: the results are summarized in Table 3 and suggest that all the $\delta^{13}\text{C}$ values fall between those characteristic of plankton (-23‰) and seagrasses (-9‰). As was noticed by PETERSON and HOWARTH (1987), for *Spartina* marsh fauna, the feeding modes are not good predictors of the $\delta^{13}\text{C}$ values, with animals from each feeding mode overlapping with one another. Nevertheless, there is a general trend for the benthic suspension and deposit-suspension feeders to display more negative values (mean: -20.8‰) than those of the omnivores and predators (mean: -18.8‰). In the same way, the isotopic ratios of animals do not seem to be influenced by habitats, although $\delta^{13}\text{C}$ of the plant carbon sources are notably different in, for example, the "AP" and "HP" biocoenoses. However, for the few genera having two closely related species, living in neighbouring but distinct biota, $\delta^{13}\text{C}$ values are significantly different. So, more particularly, are the two *Leptomysis* (Crustacea: Mysidacea) species. *L. lingvura* lives typically in shallow waters, in the "AP" biocoenose (WITTMANN, 1977; DAUBY, 1985a) and is a deposit-suspension feeder; the vicariant species, *L. gracilis*, feeds exactly in the same way, living in either "SVMC" or in "DC" biota. Examination of the $\delta^{13}\text{C}$ contents of both species reveals a mean difference of 3.3‰ ($-18.6 > -21.9\text{‰}$). Similarly, the two fishes *Serranus cabrilla* and *S. scriba* (Labridae), with the former living in the algal and the latter in the seagrass biota [although they feed on the same material (crabs and mysid shrimps)] display, respectively, mean $\delta^{13}\text{C}$ values of -17.8 and -15.8‰ . These differences must be attributed to a preponderance of organic matter, originating from *Posidonia* and/or algae in the diet of *L. lingvura* and *S. cabrilla*; they are indicative of the feeding sources of their preys.

Table 3. Feeding modes, habitats, sampling depths and $\delta^{13}\text{C}$ values of various consumers of the Gulf of Calvi. H, herbivores; SF, suspension feeders; DSF, deposit-suspension feeders; DF, deposit feeders; O, omnivores; P, predators. See "Study Area" section for explanation of habitats abbreviations

Species	Biota	Depth (m)	Remarks	$\delta^{13}\text{C}$
Sponges				
<i>Haliclona mediterranea</i>	C	30	SF	-22.5
<i>Axinella polypoides</i>	C	30	SF	-21.3
<i>Ircinia muscarum</i>	AP	5	SF	-18.7
Cnidarians				
<i>Pelagia noctiluca</i>	Plank.	2	P	-18.7
<i>Abylopsis tetragona</i>	Plank.	100	P	-23.1
<i>Anemonia sulcata</i>	HP	15	P	-17.9
<i>Aglaophenia</i> sp.	C	30	SF	-22.2
<i>Paramuricea chamaeleon</i>	C	40	SF	-15.4
<i>Eunicella stricta</i>	C	30	SF	-14.2
<i>Eudendrium racemosum</i>	C	30	SF	-22.8
<i>Parazoanthus axinellae</i>	C	20	DSF	-20.7
Annelids				
<i>Salmacina disteri</i>	C	35	SF tubes	+1.2
<i>Spirographis spalanzani</i>	HP	10	SF	-20.3
<i>Sabella pavonina</i>	DC	60	SF	-15.5
Mollusks				
<i>Sepia officinalis</i>	HP	8	P eggs	-17.3
<i>Sepia officinalis</i>	HP	15	P mantle	-16.3
<i>Haliotis tuberculata</i>	AP	6	H shell	+1.8
<i>Octopus vulgaris</i>	HP	35	P eggs	-18.0
<i>Mytilus galloprovincialis</i>	AP	10	SF	-21.7
<i>Patella coerulea</i>	Intertidal		H	-17.6
<i>Peltodoris atromaculata</i>	C	30	P	-18.1
<i>Rissoidae</i> (mixed spp.)	AP	5	DF	-24.2
<i>Cerithium vulgare</i>	AP	5	DF	-22.7
Echinoderms				
<i>Paracentrotus lividus</i>	AP	5	H test	-1.1
<i>Paracentrotus lividus</i>	AP	5	H viscera	-17.8
<i>Echinaster sepositus</i>	HP	8	P	-15.2
<i>Ophiothrix</i> sp.	VTC	120	DF	-16.5
Crustaceans				
Copepods (mixed)	Plank.	1000	SF	-21.6
Copepods (mixed)	Plank.	3	SF	-23.8
<i>Leptomysis lingvura</i>	AP	5	DSF	-18.6
<i>Leptomysis gracilis</i>	DC	35	DSF	-21.9
<i>Pachygrapsus marmoratus</i>	Intertidal		O	-18.1
<i>Ethusa mascarone</i>	HP	8	O	-19.3
<i>Lepas anatifera</i>		surf.	SF	-20.9
<i>Paguristes oculatus</i>	AP	5	DF	-16.7
<i>Galathea</i> spp.	AP	5	O	-20.8
<i>Macropipus corrugatus</i>	HP	10	O	-17.5
<i>Pisa armata</i>	C	35	O	-17.6
Bryozoans				
<i>Myriozoum truncatum</i>	C	35	SF test	-0.5
<i>Myriozoum truncatum</i>	C	35	SF	-21.1
Tunicates				
<i>Thalia democratica</i>	Plank.	5	SF	-24.2
<i>Phallusia mamillata</i>	HP	10	SF tunic	-23.6
<i>Phallusia mamillata</i>	HP	10	SF viscera	-24.4
<i>Halocynthia papillosa</i>	C	35	SF	-22.2

Table 3. *Contd.*

Species	Biota	Depth (m)	Remarks	$\delta^{13}\text{C}$
Fishes				
<i>Scorpaena scrofa</i>	AP	5	P muscles	-15.6
<i>Symphodus ocellatus</i>	AP	5	P <i>in toto</i>	-20.0
<i>Coris julis</i>	AP	5	P <i>in toto</i>	-17.7
<i>Serranus scriba</i>	HP	10	P muscles	-15.8
<i>Serranus cabrilla</i>	AP	8	P muscles	-17.8
<i>Corvina nigra</i>	AP	10	P muscles	-17.7
<i>Solea</i> sp.	SVMC	15	P <i>in toto</i>	-17.1
Birds				
<i>Phalacrocorax aristotelis</i>			P muscles	-19.0
Means				
All animals:		-19.4		
Suspension and deposit feeders:		-20.8		
Benthic omnivores:		-18.7		
Benthic predators:		-18.8		

DISCUSSION AND CONCLUSIONS

Data are available on stable carbon isotope composition of different organisms living in various seagrass communities (FRY and PARKER, 1977; FRY *et al.*, 1977, 1982, 1983; THAYER *et al.*, 1978; McCONAUGHEY and McROY, 1979b) of the American and Australian continental shelves; no study has yet been performed, however, on temperate Mediterranean waters and, especially, on *Posidonia oceanica* beds. These seagrasses differ from the eelgrasses *Zostera* or *Thalassia*, studied by the aforesaid authors, by their location in marine ecosystems (i.e. they live deeper in the infralittoral zone), by their growth mode (the mat of rhizomes can grow vertically as sediment accumulates), and by their leathery consistency. The "toughness" of *Posidonia* leaves certainly explains why very few organisms feed directly on them. At Calvi, only the sea-urchin *Paracentrotus lividus* grazes on seagrasses, but its population is scarce in the meadows (BAY, 1984). The only transfer route for the *Posidonia* carbon into the benthic food webs is through decomposition. Such seagrass carbon rejoins the pool of detrital organic carbon originating from the other producers, phytoplankton, algae and terrestrial plants; it is consumed then by suspension and deposit-suspension feeders.

In the Gulf of Calvi, true benthic herbivores are not numerous and most of the animals use particulate organic matter for their diet. This characteristic is shown in Fig. 2 which summarizes all the $\delta^{13}\text{C}$ values collected on producers, consumers and sediments. Plant carbon sources range from -6 to -32‰, with three or more important values (in terms of biomass) for seagrasses, brown algae and phytoplankton (respectively, -9, -19 and -23‰). Isotopic ratios of invertebrates fall within the range -14 to -24‰ (mean -20.8‰), which suggests that they feed either mainly on algae or on a mixture of carbon from various plants. Predator fishes display $\delta^{13}\text{C}$ values which are, on average, 2‰ higher than those of their common preys; this is in good agreement with the observations of MOSORA *et al.* (1971), DE NIRO and EPSTEIN (1978), FRY and ARNOLD (1982) or MACKO *et al.* (1982) on laboratory grown animals.

The problem of recognition of the origin of organic matter entering into the diet of

invertebrates can be solved partially by calculating the relative percentages of each plant carbon source in the POC available to the animals. If two carbon sources, A and B, are considered, we have

$$xR_A + yR_B = R_{\text{POC}}, \quad (1)$$

where x and y are the respective fractions of the two sources in the total POC pool; R_A , R_B and R_{POC} are the $^{13}\text{C}/^{12}\text{C}$ ratios in the three reservoirs. From (1), one can derive

$$x = (\delta_{\text{POC}} - \delta_B)/(\delta_A - \delta_B) \quad (2)$$

and

$$y = 1 - x.$$

If three carbon sources, A, B and C, are present, one derives

$$xR_A + yR_B + zR_C = R_{\text{POC}}. \quad (3)$$

This equation sustains, in most cases, an infinity of solutions; for x varying from 0 to 1, one has

$$y = (\delta_{\text{POC}} - \delta_C - x(\delta_A - \delta_C))/(\delta_B - \delta_C) \quad (4)$$

and

$$z = 1 - x - y.$$

However, for some x values, equation (4) gives y and/or z negative or greater than 1; these x values and the corresponding y and z ones must, consequently, be cancelled. Thus, this equation derives the ranges of possible contributions from three carbon sources to the total POC (if, of course, the different $\delta^{13}\text{C}$ are known).

In the Calvi coastal ecosystem, the suspended and bottom particulate organic matter comes from the decomposition of:

(1) Phytoplankton (mean $\delta^{13}\text{C}$: -23‰), with annual local production of about 1000 tons C, which is theoretically hardly sufficient to satisfy the dietary requirements of zooplankton populations (DAUBY, 1985a,b).

(2) Zooplankton (mean $\delta^{13}\text{C}$: -22‰), which is close to the value of its main food source with a yearly production of about 250 tons C (DAUBY, 1985a)—contributions to POC is through excretion, mortality and moulting processes.

(3) Seagrasses (mean $\delta^{13}\text{C}$: -9‰), with the highest value for primary producers (blue-green algae excepted), also the highest value of organic carbon production, 2000 tons C y^{-1} . Nevertheless, a large fraction of this is exported towards the beaches, during storms in winter, and is lost consequently to marine consumers.

(4) Seaweeds (mean $\delta^{13}\text{C}$: -19‰ , with a large range of values), the total organic production unknown, but presumably of the same magnitude than the seagrasses, according to the data of MESUREUR (1981) on *Posidonia* epiphytes and of DEMOULIN and RENARD (personal communication) on *Cystoseira balearica*.

(5) Dead benthic consumers (mean $\delta^{13}\text{C}$: -19‰), with no evaluation of biomass or production.

(6) Terrestrial communities (mean $\delta^{13}\text{C}$: -25‰), with fluctuating and invaluable inputs.

These possible sources of particulate organic matter can be arranged in three distinct

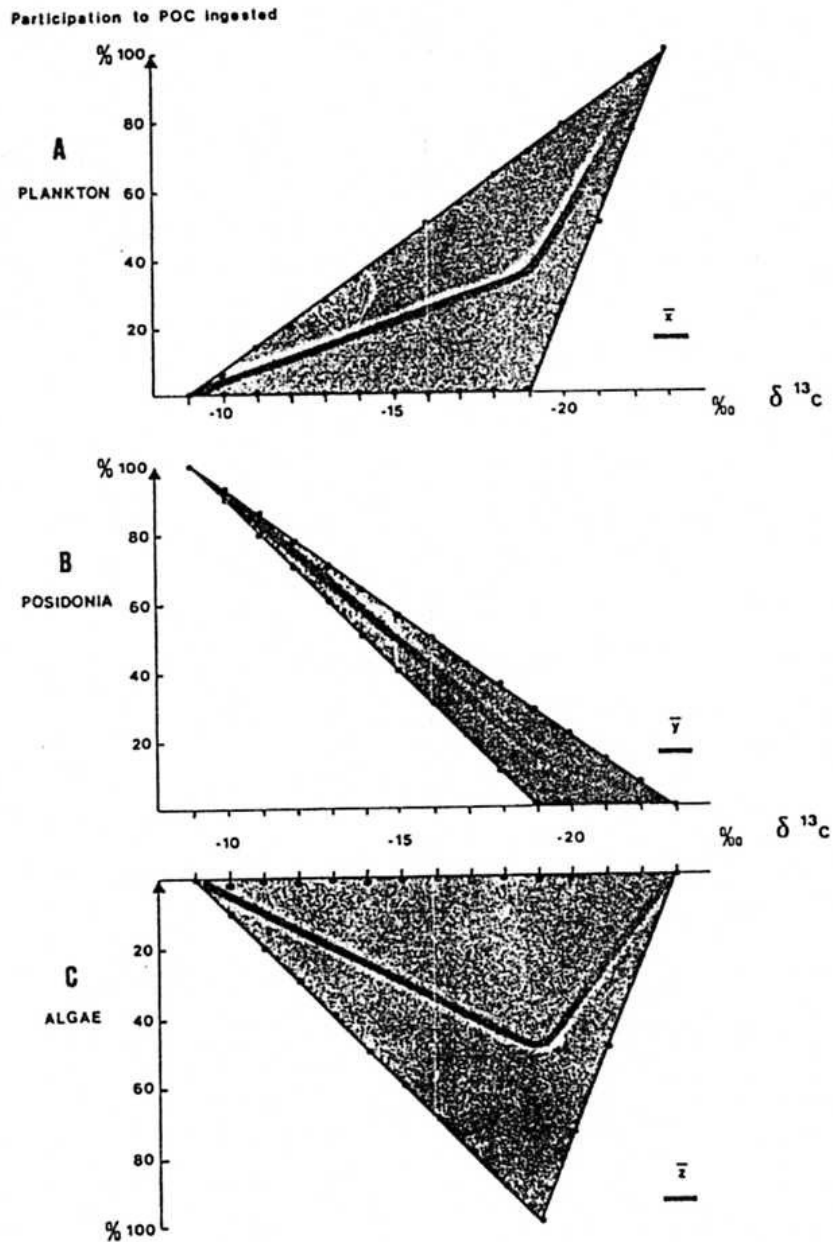


Fig. 3. Ranges of possible contributions of the three main carbon sources, (plankton, *Posidonia* and algae) to the constitution of particulate organic carbon weighing from -9 to -23 ‰; computations obtained from equation (4). (C) is inverted compared to (A) and (B), showing an increase in the proportions of plankton and *Posidonia* carbon inducing a decrease of the algal fraction.

groups, each with a relatively well-defined $\delta^{13}\text{C}$ value: (A) the planktonic-terrestrial pool, with the most negative value ($\delta_A = -23\text{‰}$); (B) the seagrasses pool, with the least negative value ($\delta_B = -9\text{‰}$); (C) the (brown) algae-zoobenthos pool, at an intermediate level ($\delta_C = -19\text{‰}$).

Using these three mean δ values and equation (4), it becomes easy to estimate the importance of the planktonic, algal or *Posidonia*'s carbon in the diet of the invertebrate species which were analysed. The δ_{POC} of the equation can be held equal either to the $\delta^{13}\text{C}$ of each of the animal species, or the δ value minus an increment of, for example, 1.0‰ to take into account the biomagnification of ^{13}C occurring because of animal respiration (DE NIRO and EPSTEIN, 1978). Figure 3 summarizes the possible ranges of contribution of the three main carbon pools, for $\delta^{13}\text{C}$ values ranging from -9 to -23‰. Table 4 gives these ranges for some invertebrate species, taking or not taking into account ^{13}C biomagnification.

The main conclusions from the results presented in this figure and table are that planktonic carbon always constitutes a large fraction of the diet of particulate feeding organisms, especially when an isotope shift between food and consumers is considered. The seaweed carbon appears as the second component (mean: 35%) of their diet, and the fraction originating from *Posidonia* seems extremely low (generally less than 20%; mean: 6%). Only the gorgons *Eunicella* (and *Paramuricea*) display relatively high $\delta^{13}\text{C}$ values, which would show that *Posidonia* carbon prevails in their diet. This observation is quite surprising when considering the sampling location of these organisms, on rocky walls (35 m depth) and far from seagrass beds. One could explain these values by a strong enrichment in ^{13}C occurring during gorgon metabolism (i.e. a large respiration/assimilation ratio; McCONNAUGHEY and McROY, 1979a). The urchin *Paracentrotus*, usually thought as a seagrass grazer, appears to feed mainly on algae; this is most likely on *Posidonia* epiphytes.

These results on the invertebrate fauna of the Gulf of Calvi are difficult to compare with those obtained for other seagrass communities. Thus, McCONNAUGHEY and McROY

Table 4. Ranges of possible contributions of the three main carbon sources in the diet of some invertebrates of the Gulf of Calvi. Values in parentheses were obtained taking into account a biomagnification of 1‰ in ^{13}C

Species	$\delta^{13}\text{C}$	% Plankton	% <i>Posidonia</i>	% Algae
<i>Axinella</i> (sponge)	-21.3	58-88 (83-95)	0-12 (0-5)	0-42 (0-17)
<i>Eudendrium</i> (hydroz.)	-22.8	97-99 (100)	0-1 (-)	0-3 (-)
<i>Eunicella</i> (gorgon)	-14.2	0-38 (0-45)	48-62 (38-55)	0-52 (0-62)
<i>Spirographis</i> (worm)	-20.3	33-81 (58-88)	0-19 (0-12)	0-67 (0-42)
<i>Mytilus</i> (mussel)	-21.7	72-91 (96-98)	0-9 (0-2)	0-28 (0-4)
<i>Paracentrotus</i> * (urchin)	-17.8		12 (2)	88 (98)
<i>Leptomysis</i> (mysid)	-18.6	0-68 (16-76)	4-32 (0-24)	0-96 (0-84)
<i>Phallusia</i> (tunicate)	-23.6	100	-	-

* Because of the herbivorous status of this species, equation (2) was used.

(1979b) found up to 50% of eelgrass (*Zostera*) carbon in many components of an Alaskan estuarine food web. Likewise, when comparing seagrass estuarine and offshore food webs, FRY and PARKER (1979, Texas) and FRY *et al.* (1983, Queensland) noticed significant $\delta^{13}\text{C}$ differences, demonstrating the importance of seagrass carbon in the animal diet. At Calvi, notwithstanding their vast extent (48% of total Gulf area) and the large amount of organic matter they produce, *Posidonia* meadows supply an extremely small proportion of carbon for consumers, compared with phytoplankton or seaweeds. This low utilization of an apparently inexhaustible carbon reservoir by zoobenthos can be partially explained by: (1) the hard consistency of *Posidonia* blades, coupled with a high crusting rate by calcareous epiphytes, making them difficult to assimilate by grazers; (2) the turnover rate of *Posidonia* leaves in the Gulf of Calvi is quite low (1.3, BAY, 1984), compared with other temperate seagrass species (McROY and McMILLAN, 1977); (3) the growth of *Posidonia* shoots is synchronous; young leaves appear in summer and grow throughout a year before sloughing off: dead leaves progressively accumulate on meadow bottoms, offering new substrates to decomposers; this period is, however, very short, autumnal and winter bad weather conditions involving strong coastal currents which sweep dead leaves ashore. On the beaches, they then pile up in large banks and are consumed by typical terrestrial fauna.

Although the proportion of dead blades leaving the marine ecosystems is difficult to estimate, these exports of material are a possible explanation for the apparent lack of *Posidonia* carbon in the benthic food webs of the Gulf of Calvi. When considering a mean $\delta^{13}\text{C}$ value of -21‰ for particulate feeders, the average ratio of plankton/*Posidonia*/algal carbons in their diet is 6/1/3; this supposes, knowing the production of planktonic and seagrass communities, that only about 10% of the *Posidonia* carbon produced enters the food web; the remainder is exported ashore. Nevertheless, these hypotheses must be regarded cautiously. In a recent investigation, BENNER *et al.* (1987) has shown that the decomposition of *Spartina* detritus in a salt marsh was accompanied by ^{13}C depletion, with the remaining detritus being richer in lighter (in term of δ) biopolymers, such as lignin. Such a process has not been demonstrated yet for seagrasses.

Notwithstanding the above, the $\delta^{13}\text{C}$ measurements on different organisms from the Calvi coastal ecosystems presented here show that they are mainly plankton-based or algae-plankton-based. The algal carbon part within the detrital organic matter can be important here (i.e. between 30 and 40%, if means are taken into consideration; up to 100% if plankton carbon is neglected) and denotes high production rates: limited data are available, however, on turnover rates of temperate seaweeds. Contrary to other seagrass species, *Posidonia* beds are not of great importance as carbon suppliers to food webs; their importance in the function of an ecosystem should not be minimized, however, owing to the great amount of oxygen they produce (i.e. the "lungs of Mediterranean"), to the quantity of sediments they trap and stabilize, and to the diversity and richness of the fauna for which they provide shelter.

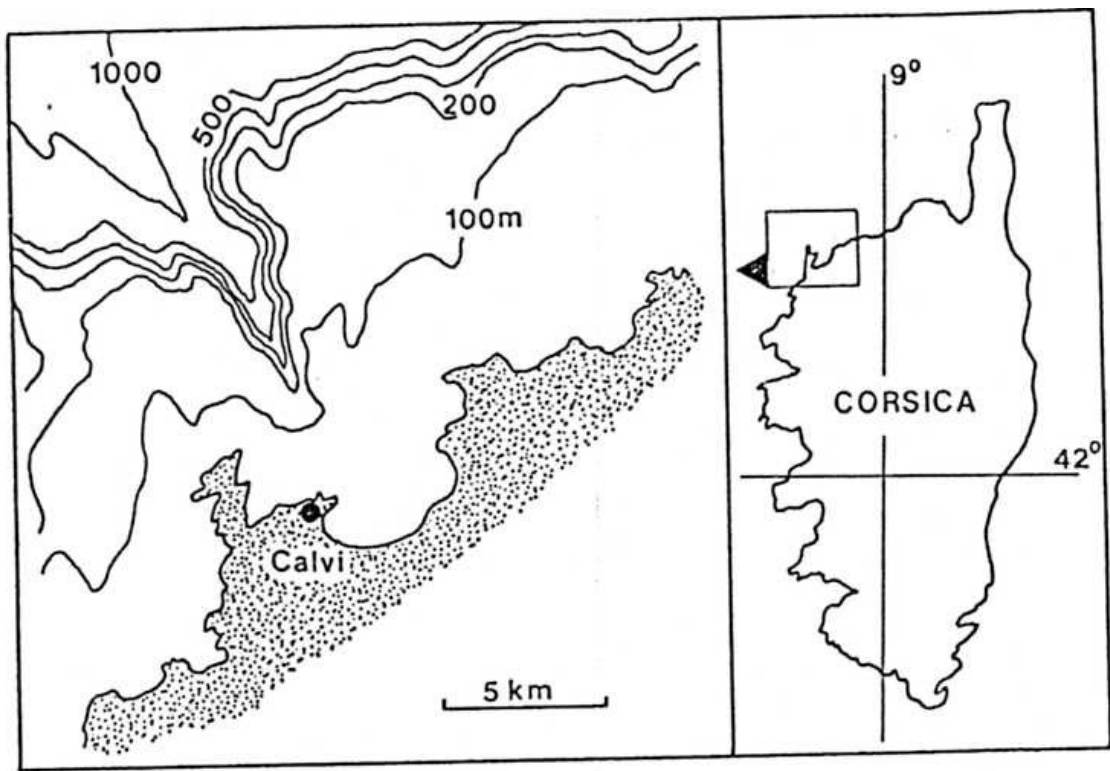
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