

## A $\delta^{13}\text{C}$ Study of the Feeding Habits in Four Mediterranean *Leptomysis* species (Crustacea: Mysidacea)

P. A. DAUBY

Laboratory of Oceanology, University of Liège, B6 Sart Tilman, B-4000 Liège, Belgium.

With 4 figures

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**Abstract.** Mediterranean *Leptomysis* species are benthic-nectonic shrimps living close to seagrass bed bottoms, forming swarms during the day and feeding on detritus and sedimentary organic matter during the night. As this matter is derived from different plant sources (phytoplankton, seagrasses, macro- and microalgae), assimilated carbon entering mysid tissues can hardly be identified on the basis of digestive tract analyses. Stable carbon isotope ratio measurements help to delineate food sources of the different studied *Leptomysis* species because plants are distinct isotopically. These  $\delta^{13}\text{C}$  measurements reinforce the view of the minor role of seagrass carbon in benthic food webs and of the importance of algae in the dynamics of these ecosystems.

### Problem

Mysids, according to their size and feeding appendages, feed on small particles, both living (diatoms, dinoflagellates, ciliates, or copepods) and non-living (detritus, fecal pellets, or terrigenous material). Most species are filter feeders and are not selective in their choice of prey. As their food is macerated, it is very difficult, sometimes impossible, to recognize it when analysing stomach content.

The purpose of the present study is to trace, using stable carbon isotope ratios, the origin of food material consumed by a common Mediterranean mysid genus, *Leptomysis*. The fractionation between stable isotopes differs in plants based on differences in their photosynthetic carbon metabolism (SMITH & EPSTEIN, 1971; BENDER, 1971; FARQUHAR *et al.*, 1989 for review), and a close relationship exists between the  $^{13}\text{C}/^{12}\text{C}$  contents of food and consumers (MOSORA *et al.*, 1971; DENIRO & EPSTEIN, 1978). Stable carbon isotope ratio analyses are therefore a useful tool in delineating carbon pathways in various ecosystems, including terrestrial and limnic (FRY *et al.*, 1978; TIESZEN *et al.*, 1979; BOUTTON *et al.*, 1980; RAU & ANDERSON, 1981), as well as coastal marine systems, especially those where distinct plant carbon sources coexist (salt marshes, estuaries, and seagrass beds) (HAINES & MONTAGUE, 1979; FRY & PARKER, 1979; MCCONNAUGHEY & McROY, 1979; FRY *et al.*, 1982, 1984; PETERSON *et al.*, 1985; DAUBY, 1989).

## Material and Methods

### 1. Study site

Sampling was carried out from the oceanographic station STARESO, Revellata Point, on the western side of the Gulf of Calvi, northwest Corsica. The gulf opens widely to the northwest and has a total area of about 22 km<sup>2</sup>. Water depth increases progressively (slope: 2%) from south to northwest, reaching 100 m. The surface water temperature has a summer maximum (about 26°C) in August and a winter minimum (13°C) in March; the water column has a seasonal thermocline from May to September.

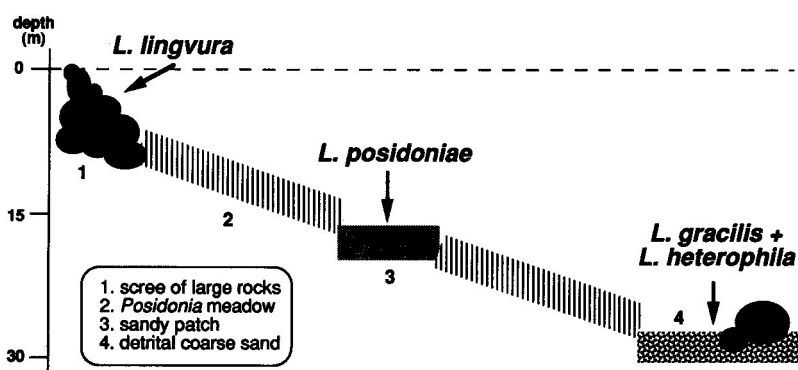


Fig. 1. Schematic cross view of the Calvi Gulf bottoms down to 35 m depth, with distribution of the biotopes and localization of *Leptomyxis* populations.

The *Leptomyxis* populations inhabit three main biotopes (Fig. 1). The first is located from the surface to 5–8 m and consists of a scree of large rocks densely covered by seaweed communities, mostly brown algae (*Halopteris* and *Cystoseira*). The second biotope, covering 48% of the gulf (BAY, 1984), is a vast *Posidonia oceanica* meadow (from 5 to 38 m) irregularly interrupted by sandy patches or small channels. The last biotope of detrital coarse sand and some scattered boulders occurs between 40 and 60 m.

### 2. Sampling and analysis

Mysid samples were collected at regular intervals from March 1983 to February 1984. Shrimps were caught alive, by SCUBA diving, using plastic bags and 'butterfly nets', and immediately frozen. Prior to isotope ratio analysis, species were determined and individuals sexed and sized. Seagrass and macroalgae samples were also collected by diving; attached microflora was removed from *Posidonia* blades by scraping before analysis. Superficial sediment samples were also taken with cores in the different biota in order to analyse edaphic microalgal material; the latter was extracted from the inorganic bulk by ultrasonication. Lastly, phytoplankton samples were filtered (20 l of surface seawater) through GF/C glassfibre filters.

Samples were slightly acidified to remove inorganic carbonates, rinsed, and oven-dried at 50°C for several days. To smooth individual variations, several specimens of each species (*e.g.*, for mysids up to 40 individuals, without separating size classes) were pooled, ground into fine powder, and combusted in the presence of copper oxide at 550°C in vacuum-sealed Pyrex® tubes (SOFER, 1980). The CO<sub>2</sub> generated was purified cryogenically and analysed on a Varian Mat CH5 mass spectrometer. All values are reported relative to the international PDB as

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

where R is the <sup>13</sup>C/<sup>12</sup>C ratio. Routine measurements are accurate to within ± 0.3%.

### 3. The mysid species

Four *Leptomysis* species are especially abundant in the gulf waters: *L. lingvura* (SARS), *L. gracilis* (SARS), *L. posidoniae* WITTMANN, and *L. heterophila* WITTMANN; the last two are relatively 'new' species (WITTMANN, 1986a, b) previously confused with *L. lingvura*.

These four species exhibit the same particular behaviour (MACQUART-MOULIN, 1973; WITTMANN, 1978; MACQUART-MOULIN & PASSELAIGUE, 1982; DAUBY, 1980, 1981, 1985; VAN DALFSEN, 1986): during daytime, individuals form swarms or shoals of various sizes and shapes which stay just above the bottom; at twilight, swarms progressively disperse and gregarious behaviour seems to decrease; during the night, all the swarms have disappeared and individuals swim actively just above the sea floor; immediately after sunrise, swarms are formed again.

Populations of the four species hardly mix, each inhabiting a well-defined biotope (Fig. 1). *Leptomysis lingvura* is restricted to the shallow rocky shore fringe, forming small swarms (a few litres in volume) generally located at the opening of recesses protected from direct sunlight. This species is only observed in shallow waters during summertime and disappears from the study area for the rest of the year. *L. posidoniae* is found throughout the year from 3 to 40 m depth; its main localization is in the *Posidonia* meadow, on sand spots or within the channels running through the seagrass bed. *L. heterophila* is also found at all depths, but is most abundant on the deep detrital coarse sand bottoms (between 25 and 50 m) near big rock formations. Populations of this species are seldom observed alone (which explains the species name) and, at Calvi, are generally associated with those of *L. gracilis*. Throughout the year they form large shoals that can cover up to several hundred square metres (several million individuals).

## Results

### 1. $^{13}\text{C}/^{12}\text{C}$ ratios of food sources

Within the Gulf of Calvi, four main sources of photosynthetically fixed carbon are available to mysid consumers either in the form of living food or as detrital material: phytoplankton of the water column, blades of *Posidonia oceanica*, thalli of benthic macroalgae, and cells or filaments of benthic microalgae (edaphic or epiphytic). Inputs of terrestrial plant material (mainly  $\text{C}_3$ , average  $-27\text{‰}$ ) can be ignored as only a small seasonal stream enters the gulf;  $\delta^{13}\text{C}$  values of sediment collected at its mouth do not differ significantly from samples collected in other parts of the gulf at similar depths.

Data on  $^{13}\text{C}/^{12}\text{C}$  ratios of macroalgae and phytoplankton have been published previously (DAUBY, 1989; DAUBY *et al.*, 1990) and will be discussed below.

*Posidonia oceanica* carbon did not show significant seasonal  $\delta^{13}\text{C}$  variations. However, its stable isotope ratio apparently decreased from about  $-9\text{‰}$  near the surface (range:  $-6.4 > -11.3$ ) to  $-12\text{‰}$  at the lower limit (range:  $-10.1 > -14.2$ ) of the seagrass bed (Fig. 2), probably due to a light intensity effect (COOPER & DENIRO, 1989). Similar depth-related variations have also been reported from plant material collected in other Western Mediterranean areas (Marseilles and Naples).

Seagrass epiphytic microflora, analysed as a whole, showed a  $\delta^{13}\text{C}$  of  $-17.5 \pm 1.2\text{‰}$ . Measurements made on single groups of species ranged from  $-15.6$  (*Dictyota*) to  $-19.6\text{‰}$  (*Peysonnellia*). Edaphic microflora (mostly diatoms) and sedimentary organic matter had a mean  $\delta^{13}\text{C}$  of  $-18.0\text{‰}$ ; this value was quite constant along the entire depth gradient, from 5 to 40 m.

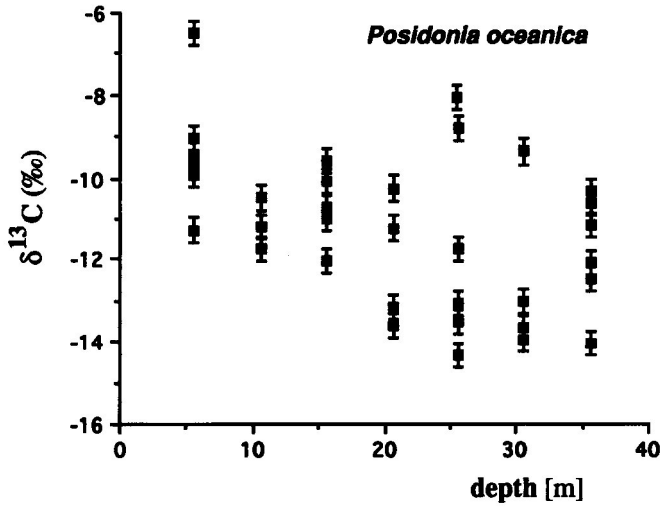


Fig. 2. Stable carbon isotope ratios of *Posidonia oceanica* in relation to depth.

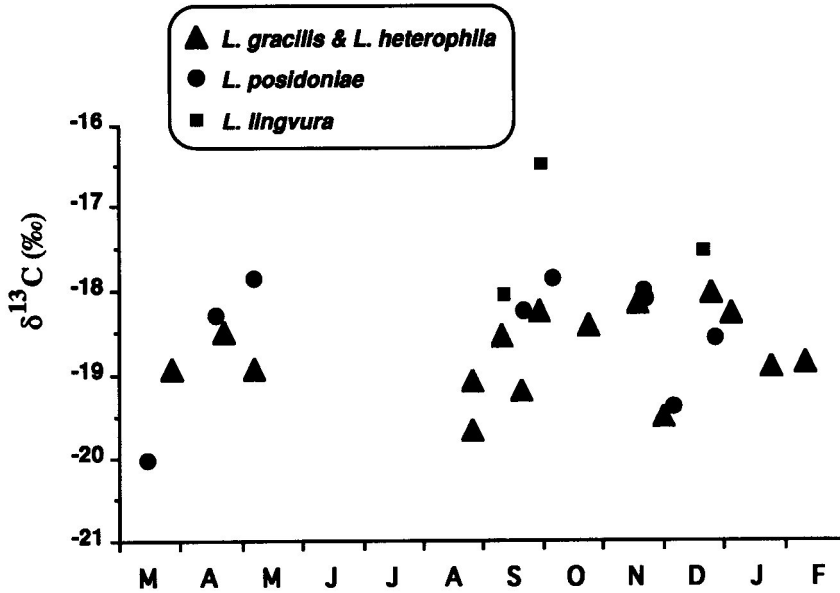


Fig. 3. Variations throughout the year of body  $\delta^{13}\text{C}$  of the different *Leptomyxis* species.

## 2. $\delta^{13}\text{C}$ of *Leptomyxis* populations (Fig. 3)

As *Leptomyxis lingvura* has only been found during summer months (several years of observation have failed to reveal their habitat during the cold season), only one season's data are available for these populations: July ( $-18.0\text{‰}$ ), August ( $-16.5\text{‰}$ ), and October ( $-17.4\text{‰}$ ). A nearly complete year's set of  $\delta^{13}\text{C}$  values was obtained for *Leptomyxis posidoniae*. They ranged from  $-17.7$  to  $-19.9\text{‰}$ , with a weak winter depression. The  $^{13}\text{C}/^{12}\text{C}$  ratios of the mixed populations of

*Leptomysis gracilis* and *L. heterophila* were variable, but with no obvious annual trend; values ranged from  $-17.9\text{‰}$  to  $-19.7\text{‰}$  over the year. Measurements of individual species at different seasons showed no significantly different  $\delta^{13}\text{C}$ .

## Discussion

The feeding behaviour of Mediterranean *Leptomysis* spp. is well-known, especially by *in situ* observations (WITTMANN, 1977; DAUBY, 1985; VAN DALFSEN, 1986); it appears to be correlated with the rhythm of formation-dissociation of swarms. During the day, when swarms are well-formed, mysids spend most of their time swimming, keeping the group quite stationary and avoiding predators. In contrast, at night, as swarms spread and disaggregate, the shrimps actively scrounge for food on the bottoms and often have miscellaneous food particles in their thoracic appendages. MAUCLINE (1969) reported, from samples collected at the surface, that generally more than half the individuals taken during the day had little or no food in the stomach. Similarly, HECQ *et al.* (1981, 1984) showed that the digestive enzymatic activity increased about five-fold during the night (with a maximum just before dawn), indicating increased feeding.

Few data are available on the dietary preferences of the different *Leptomysis* species. MAUCLINE (1969) examined the stomach contents of *L. gracilis* from the west coast of Scotland over an annual cycle and found identifiable material, mainly detritus and terrigenous particles. In his detailed study of Adriatic populations of *Leptomysis*, WITTMANN (1978) also analysed stomach contents of different species; he noted the presence of miscellaneous materials such as pieces of *Posidonia* and algae, diatoms, dinoflagellates, foraminifera, parts of worms and small crustaceans or sponge spicules, but also inorganic bodies such as sand grains. The same diversity was found in the stomach contents of the Corsican populations of the four species (DAUBY, 1985). GAUDY & GUÉRIN (1979) observed that *L. lingvura* under laboratory conditions fed both on living harpacticoid copepods (*Tisbe*) as well as on artificial food flakes. Lastly, HECQ *et al.* (1981, 1984), analysing the digestive enzymatic activities of *L. lingvura*, found that the amylasic activity was about four times more important than the proteolytic activity; this suggests that this species is more 'herbivorous' than 'carnivorous'.

Thus it appears that *Leptomysis* species are not selective feeders and that they are broadly omnivorous. The size of seized 'prey' is also not a key factor. Mysids are often seen gripping pieces of food several millimetres long (mean body length of adults = 9 mm) and cannibalism has been observed (WITTMANN, 1978; DAUBY, 1985).

The remaining questions are: which part of the swallowed food is effectively digested? Where does the assimilated carbon come from? The stable isotope technique provides pertinent information: laboratory and field studies clearly demonstrate a good agreement between  $\delta^{13}\text{C}$  of food and consumers (DENIRO & EPSTEIN, 1978; FRY *et al.*, 1978), the latter being on the average slightly enriched in  $^{13}\text{C}$  (less negative  $\delta^{13}\text{C}$  values) relative to their diets by about 0.5 to 1‰. The *Leptomysis* populations (all species combined) display  $\delta^{13}\text{C}$  values ranging from  $-17$  to  $-20\text{‰}$ , and must thus feed on materials with combined isotopic ratios roughly falling within the range  $-17.5$  to  $-21\text{‰}$ .

Available carbon sources of mysid shrimps in the Gulf of Calvi include: (i) living microplankton (phyto- and zoo-) whose  $\delta^{13}\text{C}$  range from  $-24\text{‰}$  during the spring diatom bloom to  $-20\text{‰}$  in summer months (DAUBY *et al.*, 1990); (ii) microalgae (edaphic or epiphytic), with a mean  $\delta^{13}\text{C}$  of  $-18\text{‰}$ , and pieces of larger benthic seaweeds whose  $\delta^{13}\text{C}$  range from  $-10.1$  to  $-30.8\text{‰}$ , with an average value of  $-19\text{‰}$  for the most common genera (the brown algae *Halopteris* and *Cystoseira*) (DAUBY, 1989); (iii) *Posidonia oceanica* blade pieces, with heavier  $\delta^{13}\text{C}$  values, between  $-9$  and  $-12\text{‰}$  for living blades and approximately  $-13\text{‰}$  for the litter; (iv) detrital suspended organic matter whose  $\delta^{13}\text{C}$  range from  $-20$  to  $-25\text{‰}$  (mean:  $-22\text{‰}$ ) in this Mediterranean area (RAU *et al.*, 1990).

These different potential carbon supplies can be amalgamated on the basis of their  $^{13}\text{C}/^{12}\text{C}$  ratios in three main food pools: a 'pelagic' one, including plankton and suspended matter, an 'algal' one, including benthic micro- and macroalgae, and a 'seagrass' one, with respective mean  $\delta^{13}\text{C}$  values of  $-22$ ,  $-18.5$ , and  $-11\text{‰}$ . A simple algorithm (DAUBY & MOSORA, 1988; DAUBY, 1989) enables computation of the maximum and minimum percentages of each of these carbon pools entering

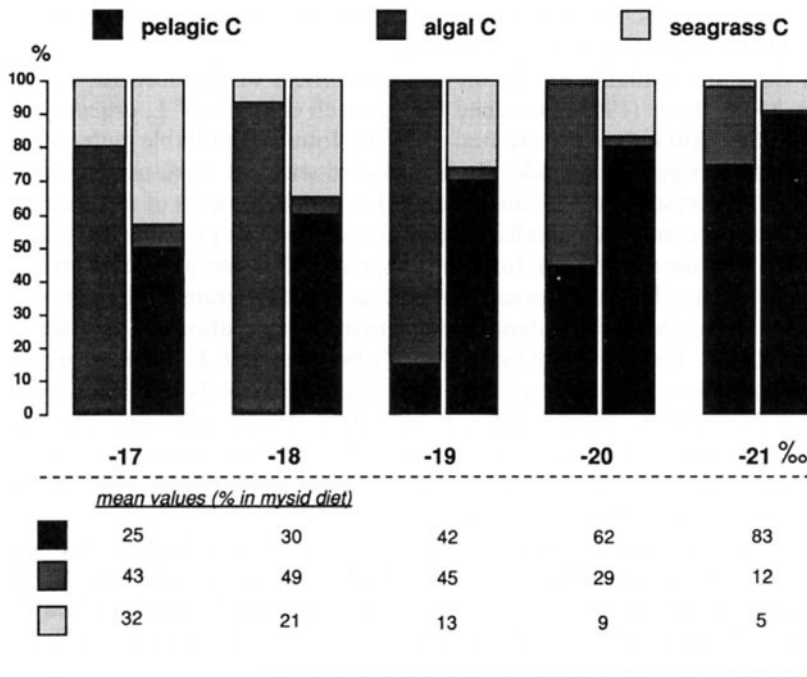


Fig. 4. Possible maximum and minimum contributions (as 100% stacked column charts) of the three main plant carbon sources in the diet of *Leptomysis*, as a function of mysid body  $\delta^{13}\text{C}$  (from  $-17$  to  $-21\text{‰}$ ). Corresponding mean values (in percent contribution).

the diet of *Leptomysis*. These proportions are shown in Fig. 4, according to the range of  $\delta^{13}\text{C}$  values observed in mysid tissues. Although the range of possible combinations in the relative share of each food source in the *Leptomysis*  $^{13}\text{C}/^{12}\text{C}$  organic constitution is clearly large, it nevertheless appears that: a. 'Pelagic' carbon is an important dietary component which contributes from min. 0–50% to max.

75–90% (average: 48%). The importance of this C source is due to the fact (i) that mysids, during daytime, actively swim in open water and thus mainly filter planktonic or detrital suspended matter, and (ii) that pelagos-originating matter constitutes a non-negligible part of bottom organic matter ( $\delta^{13}\text{C}$ :  $-18\text{‰}$ ) on which mysid feed during the night. It should be noted here that zooplankton collected offshore or large crustaceans inhabiting deeper waters, like the euphausiid *Meganycitiphanes norvegica*, clearly display  $\delta^{13}\text{C}$  values ( $-20.5$  to  $-22.5\text{‰}$ ) close to those of their only available food source, *i.e.*, phytoplankton; b. algae apparently constitute the second C source, with a range of 1–23% to 5–93% (average: 36%). Albeit less important than seagrasses in terms of instantaneous standing stock, algae (especially inconspicuous species) show very high growth rates and likely produce as much (or even more) organic matter than *Posidonia* does annually. This was recently confirmed by *in situ* comparative measurements of C uptake by seaweeds and seagrasses in the bay of Calvi using the  $^{14}\text{C}$  technique (DAUBY *et al.*, unpubl.); c. *Posidonia*-originating carbon clearly provides the lowest fraction in the mysid diet (min: 2–9% to max: 20–43%) (average: 16%). The apparent lack of this carbon in the diet of the four *Leptomysis* species (and especially in that of *L. posidoniae*) has several possible explanations: (i) the seagrass leaves—even as litter—are ‘inedible’: they have a hard consistency (due to the high proportion of fibers) and contain a relatively high amount of poorly digestible carbohydrates (insoluble carbohydrates make up to 40% of total *Posidonia* organic matter; BELKHIRIA, unpubl.) such as pectine or suberine (B. VELIMIROV, pers. comm.); they are highly encrusted by calcareous epiphytes (*Melobesia*) and are naturally very slowly degraded; (ii) the decaying and dead leaves are largely exported, swept ashore by autumn and winter storms, and pile up in large banks on the beaches (‘banquettes’); another fraction is transported to deep bottoms (*Posidonia* fibres were found down to 2000 m in Calvi Canyon’s sedimentary matter). Thus, only a minor share of the total litter biomass is accessible to marine consumers; (iii) the bacterial degradation of *Posidonia* blades could be accompanied by a shift in its  $\delta^{13}\text{C}$ , with a depletion in  $^{13}\text{C}$ ; such a physiology has been observed for salt marsh *Spartina*-derived detritus (BENNER *et al.*, 1987, 1991), depending on the relative degradation rate of the different biochemical components of the plant; for seagrasses, however, such a shift should be small, ca. 1‰ (FRY *et al.*, 1987).

These different hypotheses, combined with the wind stress-induced high orbital velocities near the shallow seafloor (at least under autumn and winter conditions) and with a mean horizontal advective current of between 5 and 10  $\text{cm} \cdot \text{s}^{-1}$ , could contribute to a high mixing rate of sedimentary organic matter originating from various plant sources. Of course, any proportional combination of these hypotheses could be proposed.

In any case, the  $\delta^{13}\text{C}$  of *Leptomysis* populations better reflects the influence of an algal carbon source, stemming either from a planktonic or a benthic pool, than a seagrass carbon input. This reinforces the view that very few consumers actually feed on *Posidonia* (OTT & MAURER, 1977). These observations, although only restricted to carbon isotopes, corroborate results from other seagrass ecosystems and underline the importance of periphyton carbon in benthic food webs (KITTING *et al.*, 1984; FRY, 1984; STEPHENSON *et al.*, 1986; FRY *et al.*, 1987; SULLIVAN & MONCREIFF, 1990). Periphyton (comprising fungi and bacteria, diatoms and flagellates, attached and drift macroalgae, encrusting species) obviously has a

higher nutritional value than (supporting) seagrasses themselves (several authors in KLUMPP *et al.*, 1989) and more easily provides nitrogen to consumers.

One should expect the different *Leptomysis* species to present different mean  $\delta^{13}\text{C}$  values, as they live in different biota characterized by different predominant primary producers (macroalgae for *L. lingvura*, seagrasses for *L. posidoniae*, and a mixture of phytoplankton and detritus for the pair *L. gracilis-L. heterophila*). Measurements over the year, however, show no significant difference between the four species'  $\delta^{13}\text{C}$ . Such a uniform  $^{13}\text{C}$  content was also observed among benthic crustaceans in the Gulf of Mexico, regardless of species, by FRY *et al.* (1984), who assumed a decrease in isotopic variations when ascending in food webs. The similarity between *Leptomysis* isotope ratios could be the result of either a feeding selectivity or an omnivorous behaviour associated with a differential assimilation of ingested foods. Even if mysid shrimps feed on seagrass detritus (PECHEN'-FINENKO & PAVLOVSKAYA, 1975) and digest cellulose (FOULDS & MANN, 1978), they probably more easily assimilate plant material with 'soft' cell walls such as algae. Such a preferential assimilation was also found for the herbivorous fish *Sarpa salpa*, which feeds on *Posidonia* blades (VELIMIROV, 1984; DAUBY & COULON, 1993), and seems to be a general rule for most benthic consumers.

## Summary

Four *Leptomysis* species inhabit three relatively closely adjoining biotopes in the Gulf of Calvi: *L. lingvura* near the surface, forming shoals within rock blocks, *L. posidoniae* in *Posidonia* seagrass beds, and the couple *L. heterophila* + *L. gracilis* at the lower border of the infralittoral zone. These three biotopes are characterized by different main plant food sources (namely macroalgae, seagrasses, and phytoplankton), which are C isotopically well separated.  $\delta^{13}\text{C}$  measurements of the different *Leptomysis* populations show that these shrimps do not feed preferentially on the carbon source prevailing in their own biotope, but rather have an isotope ratio ( $-16.5$  to  $-20\%$ ) close to the algal ratio. These observations can either be explained by feeding selectivity or by a differential assimilation rate of ingested material; in any case, they corroborate the role of algae in the trophodynamics of Mediterranean seagrass ecosystems.

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