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EVALUATION OF PHOTOSYNTHETIC PATHWAYS OF VEGETATION, AND OF SOURCES OF SEDIMENTARY ORGANIC MATTER THROUGH $\delta^{13}C$ IN TERMINOS LAGOON, CAMPECHE, MEXICO

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RESUMEN

La vegetación sumergida se caracterizó isotópicamente con el objeto de reconocer el mecanismo fotosintético utilizado por la vegetación y su adaptación a un medio lagunar tropical de salinidad variable. La composición isotópica ($\delta^{13}C$) varió poco para *Thalassia testudinum* de -11.6 a -15.9‰ (C_3) y *Dictyota sp.* de -16.8 a -18.7‰ (C_4). Para *Halodule wrightii* y las algas rodofitas se registraron dos intervalos de $\delta^{13}C$: *H. wrightii* (C_3) de -15.2 a -17.0‰ al noreste de la laguna y de -23.6 a -27.6‰ en el resto del sistema, y las rodofitas de -17.2‰ (C_4) en el sublitoral (Bahamita) y de -23.3 a -27.1‰ (C_3) dentro de la laguna. Se discute el registro de los dos intervalos de valores isotópicos para los dos últimos tipos de vegetación, la relación de los intervalos con la distribución de la vegetación en el sistema y con las características ambientales de cada localidad, y su implicación a nivel fotosintético. El detrito y sedimento superficial se caracterizaron isotópicamente para determinar las fuentes naturales de los aportes de carbono orgánico y la distribución de éste en el sistema lagunar. Se aplicó un análisis de conglomerados con los datos hidrológicos, sedimentarios e isotópicos para determinar agrupaciones de localidades similares. La laguna se dividió en dos áreas: Area 1, al norte-noreste con un $\delta^{13}C\bar{x}=-15.5$‰ lo cual indica que la materia orgánica de las praderas de pastos y algas constituye la fuente de carbono orgánico; área 2, el resto del sistema con un $\delta^{13}C\bar{x}=-20.3$‰ que refleja la predominancia del carbono orgánico de origen terrestre.

Palabras clave: $\delta^{13}C$, vegetación sumergida, fotosíntesis, sedimento, detrito, Laguna de Términos, México.

ABSTRACT

Submerged vegetation was isotopically characterized in order to determine the photosynthetic mechanism used by each species and its adaptation to a tropical lagoonal environment of variable salinity. Isotopic composition ($\delta^{13}C$) for *Thalassia testudinum* of -11.6 to -15.9‰ (C_3) and *Dictyota sp* of -16.8 to -18.7‰ (C_4) was registered. For *Halodule wrightii* and the red algae two $\delta^{13}C$ intervals were registered: *H. wrightii* (C_3) from -15.2 to -17.0‰ to the northeast of the lagoon and from -23.6 to -27.6‰ throughout the rest of the system, and the red algae of -17.2‰ (C_4) on the sublittoral (Bahamita) and from -23.3 to -27.1‰ (C_3) within the lagoon. The registration of the two intervals of isotopic values for these last two types of vegetation, the manner in which these intervals are related to the distribution of the vegetation within the system and to the environmental characteris-

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tics of each locality, and the implications with respect to photosynthesis, are discussed. Surface sediment and detritus were isotopically characterized in order to identify the natural sources of organic carbon and its distribution within the lagoon. A cluster analysis was applied to hydrological, sedimentary and isotopic data to define groups of similar localities. The lagoon was divided into two areas: Area 1 to the north and northeast with an average $\delta^{13}C$ of −15.5‰ which indicates that the organic matter of seagrass and algae beds is the source of organic carbon, and Area 2, the rest of the system with an average $\delta^{13}C$ of −20.3‰ that indicates a predominance of organic carbon of terrestrial origin.

Key words: $\delta^{13}C$, submerged vegetation, photosynthesis, sediment, detritus, Terminos Lagoon, Mexico.

INTRODUCTION

Submerged vegetation uses both CO^2 and HCO^-_3 as substrate for photosynthesis. However, it relies more on HCO^-_3 than CO^2 as the first is more abundant in sea water. Inorganic carbon can be found in nature in two stable isotopic forms: ^{12}C and ^{13}C. The proportion in which ^{13}C is discriminated in the leaves of plants during photosynthesis (represented as $\delta^{13}C$) has been used as an indicator of photosynthetic pathways.

There are three types of pathways: the C3 (Calvin) pathway which is characterized by $\delta^{13}C$ values of −23.0 to −34.3‰, the C4 (Hatch-Slack) pathway with values of −3.0 to −19.0‰, and the CAM (crassulacean acid metabolism) which is represented by an ample range of $\delta^{13}C$ values. CAM is present in a genetically undefined group of plants that are commonly subjected to environmental stress (Beer and Wetzel, 1982).

These values stand and serve as references for different vegetation types, notwithstanding that cases have been recorded of intra and interspecific variation with respect to the photosynthetic mechanism that is used (Smith and Epstein, 1971; Beer and Waisel, 1979; McMillan *et al.,* 1980).

In the case of seagrasses, the $\delta^{13}C$ is related to: 1) the form of inorganic carbon that is used as substrate, 2) the fractionation of ^{12}C and ^{13}C that accompanies the isotopic equilibrium of CO^2 and HCO^-_3 in sea water, 3) the initial carboxilation reaction, and 4) photorespiration. In C3 terrestrial vegetation, photorespired CO^2 has more ^{13}C than is found in the tissue of the leaves, and the loss of $^{13}CO^2$ can be due to a preferential refixation of $^{12}CO^2$ from the pool of photorespired CO^2. The total carbon of the plant is therefore enriched in ^{12}C and the $\delta^{13}C$ value is lighter and more negative. The carbon fixation takes place in an open system where internal CO^2 is balanced with atmospheric CO^2 (Benedict *et al.,* 1980).

In seagrasses such as *Thalassia sp.* there is little photorespiration for two reasons: 1) resistance at the cell wall or the membrane to CO^2 diffusion, and 2) resistance by the surrounding water to CO^2 diffusion. Both prevent the loss of photorespired CO^2 which results in its refixation and the elimination of any isotopic effect of photorespiration on the $\delta^{13}C$. This is a diffusion-limited system where internal CO^2 is not balanced with external CO^2 (Benedict *et al.,* 1980).

Plants that photosynthesize by means of the C3 and C4 pathways have been classified on the basis of their initial photosynthetic CO^2 incorporation patterns. The C3 incorporation pattern initially fixes carbon to produce 3-PGA (3-phosphoglyceric acid), then phosphate esters, and then sugars. It is also related to the use of CO^2 as substrate for photosynthesis and of RuBP-case (ribulosebiphosphate carboxylase) as principal photosynthetic enzyme.

The C4 pattern presents a high initial carbon incorporation rate into malate and other organic acids, and it can use HCO^-_3 as substrate and the enzyme PEP-case (phosphoenolpyruvate carboxylase). The malate and organic acids produced initially by this pathway are called photosynthetic intermediaries as they are rapidly decarboxylated by which process they form CO^2 that is refixed via RuBP-case (Holladay and Bowes, 1980).

RuBP-case differs from PEP-case in that it is more salt-sensitive, is such a way that RuBP-case/PEP-case activity ratios are in favour of the latter enzyme in saltier waters. It has also been found that a high RuBP-case/PEP-case activity ratio indicates a C3 plant, while a low ratio indicates a C4 plant, as in the case of *Cymodocea nodosa.*

The CAM pattern is more complicated as it relies on RuBP-case by day and of PEP-case by night, and so presents a combination of C3 and C4 characteristics (Holladay and Bowes, 1980).

Aquatic plants have been placed in a group intermediate between the classical terrestrical C3 and C4 groups by several authors, as the relationship between $\delta^{13}C$ and photosynthetic pathway is not as strict as in terrestrial plants. An example of this is the case of some seagrass species for which high $\delta^{13}C$ values, characteristic of terrestrial C4 plants, have been recorded (Smith and Epstein, 1971) in spite of the fact that these species do not have bundle sheath cells and belong to the C3 group of plants (Beer *et al.,* 1980; Beer and Wetzel, 1982).

The isotopic composition of the substrate, determined by means of the $\delta^{13}C$ of sedimentary organic matter and of detritus, depends directly on the isotopic composition of the plant source. From data obtained in previous studies a gradient of sedimentary $\delta^{13}C$ has been established that varies from lighter values (–25.0 to –27.5‰) in areas that receive contributions of organic carbon of terrestrial origin, to heavier values (–21.0 to –22.8‰) in estuarine environments and those that are influenced by sea water (Shultz and Calder, 1976; Rashid and Reinson, 1979; Tan and Strain, 1979; Botello *et al.,* 1980; Botello and Macko, 1982; Fry and Sherr, 1984).

Terminos Lagoon, Campeche, has a variety of species of submerged vegetation, among which seagrasses and red algae form extensive beds. These beds play an important role as environmental stabilizers and reservoirs of organic matter, and provide nursing areas for commercially important animal species. The distribution of the species of submerged vegetation within the system is determined by the characteristics of the water column and of the substrate, such as salinity, turbidity and the textural and compositional properties of the sediment. These, in turn, are related to freshwater, marine and terrestrial inputs, as well as to autocthonous inputs derived from the beds of submerged vegetation.

Taking this into account, the purpose of this study was to characterise Terminos Lagoon into isotopically different areas through: (1) the isotopic characterization of the dominant species of submerged vegetation within the lagoon and adjacent areas (the seagrasses *Thalassia testudinum* Banks ex König and *Halodule wrightii*

Aschers., the red algae, and the brown alga *Dictyota sp.*), (2) the determination of the relationship between the $\delta^{13}C$ values and the photosynthetic mechanism used by each species of vegetation, (3) the isotopic characterization of the sediment and detritus of 18 localities of the lagoon and adjacent areas, and (4) the identification of the natural sources of the organic carbon that is incorporated into the substrate and the description of its distribution throughout the system.

STUDY AREA

Terminos Lagoon, Campeche lies between 91° 15′ and 91° 51′ W and between 18° 27′ and 18° 50′ N. It is separated from the Gulf of Mexico by Isla del Carmen, and communicates with it through Boca de Puerto Real to the northeast and Boca del Carmen to the northwest. The main rivers that flow into the lagoon are the Palizada to the southwest, the Chumpán to the south, and the Candelaria to the southeast. The Rio Palizada is a derivative of the Grijalva-Usumacinta system that drains lateritic substrates and carries terrestrial materials of silty-clay texture into Terminos Lagoon through the Laguna del Vapor and the Laguna San Francisco. To the east of the Rio Palizada sediments are clear and the basins of the rivers Chumpán and Candelaria are predominantly calcareous (Cruz-Orozco, 1980) (Figs. 1, 2).

The surrounding vegetation of the lagoon is mainly mangrove and palm trees, and among the submerged vegetation the seagrasses *T. testudinum, H. wrightii* and *Syringodium filiforme* Kütz are dominant. These are distributed in beds along the inner margin of Isla del Carmen and along the eastern and southern margins of the lagoon. They form extensive beds that play an important role as nursing areas for the juvenile phases of several species of commercially important shrimp and fish. Red algae of the genera *Gracilaria, Hypnea* and *Acantophora* are also found mainly to the southwest, south and centre of the system, as well as green algae of the genus *Caulerpa* and brown algae of the genus *Dictyota* (C. Candelaria, personal communication).

The variety of allocthonous as well as autocthonous sources that provide organic and inorganic materials to the system give rise to an heterogeneity of sedimentary characteristics that are distributed throughout the system in gradients determined by the proximity of the river systems and of the communications to the sea. The Rio Palizada contributes a great quantity of detritus of terrestrial origin to the western and southwestern sections of the lagoon, and in contrast organic residues of submerged vegetation associated with seagrass beds are predominant towards the north and northeastern sections.

MATERIALS AND METHODS

Field trips were organised during March (dry season), August (rainy season) and November (season of northers) of 1984 in order to determine possible seasonal fluctuations in the isotopic data. Eighteen localities that included the main river

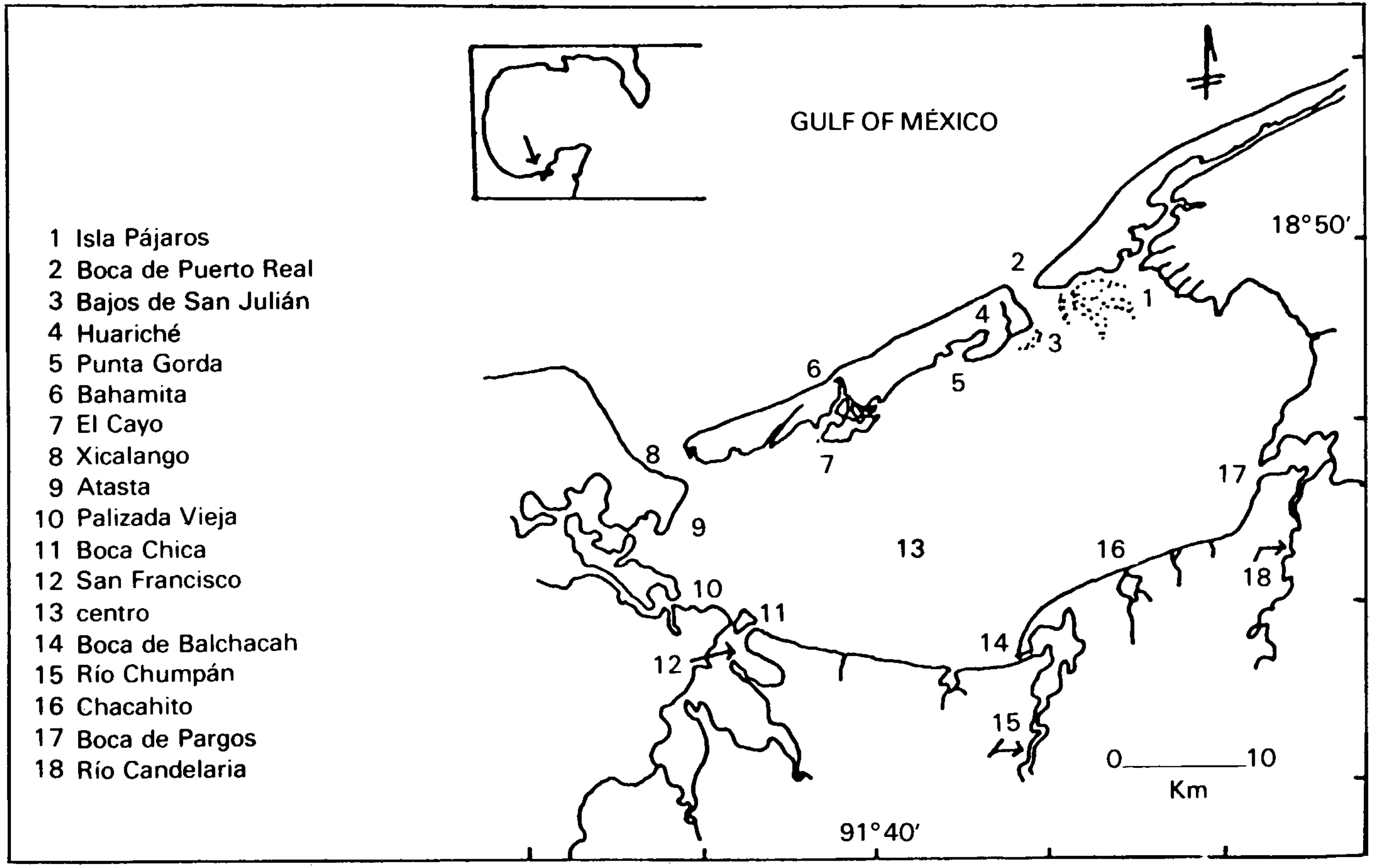

Fig. 1. Terminos Lagoon, Campeche showing sampling localities.

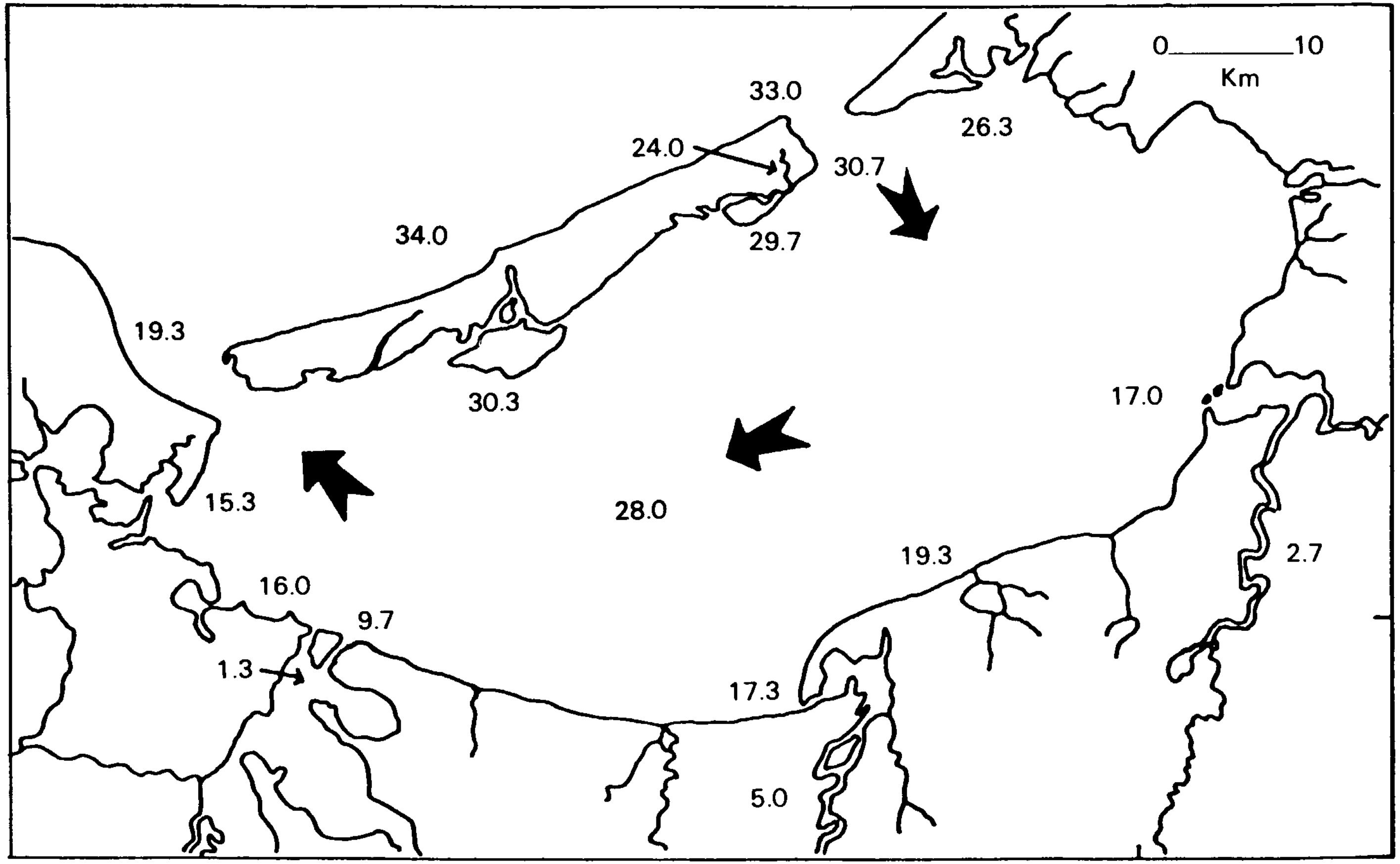

Fig. 2. Salinity values (‰) and main circulation flow in Terminos Lagoon.

systems that empty into the lagoon and their mouths, the margins and the centre of the lagoon, the communications of Boca del Carmen and Boca de Puerto Real, and the sublittoral of Isla del Carmen were selected taking into account the marked differences in environmental characteristics within the system.

Surface water temperature and salinity were measured in each sampling locality. Salinity values used in the text represent average values for the three months. The dominant species of submerged vegetation were selected for the isotopic analysis: the seagrasses *T. testudinum* and *H. wrightii*, the red algae of the genera *Gracilaria* and *Hypnea*, and the brown alga *Dictyota sp.* Several plants of each species were pooled and from this compound sample a subsample was analysed. The plants were collected with a Renfro beam net with an opening of 1.8 × 0.7 m and a 0.8 mm mesh (Renfro, 1962) and a trawling net with an opening of 5 m, a length of 10 m and a 13 mm mesh. Surface sediment was collected with a 3 lt. van Veen sampler and detritus with a Renfro beam net. Detritus was generally composed of plankton, plant and animal fragments, and unidentifiable organic matter.

Samples were preserved in ice until they were processed. They were then dried, ground and sifted through a 0.25 mm mesh, carbonates were eliminated with 10% HCl, and $\delta^{13}C$ was determined following the sealed tube combustion method (Boutton *et al.*, 1983). The internal standard that was used (CO^2 gas) a value of −41.550‰ (S. Ramos, personal communication) with respect to the PDB calcareous standard (*Belemnitella americana*, the fossil belemnite of the PeeDee Formation of Southern Carolina, USA) of Chicago University. The average isotopic variation of each analysis was ±0.1‰.

Sediment was also analysed with respect to three texture groups: gravel (>2 mm), sand (0.0625 to 2 mm) and silt-clay (<0.0625 mm) (Shackley, 1975), as well as for its total organic matter (Dean, 1974) and carbonate content (Shackley, 1975) as part of the sedimentary characterization.

The Kruskal-Wallis test (Zar, 1974) was applied for each locality, to the $\delta^{13}C$ data of the three months. Results were significantly similar for which reason all variables are represented by their average value. The relationship between variables was determined by means of linear correlations (Zar, 1974).

In order to determine groups of environmentally similar localities in the system, the "mean link" method of the Cluster Analysis Programme (Espinosa *et al.*, 1978; Espinosa y López, 1986) was applied to the following variables: water temperature and salinity, gravel, sand, silt-clay, total organic matter and carbonate content and $\delta^{13}C$ of sediment, and $\delta^{13}C$ of detritus and of submerged vegetation.

RESULTS AND DISCUSSION

Average values of water temperature and salinity and of sedimentary variables are presented in Table 1.

Submerged vegetation. The greater part of the $\delta^{13}C$ values of the submerged vegetation of Terminos Lagoon reflects a light isotopic composition in the vegetation that was collected to the west and southwest, and a heavy isotopic composition in the vegetation found to the northeast of the lagoon (Table 2).

TABLE 1

AVERAGE VALUES OF WATER AND SEDIMENT VARIABLES OF EACH LOCALITY OF TERMINOS LAGOON AND ADJACENT AREAS*

Locality	T °C	S ‰	GR	SA	S-C	TOM	$CO_3^=$
El Cayo	28.7	30.3	8.0	66.3	25.7	13.3	44.8
Bajos de San Julián	28.0	30.7	4.6	60.6	34.9	12.6	59.5
Isla Pájaros	29.0	26.3	2.7	27.5	69.8	20.0	65.9
Punta Gorda	28.7	29.7	2.2	78.4	19.3	12.5	45.1
Boca de Puerto Real	29.0	33.0	51.8	46.9	1.3	10.7	54.0
Huariché	26.0	24.0	0.6	32.8	66.6	16.8	69.6
Boca de Pargos	30.0	17.0	19.6	39.8	40.5	16.7	57.6
Bahamita	31.0	34.0	0.3	98.9	0.8	2.0	36.2
Boca de Balchacah	28.3	17.3	22.4	24.5	53.1	12.4	22.3
Xicalango	28.0	19.3	14.7	49.8	35.5	11.4	36.2
Boca Chica	29.0	9.7	0.9	20.2	78.9	13.7	19.7
centro	29.5	28.0	17.4	20.7	61.8	24.4	60.2
Chacahito	28.7	19.3	4.9	36.6	58.5	10.0	16.4
Atasta	28.7	15.3	4.6	13.0	82.5	17.8	32.9
San Francisco	28.3	1.3	0.2	40.5	59.3	11.1	17.3
Palizada Vieja	29.0	16.0	0.0	0.4	99.6	18.2	33.1
Río Chumpán	28.7	5.0	33.6	56.1	40.3	4.5	3.8
Río Candelaria	28.7	2.7	5.1	59.1	35.8	15.0	40.0

* Symbols: T °C = surface water temperature (°C), S ‰ = salinity (‰), GR = gravel (%), SA = sand (%), S-C = silt-clay (%), TOM = total organic matter (%), $CO_3^=$ = carbonates (%).

TABLE 2

AVERAGE VALUES OF $\delta^{13}C$ OF SUBMERGED VEGETATION OF TERMINOS LAGOON AND ADJACENT AREAS*

Locality	δTh	δHal	δreds	δDict
El Cayo	-13.5	—	—	—
Bajos de San Julián	-13.8	-17.0	—	-16.8
Isla Pájaros	-12.0	-15.2	—	—
Punta Gorda	-14.1	-16.5	—	-18.7
Boca de Puerto Real	-12.4	—	—	—
Huariché	—	—	—	—
Boca de Pargos	—	-26.4	-23.8	—
Bahamita	-11.6	—	-17.2	—
Boca de Balchacah	—	—	-24.2	—
Xicalango	-12.4	—	—	—
Boca Chica	—	—	-25.2	—
centro	—	—	-27.1	—
Chacahito	-15.9	—	-23.3	—
Atasta	—	-23.6	—	—
San Francisco	—	—	—	—
Palizada Vieja	—	—	—	—
Río Chumpán	-13.2	—	—	—
Río Candelaria	—	-27.6	—	—

* Symbols: δTh = $\delta^{13}C$ of *T. testudinum*, δHal = $\delta^{13}C$ of *H. wrightii*, δ reds=^{13}C of red algae, δDict = $\delta^{13}C$ of *Dictyota sp.*

The species *T. testudinum* presented an interval of values of −11.6 to −15.9‰ and was distributed in beds throughout the lagoon (Fig. 3). *H. wrightii* registered values of −15.2 to −17.0‰ to the northeast and of −23.6 to −27.6‰ in the rest of the system (Fig. 4). Red algae had a $\delta^{13}C$ of −17.2‰ on the sublittoral of the island barrier (Bahamita) and of −23.3 to −27.1‰ in the rest of the lagoon (Fig. 5). *Dictyota sp.* registered −16.8 to −18.7‰ to the northeast of the system (Fig. 6).

$\delta^{13}C$ values of −11.6 to −15.9‰ of *T. testudinum* (Fig. 3) are similar to those of McMillan *et al.* (1980), and Fry and Sherr (1984), and are enriched in ^{12}C by 2‰ with respect to those reported by Smith and Epstein (1971), Botello and Gallegos (1981) and Fry *et al.* (1982) of −9.3 to −13.2‰.

If one based the determination of the photosynthetic pathway used by plants on their $\delta^{13}C$ values, these would, in the case of this species, indicate that *T. testudinum* is a characteristically C4 plant in Terminos Lagoon. However, this species forms part of the C3 group which implies that it enjoys a high refixation rate of photorespired CO_2 without presenting the typical Kranz anatomy in the leaves, such as is common in terrestrial C4 plants (Beer and Wetzel, 1982).

Beer *et al.* (1980) have explained the processes by which this and other seagrass species belong to the C3 group and record such high $\delta^{13}C$ values. At a later date, Beer and Wetzel (1982) considered *T. testudinum* to be an intermediate between a C3 and a C4 plant, as it registers high initial carbon incorporation rates into malate and other organic acids. This may be partly caused by high PEP-case activities, such as are typical of many seagrass species (Beer *et al.*, 1980).

For the seagrass *H. wrightii* an isotopic variation of 9.7‰ between the $\delta^{13}C$ average of the specimens collected to the northeast of the lagoon (−15.2 to −17.0‰) and the average of those collected in the rest of the system (−23.6 to −27.6‰) was recorded (Fig. 4).

The second interval differs from the typical $\delta^{13}C$ values of seagrasses, and this can be due to the interaction of several factors such as:

1. The isotopic ratio of dissolved inorganic carbon (HCO^-_3) is ≈ 0‰ in marine waters and −5 to −10‰ in less saline waters. The lighter $\delta^{13}C$ values of *H. wrightii* were recorded in the localities of Atasta, the Rio Candelaria and Boca de Pargos where salinity was 15.3, 2.7 and 17.0‰ respectively. It is expected that this salinity will reduce the isotopic ratio of HCO^-_3 used as active substrate which causes a lower isotopic composition in the vegetation of these localities.

2. The degree of discrimination against ^{13}C by the enzymes that are responsible for the carbon fixation in photosynthesis (phosphoenolpyruvate carboxylase (PEP-case) in the C4 pathway, and ribulosebiphosphate carboxylase (RuBP-case) in the C3 pathway). Discrimination is reduced and results in a higher $\delta^{13}C$ value in the case of the first enzyme, and is greater and results in a lower $\delta^{13}C$ value in the case of the second enzyme. In the case of the specimens that were collected in Atasta, the Rio Candelaria and Boca de Pargos, the more negative $\delta^{13}C$ may be interpreted as the result of the greater isotopic discrimination of the enzyme RuBP-case, which according to Smith and Epstein (1971), Beer and Waisel (1979), and McMillan *et al.* (1980), means that these specimens used the C3 photosynthetic pathway.

3. A high resistance to CO_2 and/or HCO^-_3 diffusion through the cellular membrane (Farquhar *et al.*, 1982) of which little is yet known. Beer and Waisel's (1979)

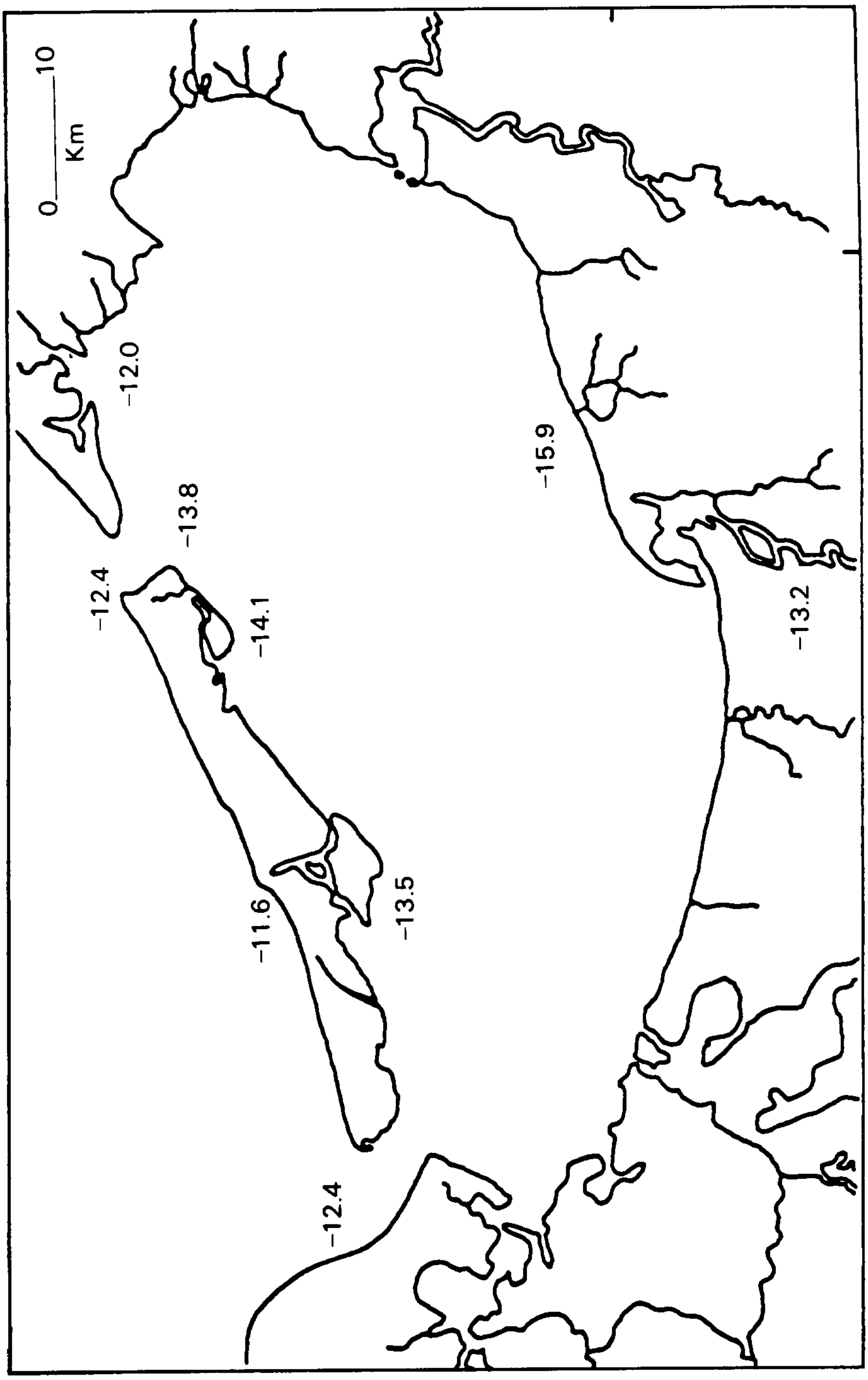

Fig. 3. *Thalassia testudinum* δ^{13}C (‰) in Terminos Lagoon.

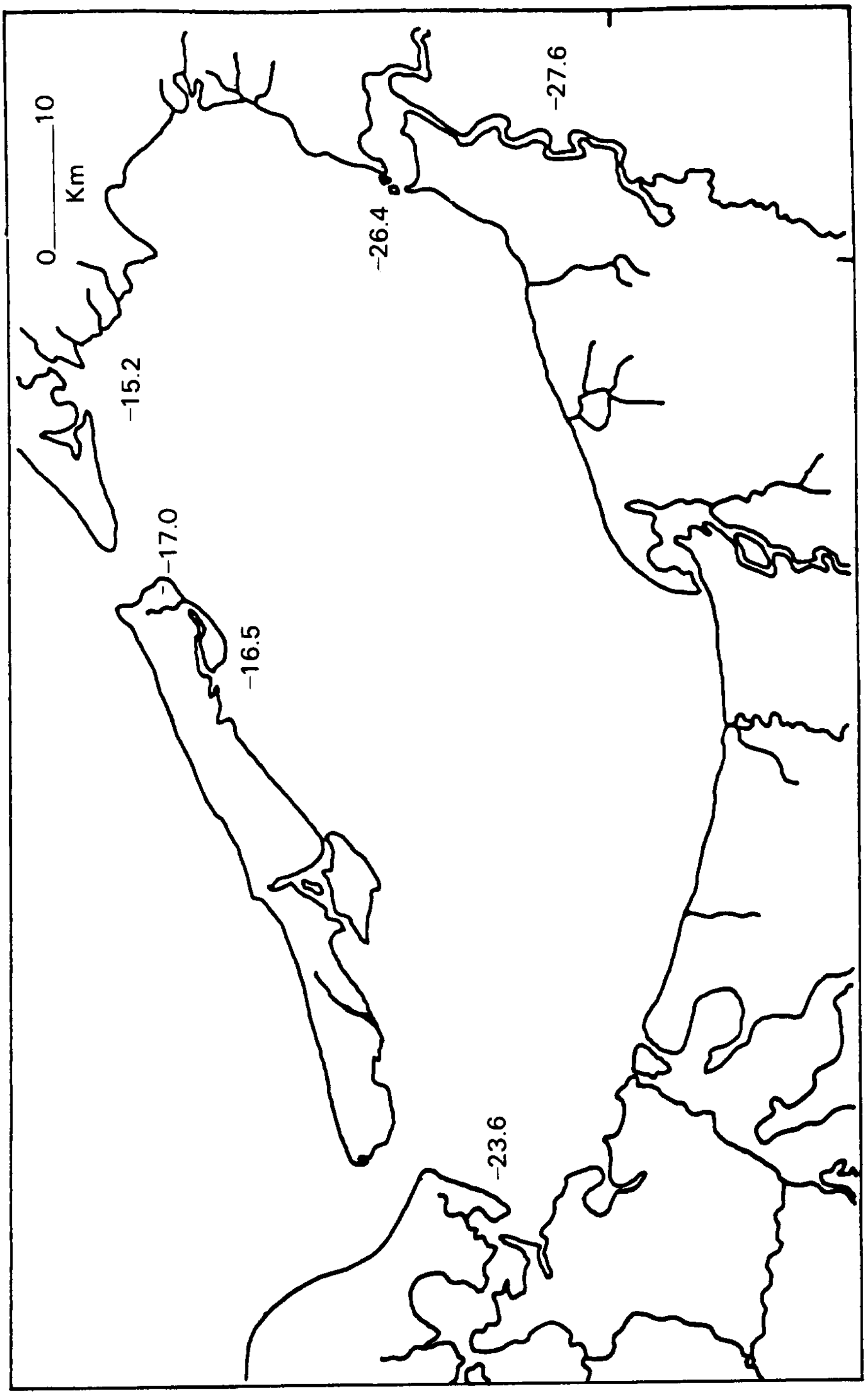

Fig. 4. *Halodule wrightii* $\delta^{13}C$ (‰) in Terminos Lagoon.

proposal can be considered here in the sense that both photosynthetic pathways can act simultaneously in seagrasses by means of a variation in the ratio of PEP-case to RuBP-case as a response to environmental changes and growth conditions, as well as by means of the dehidration of HCO^-_3 to CO_2 with the resulting change in the photosynthetic plathway that is used.

The specimens of *H. wrightii* that were collected to the northeast of the lagoon registered a $\delta^{13}C$ interval of −15.2 to −17.0‰ (Fig. 4). The higher $\delta^{13}C$ values are due to a physiological adaptation on the part of the seagrass towards a more efficient photosynthetic carbon fixation, as a response to extreme and variable environmental conditions, such as are found in aquatic and xeric habitats (Smith and Epstein, 1971).

An important variable in this sense is salinity as it presents submerged vegetation with an environmental stress element that may result in a change in photosynthetic pathway on the part of such vegetation. This possibility has been established by Beer and Waisel (1979). In relation to this, the above-mentioned higher isotopic values of *H. wrightii* are closely related to the high salinities of 26.3 to 30.7‰ that were registered to the northeast of the lagoon (Raz-Guzmán, 1987). Also related to high salinity is the isotopic ratio of $\approx$ 0‰ of the HCO^-_3 that is used in aquatic environments as active substrate for photosynthesis. These $\delta^{13}C$ values also indicate that the specimens that were collected in this area photosynthesize by means of the C4 pathway (Smith and Epstein, 1971). These values are similar to those reported by Fry and Parker (1979), McMillan *et al.* (1980) and Fry *et al.* (1982).

The difference between the two $\delta^{13}C$ intervals that were recorded for *H. wrightii* indicates the possibility of a great variation in the isotopic composition of one species as a result of different physiological adaptations to the environment (Smith and Epstein, 1971), as well as of different operative photosynthetic pathways in seagrasses in general (McMillan *et al.*, 1980).

In this respect Beer and Wetzel (1982) included *H. wrightii* with *T. testudinum* as a species intermediate between the C3 and C4 plant groups for the reasons stated above for *T. testudinum.*

The macroalgae group is made up of approximately 16,000 species of world distribution (Ortega, 1984). As a result of such a diversity of species it is common to register a $\delta^{13}C$ interval of −8 to −27‰ (Fry and Sherr, 1984) for this vegetation. This interval is one of the most ample and indicates that these plants use both photosynthetic pathways, as Beer and Waisel (1979) have mentioned.

$\delta^{13}C$ values of −23.3 to −27.1‰ were reecorded for the red algae collected in the lagoon (Fig. 5). These values are similar to that of −22.3‰ that Haines and Montague (1979) recorded for *Gracilaria sp.* and they reflect the use, on the part of this vegetation, of the C3 photosynthetic pathway.

In contrast, the red algae that were collected in Bahamita registered a $\delta^{13}C$ of −17.2‰ (Fig. 5) which is similar to those of −18.9 to −19.9‰ recorded by Fry *et al.* (1982) for *Gracilaria sp.* and *Hypnea sp.* The $\delta^{13}C$ of −17.2‰ in Bahamita can be the result of two processes: 1.- the combination of a lighter $\delta^{13}C$ such as those that were registered for the red algae in the lagoon with the $\delta^{13}C$ of $\approx$0‰ of the disssolved inorganic carbon of marine water (34%. salinity in Bahamita), and 2.- the use of the C4 photosynthetic pathway as a response to environmental conditions, as in the

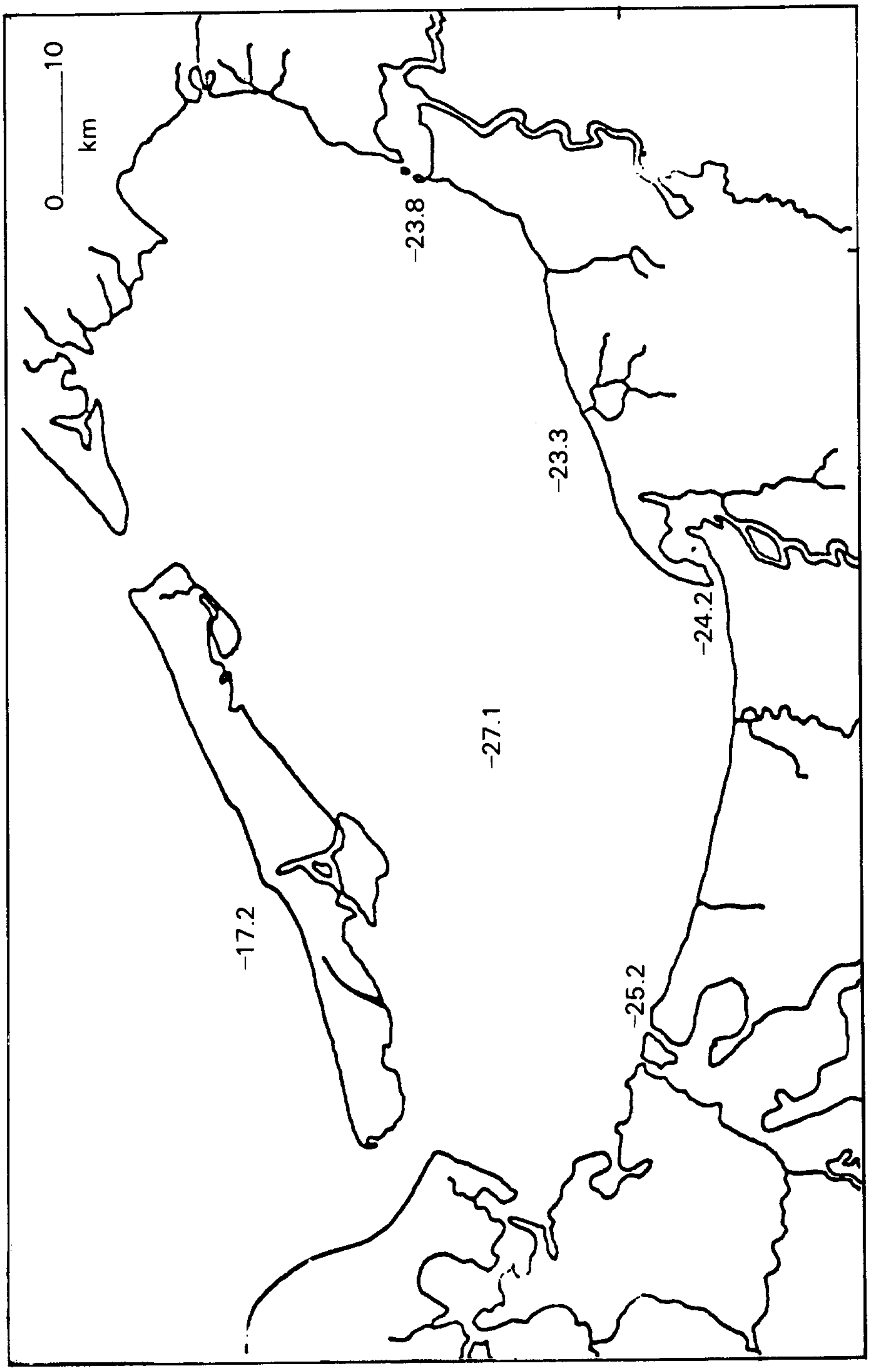

Fig. 5. *Red algae* $\delta^{13}C$ (‰) in Terminos Lagoon.

case of the *H. wrightii* specimens collected to the northeast of the lagoon. Both processes remain subject to confirmation through future analysis of the red algae along the coast.

The $\delta^{13}C$ interval of −16.8 to −18.7‰ of the brown alga *Dictyota sp.* (Fig. 6) indicates that this is a C4 plant. This interval of values is approximatelly 3% more negative than that registered for this genus by Fry *et al.* (1982) of −12.7 to −14.1‰ However, the values recorded here lie within the $\delta^{13}C$ interval of macroalgae of −8 to −27‰ (Fry and Sherr, 1984) and the difference is related to environmental conditions in widely separated geographical areas.

The distribution of the $\delta^{13}C$ values of the submerged vegetation is similar to that of sedimentary $\delta^{13}C$ values and so conforms to a simple terrestrial-marine mixing model. The model however is altered in the areas to the south and west of the system with respect to the seagrass *T. testudinum.* An approximately uniform heavy isotopic composition was registered for this species throughout the system and this results in a dissimilarity between its $\delta^{13}C$ values and those of sediment, detritus and other types of submerged vegetation in these areas.

With the exception of *T. testudinum,* the isotopic composition of the submerged vegetation is closely related to salinity, as can be observed in the graphic representation in figure 7. More negative $\delta^{13}C$ values for vegetation are registered in localities with low salinities and vice-versa. This in turn implies a relationship between the isotopic composition of the vegetation and that of the dissolved inorganic carbon that is used by these plants as a source of carbon.

Sediment and detritus. Sedimentary and detritus $\delta^{13}C$ values are presented in Table 3 The cluster analysis that was applied to all the variables in this study resulted in the formation of two groups of lagoonal localities and left out the locality of Bahamita on the sublittoral of Isla del Carmen (Fig. 8). The variables that had the strongest effect in the clustering were salinity and sediment $\delta^{13}C$.

The first group (Area 1) was formed by the localities of El Cayo, Punta Gorda, Bajos de San Julián, Isla Pájaros, Huariché, and Boca de Puerto Real to the north and northeast of the lagoon, and was characterized by polyhaline to euhaline waters (24 to 33‰). The heavier $\delta^{13}C$ values of −12.0 to −19.0‰ ($\bar{x}$=−15.5‰) were recorded in this area of the lagoon.

The second group (Area 2) was formed by the other localities to the southeast, south, southwest, west, northwest and centre of the lagoon, with salinity records that ranged from 1.3 to 28.0‰ as a result of the contributions of fresh and sea water to the lagoon. $\delta^{13}C$ values were lighter in this area of the lagoon and varied between −12.4 and −28.2‰ ($\bar{x}$=−20.3‰).

The locality of Bahamita was environmentally different with respect to the localities within the estuarine system, which is to be expected considering its position on the sublittoral of Isla del Carmen.

$\delta^{13}C$ values of −16.9‰ for detritus and of −14.6 to −19.0‰ for sediment were recorded in Area 1, and in Area 2 values were of −25.7 to −27.7‰ for detritus and of −21.8 to −28.2‰ for sediment (Figs. 9, 10).

Sediment $\delta^{13}C$ values are clearly distributed along a gradient, as can be graphically seen in Table 4: −28.2‰ in the Rio Candelaria, from −24.2 to −25.4‰ to the southwest and in the Rio Chumpán, from −21.8 to −22.9‰ to the northwest, west,

TABLE 3

AVERAGE VALUES OF $\delta^{13}C$ OF DETRITUS AND SEDIMENT OF TERMINOS LAGOON AND ADJACENT AREAS*

Locality	δdetr	δsed
El Cayo	—	−14.6
Bajos de San Julián	−16.9	−16.2
Isla Pájaros	—	−16.3
Punta Gorda	—	−17.0
Boca de Puerto Real	—	−18.2
Huariché	—	−19.0
Boca de Pargos	—	−21.8
Bahamita	—	−22.0
Boca de Balchacah	—	−22.2
Xicalango	—	−22.7
Boca Chica	−26.2	−22.9
centro	—	−22.9
Chacahito	—	−22.9
Atasta	−25.7	−24.2
San Francisco	−27.7	−24.3
Palizada Vieja	—	−24.5
Río Chumpán	−26.6	−25.4
Río Candelaria	—	−28.2

* Symbols: δdetr = $\delta^{13}C$ of detritus, δsed = $\delta^{13}C$ of sediment.

TABLE 4

DISTRIBUTION OF SEDIMENT $\delta^{13}C$ OF LOCALITIES OF TERMINOS LAGOON AND ADJACENT AREAS

$\delta^{13}C$	−30	−25	−20	−15
El Cayo				×
Bajos de San Julián				×
Isla Pájaros				×
Punta Gorda				×
Boca de Puerto Real				×
Huariché			×	
Boca de Pargos			×	
Bahamita			×	
Boca de Balchacah			×	
Xicalango		×		
Boca Chica		×		
centro		×		
Chacahito		×		
Atasta		×		
San Francisco		×		
Palizada Vieja		×		
Río Chumpán		×		
Río Candelaria	×			

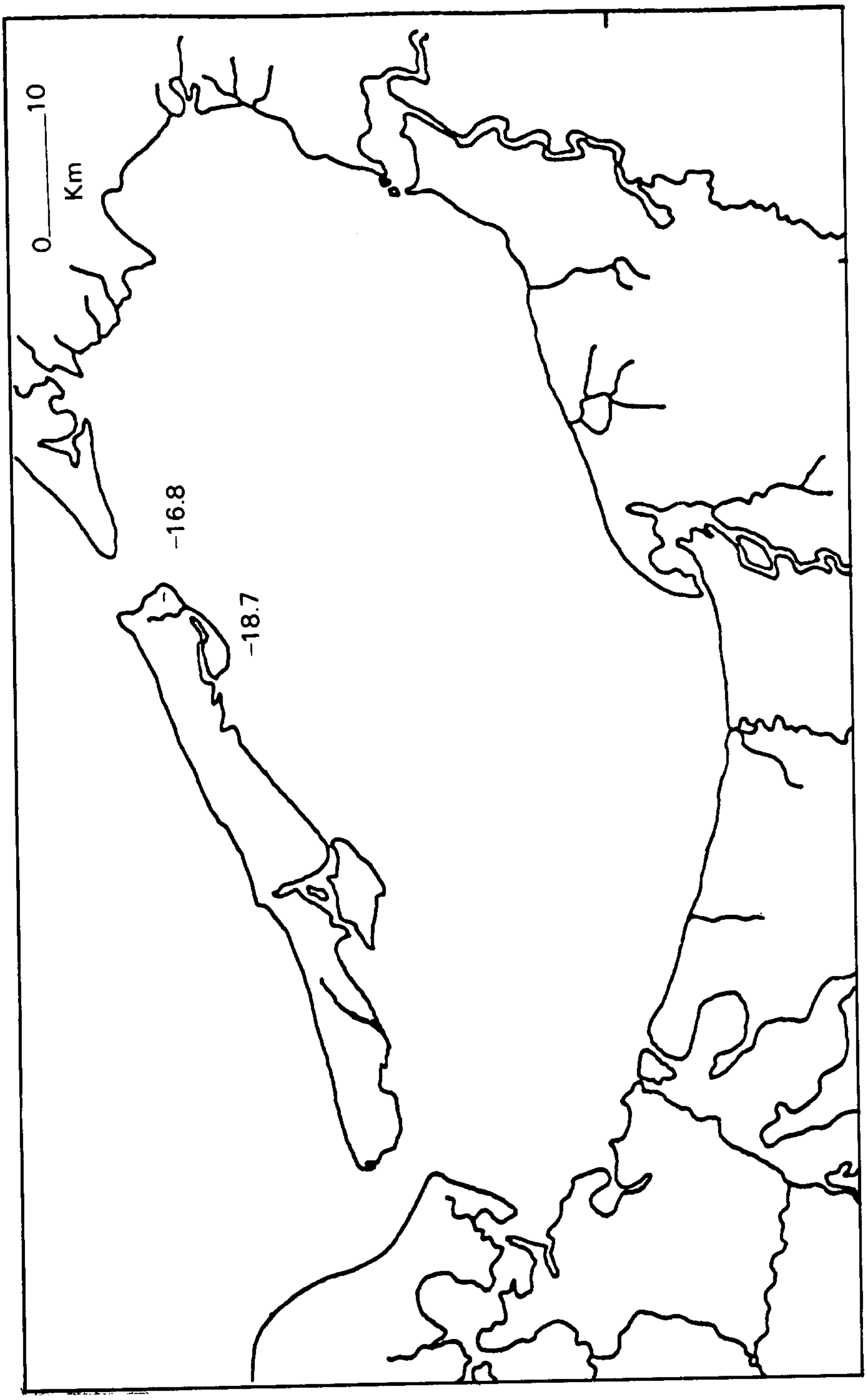

Fig. 6. *Dictyota sp.* $\delta^{13}C$ (‰) in Terminos Lagoon.

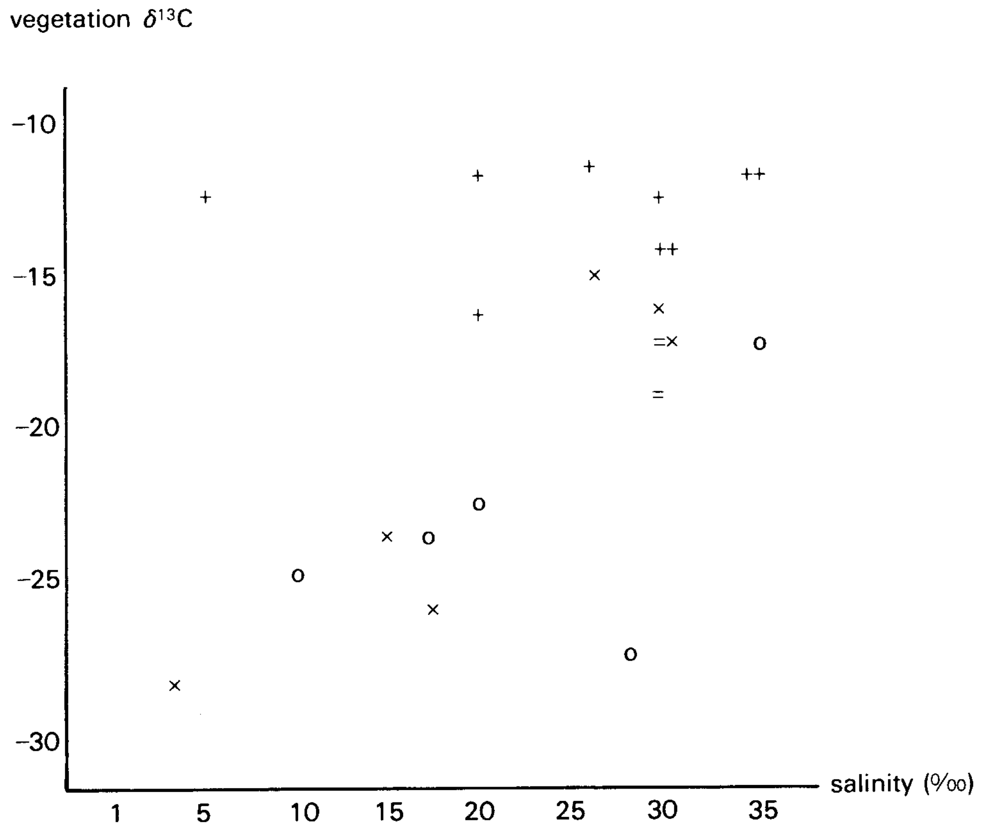

Fig. 7. Relationship between *T. testudinum* (+), *H. wrightii* (×), red algae (o) and *Dictyota sp.* (=) $\delta^{13}C$, and salinity throughout Terminos Lagoon, Campeche.

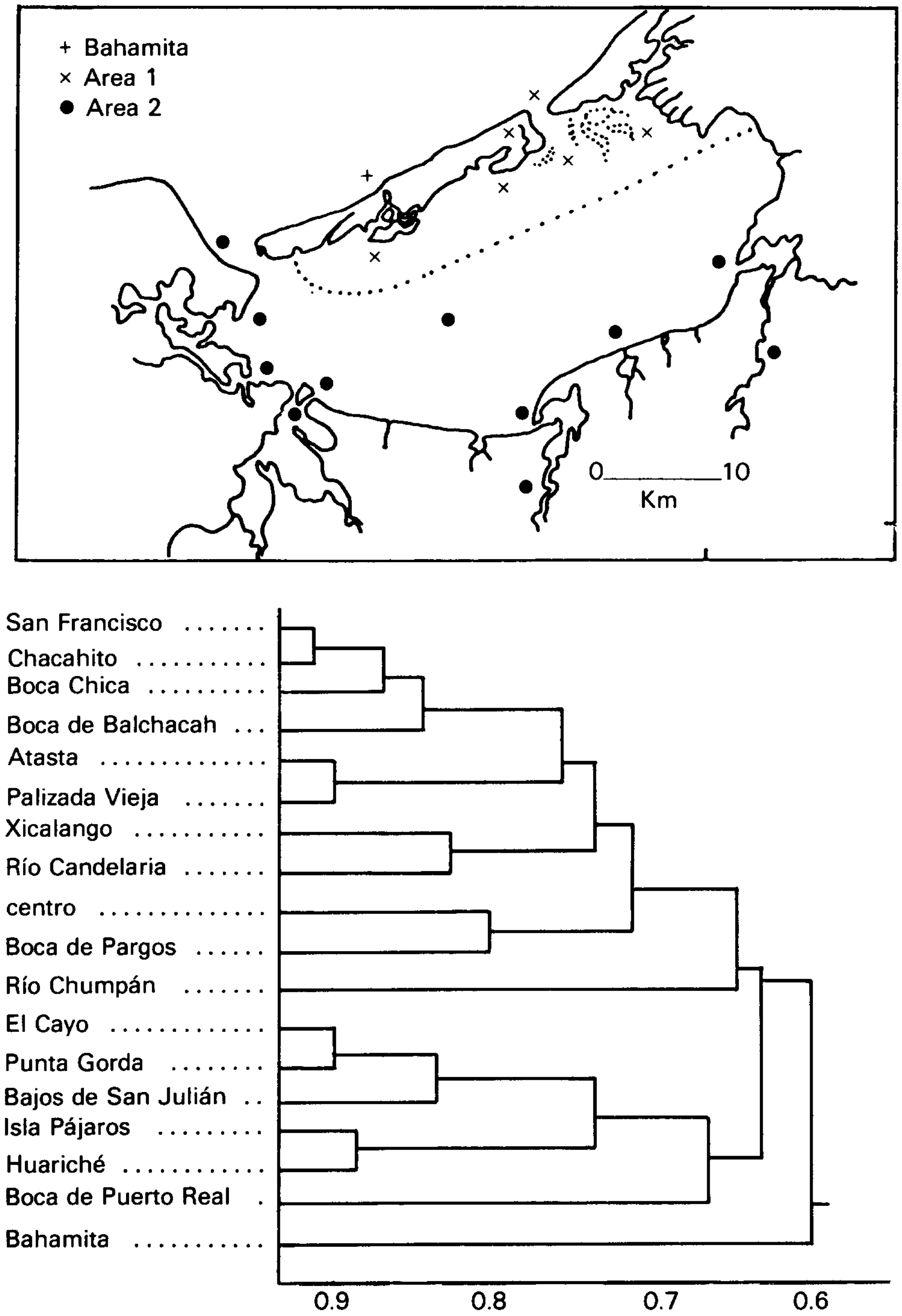

Fig. 8. Cluster of submerged vegetation, sediment and detritus, and Area 1 and Area 2 of Terminos Lagoon, Campeche.

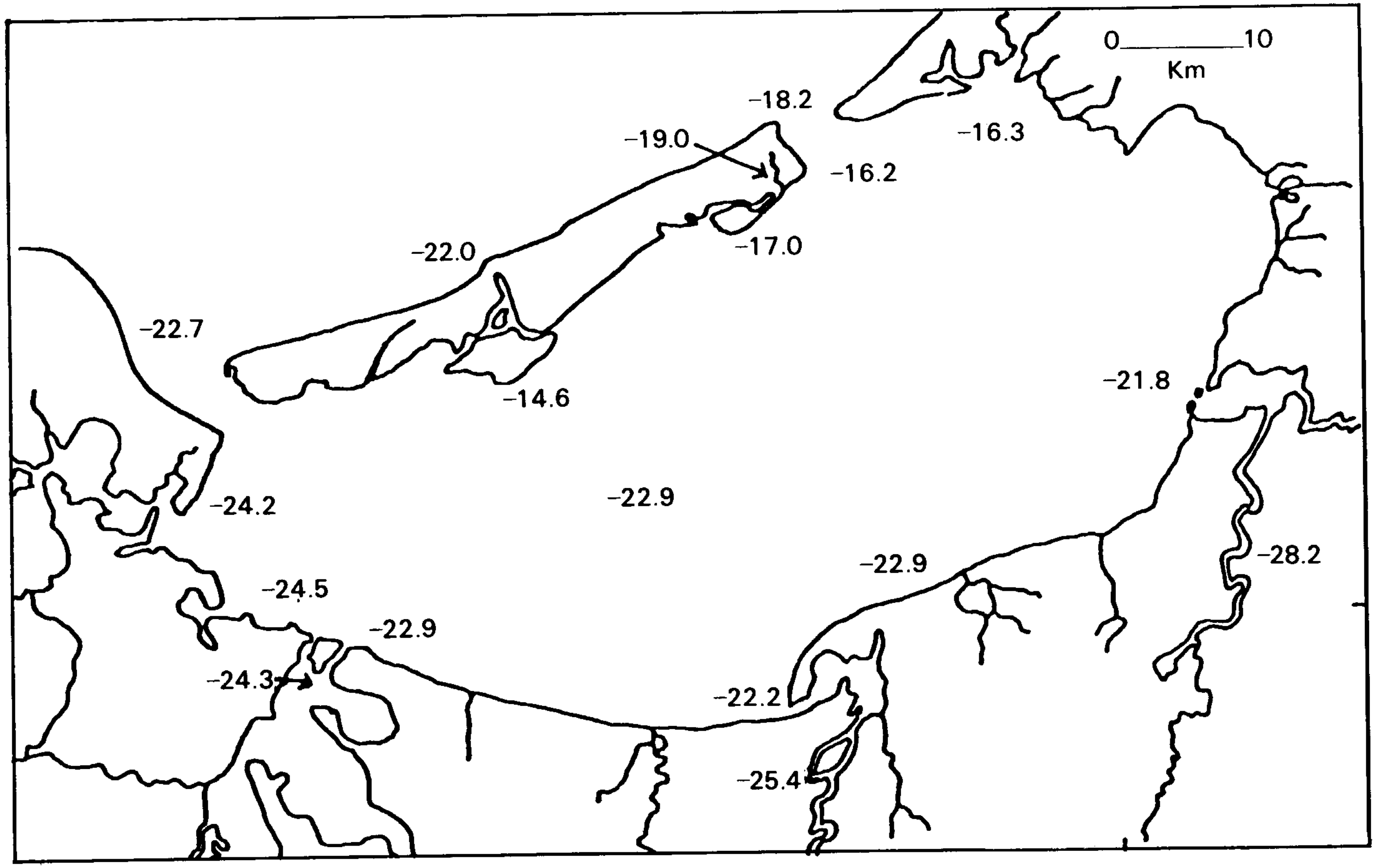

Fig. 9. Sediment $\delta^{13}C$ (‰) in Terminos Lagoon.

centre and south, and from −14.6 to −19.0‰ to the northeast (Fig. 9). As a result of this distribution, three isotopically different areas are clearly delimited within the lagoon.

1. The most negative $\delta^{13}C$ values were registered to the south and southwest of Area 2: −28.2‰ in the Rio Candelaria, −25.4‰ in the Rio Chumpán, −24.3‰ in Laguna San Francisco, −24.5‰ in Palizada Vieja and −24.2‰ in Atasta. These records indicate that the main organic carbon inputs deposited in this area are of terrestrial origin. These contributions reduce sedimentary $\delta^{13}C$ due to the enrichment in ^{12}C of the organic carbon of the terrestrial vegetation that is carried by the three river systems from the deltaic plains into the lagoon. This area receives great quantities of detritus that is isotopically similar to the terrestrial vegetation from which it derives. This similarity is due to the fact that the isotopic composition of the material that is produced as a result of the decomposition of vascular plants changes minimally (Schwinghamer *et al.,* 1983; *vide in* Fry and Sherr, 1984). Detritus $\delta^{13}C$ of −25.7 to −27.7‰ (Fig. 10) is directly related to sedimentary $\delta^{13}C$ ($r=0.999$; $P<0.05$) and this reflects the isotopic similarity that exists between them, as has been previously observed by Fry and Sherr (1984).

2. The other localities of Area 2, Boca de Pargos, Chacahito, Boca de Balchacah, Boca Chica, Xicalango and the centre of the lagoon (Fig. 9) represent a mixing area that is influenced by the circulation of the water inside the lagoon. In this area, isotopically lighter organic carbon of terrestrial origin is combined with isotopically heavier carbon of the seagrass beds along the southern littoral of the lagoon. This results in a uniformity of sedimentary $\delta^{13}C$ values with a variation of −21.8 to −22.9‰.

The $\delta^{13}C$ values that were registered in Area 2 are similar to those that were registered by Shultz and Calder (1976), Rashid and Reinson (1979), Tan and Strain (1979), Botello and Macko (1982), and Sherr (1982) of −19.0 to −29.2‰ in environments that receive similar contributions of organic carbon of terrestrial origin.

3. In Area 1, the isotopic composition of the organic carbon that is provided by the seagrasses is reflected in the heavier sedimentary $\delta^{13}C$ values of −14.6 to −19.0‰ These values are similar to those reported by Haines (1976), Fry *et al.* (1977), Fry and Parker (1979) and Sherr (1982) of −10.1 to −19.9‰ for characteristically estuarine environments similar to this area. The seagrasses *T. testudinum* and *H. wrightii* and the brown alga *Dictyota sp.* play an important role in the contribution of detritus to the substrate. The detritus $\delta^{13}C$ of −16.9‰ of Bajos de San Julián (Fig. 10) reflects the isotopic composition of the above-mentioned species of submerged vegetation (−13.8 to −17.0‰) and is similar to that of the sedimentary organic carbon (−16.2‰) of that locality.

On the other hand, considering that it was in this area that some of the highest concentrations of carbonates were registered, another explanation of the increase in sedimentary $\delta^{13}C$ is based on the isotopic exchange reactions between gaseous CO_2 and aqueous carbonate species, which cause sedimentary carbonates to be enriched in ^{13}C (Faure, 1977) and consequently the organic fraction of the sediment. This is corroborated by the direct relationship that was registered between the sedimentary $\delta^{13}C$ and the carbonate content in the sediment ($r=0.6$; $P<0.05$).

The interval of $\delta^{13}C$ values of −12.4 to −25.9‰ that were registered for Termi-

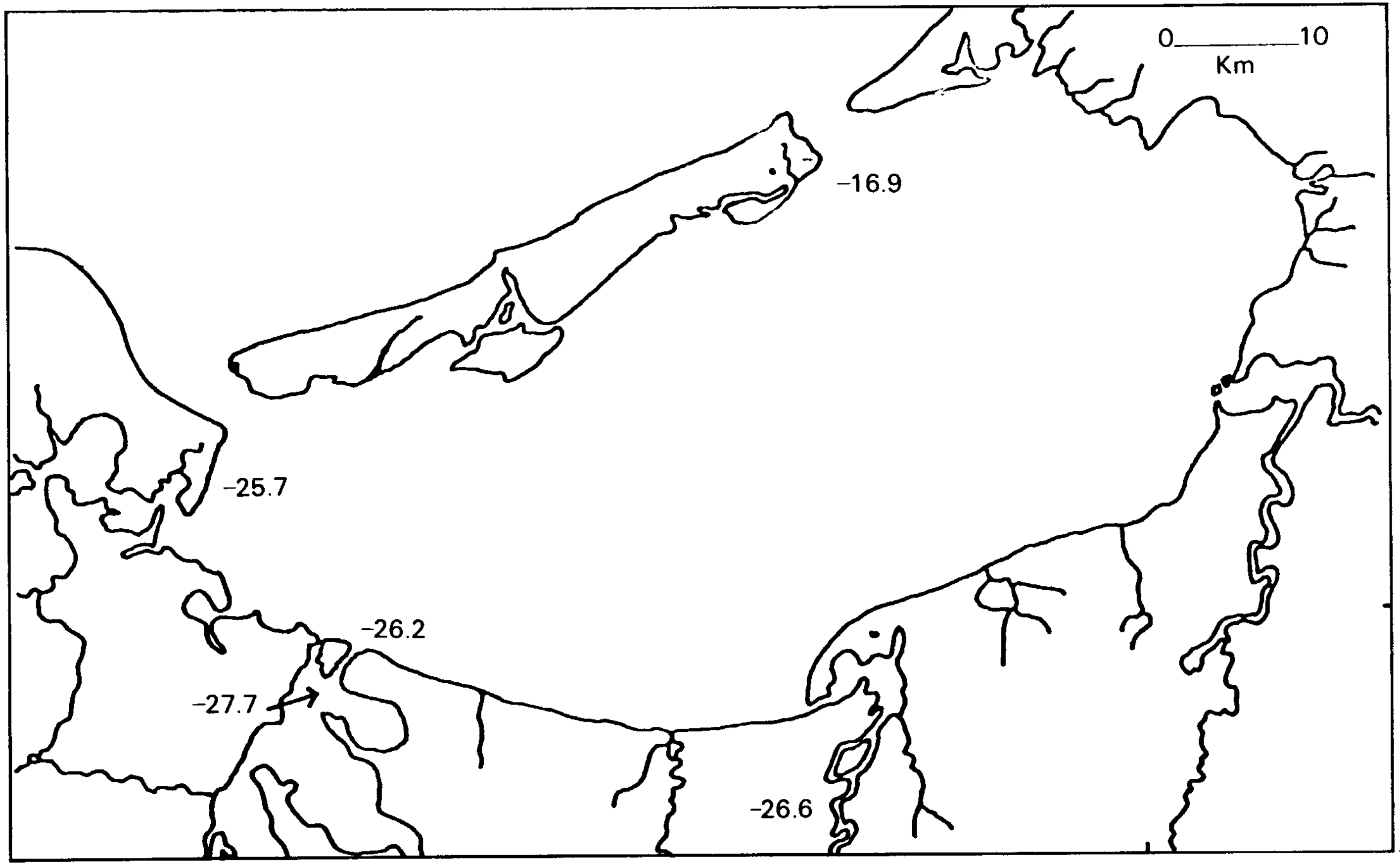

Fig. 10. Detritus $\delta^{13}C$ (‰) in Terminos Lagoon.

nos Lagoon sediments by Botello and Gallegos (1981), Botello and Soto (1981) and Botello and Macko (1982) is extended here up to −28.2‰ and this is because the samples that were collected in this study include the interior lagoon of San Francisco, the rivers Chumpán and Candelaria and other localities not previously sampled.

The sedimentary $\delta^{13}C$ of −22.0‰ recorded in Bahamita (Fig. 9) bears no relationship to the $\delta^{13}C$ of the submerged vegetation (*T. testudinum*=−11.6‰ and red algae=−17.2‰) in contrast to the case of the localities within Terminos Lagoon. Due to the setting of Bahamita it can be considered that the $\delta^{13}C$ of the sediment reflects the isotopic composition of the organic carbon of marine origin (planktonic $\delta^{13}C$, $\bar{x}$=−21‰) which is deposited and becomes part of the substrate, such as Fry *et al.* (1977) found in their study.

The gradient of sedimentary and detritus $\delta^{13}C$ values that is described above is consistent with a simple mixing terrestrial-marine model, such as is mentioned by Sackett and Thompson (1963), Shultz and Calder (1976) and Tan and Strain (1979) in which hydrodynamics, sedimentation processes and input-output all play a part.

In general, as in the case of submerged vegetation, there is a marked relationship between the isotopic composition of sedimentary organic matter and that of detritus ($r=0.956$; $P<0.05$) and between the $\delta^{13}C$ of sedimentary organic matter and salinity ($r=0.674$; $P<0.05$) (Fig. 11). Heavier $\delta^{13}C$ values are related to high salinities and lighter $\delta^{13}C$ values are related to low salinites, where input of land-derived organic matter is high.

Terminos Lagoon is characterized by two isotopically different areas. Less negative $\delta^{13}C$ values ($\bar{x}$=−15.5‰) were recorded along the inner margin of Isla del Carmen and Isla Aguda, as well as in Boca de Puerto Real (Area 1). These are the result of the contribution of organic carbon from *T. testudinum, H. wrightii* and *Dictyota sp.* (−12.0 to −14.1‰, −15.2 to −17.0‰, and −16.8 to −18.7‰, respectively) to sedimentary organic matter and detritus (−14.6 to −19.0‰). Additionally, the enrichment in ^{13}C of the carbonates in the sediment contributes to an increase in the sedimentary $\delta^{13}C$ of this area.

Lighter $\delta^{13}C$ values ($\bar{x}$=−20.3‰) were recorded in the rest of the system, including Laguna San Francisco and the rivers Chumpán and Candelaria (Area 2). These are the result of the contribution of organic carbon of terrestrial origin by the three rivers (Palizada, Chumpán and Candelaria) that flow into the system to the south, southwest and west, to sedimentary organic matter and detritus (−21.8 to −28.2‰).

In general terms, sedimentary $\delta^{13}C$ values show a gradient from the north and northeast to the south, southwest and west within the system. The distribution of sedimentary $\delta^{13}C$ values is achieved through estuarine sedimentation processes that are governed by the circulation pattern within the system.

The distribution of $\delta^{13}C$ values here presented for Terminos Lagoon is characteristic of estuarine systems that have a permanent input both of freshwater and seawater, and may be applied as a descriptive model to other typically estuarine systems.

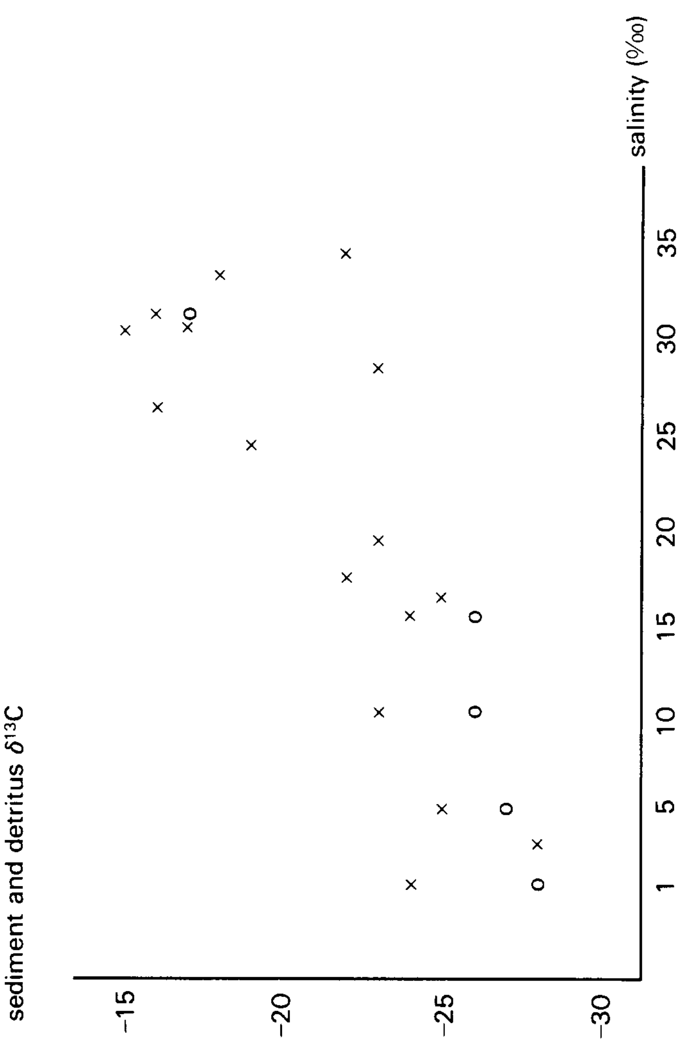

Fig. 11. Relationship between sediment (×) and detritus (o) $\delta^{13}C$, and salinity throughout Terminos Lagoon, Campeche.

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LITERATURE CITED

BEER, S. AND Y. WAISEL. 1979. Some photosynthetic carbon fixation properties of seagrasses. *Aquat. Bot. 7:* 129-138.

BEER, S. AND R.G. WETZEL. 1982. Photosynthetic carbon fixation pathways in *Zostera marina* and three Florida seagrasses. *Aquat. Bot. 13:* 141-146.

BEER, S., A. SHOMER-ILAN AND Y. WAISEL. 1980. Carbon metabolism in seagrasses. II. Patterns of photosynthetic incorporation. *J. Exp. Bot. 31(123):* 1019-1026.

BENEDICT, C.R., W.W.L. WONG AND J.H.H. WONG. 1980. Fractionation of the stable isotopes of inorganic carbon by seagrasses. *Plant Physiol. 65:* 512-517.

BOTELLO, A.V. AND M. GALLEGOS. 1981. *Estudios ecológicos y químicos sobre praderas de Thalassia testudinum Konig: en la Laguna de Términos, Campeche, México.* Reporte técnico. Instituto de Ciencias del Mar y Limnología Universidad Nacional Autónoma de México. 13 p.

BOTELLO, A.V. AND S. MACKO. 1982. Oil pollution and the carbon isotope ratio in organisms and recent sediments of coastal lagoons in the Gulf of Mexico. *Oceanologica Acta no. SP:* 55-62.

BOTELLO, A.V. AND L.A. SOTO. 1981. Proyecto: "Cuantificación de hidrocarburos fósiles y metales pesados en sedimentos y organismos marinos de la Sonda de Campeche." Primer informe final presentado al "Programa Coordinado de Estudios Ecológicos en la Sonda de Campeche." Centro de Ciencias del Mar y Limnología Universidad Nacional Autónoma de México., México. 66 p.

BOTELLO, A.V., E.F. MANDELLI, S. MACKO AND P.L. PARKER. 1980. Organic carbon isotope ratios of recent sediments from coastal lagoons of the Gulf of Mexico, Mexico. *Geochim. et Cosmochim. Acta 44:* 557-559.

BOUTTON, T.W., W.W. WONG, D.L. HACHEY, L.S. LEE, M.P. CABRERA, AND P.D. KLEIN. 1983. Comparison of quartz and pyrex tubes for combustion of organic samples for stable carbon isotope analysis. *Anal. Chem. 55:* 1832-1833.

CRUZ-OROZCO, R. 1980. Estudio del sistema fluvio-lagunar deltáico de la región de Campeche, Tabasco, en particular de la Laguna de Términos y areas adyacentes, para su mejor uso y aprovechamiento. Tercer reporte presentado al Consejo Nacional de Ciencia y Tecnología. México. 61 p.

DEAN, N.D. JR. 1974. Determination of carbonate and organic matter in calcereous sediments and sedimentary rocks by loss on ignition; Comparison with other methods. *J. Sedim. Petrol. 44(1):* 242-248.

ESPINOSA, G. AND A. LÓPEZ. 1986. *Introducción a los métodos jerárquicos de análisis de cúmulos.* Comunicaciones técnicas. Serie verde: Notas. Vol. 1. No. 9. 2a. reimpresión. Instituto de Investigaciones Matemáticas Aplicadas y de Sistema Universidad Nacional Autónoma de México., México. 77 p.

ESPINOSA, G., A. LÓPEZ AND L. REYES. 1978. Análisis/Cúmulos: un programa para análisis de cúmulos. Comunicaciones técnicas. Serie amarilla: Desarrollo. Vol. 1. No. 6. Instituto de Investigaciones Matemáticas Aplicadas y de Sistema. Universidad Nacional Autónoma de México., México. 27 p.

FARQUHAR, G.D., M.C. BALL, S. VON CAEMMERER AND Z. ROKSANDIC. 1982. Effect of salinity and humidity on $\delta^{13}C$ value of halophytes —evidence for diffusional isotope fractionation determined by the ratio of intercellular atmospheric partial pressure of CO_2 under different environmental conditions. *Oecologia 52:* 121-124.

FAURE, G. 1977. *Principles of isotope geology.* John Wiley and Sons, Inc. New York. 464 p.

FRY, B. AND P.L. PARKER. 1979. Animal diet in Texas seagrass meadows: $\delta^{13}C$ evidence for the importance of benthic plants. *Est. Coast. Mar. Sci. 8:* 499-509.

FRY, B. AND E.B. SHERR. 1984. $\delta^{13}C$ Measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib. Mar. Sci. 27:* 13-47.

FRY, B., R.S. SCALAN AND P.L. PARKER. 1977. Stable carbon isotope evidence for two sources of organic matter in coastal sediments: seagrasses and plankton. *Geochim. et Cosmochim. Acta 41:* 1875-1877.

FRY, B., R. LUTES, M. NORTHAM AND P.L. PARKER. 1982. A $^{13}C/^{12}C$ comparison of food webs in Caribbean seagrass meadows and coral reefs. *Aquat. Biol. 14:* 389-398.

HAINES, E.B. 1976. Stable carbon isotope ratios in the biota, soils and tidal water of a Georgia salt marsh. *Est. Coast. Mar. Sci. 4:* 609-616.

HAINES, E.B. AND C.L. MONTAGUE. 1979. Food sources of estuarine invertebrates analysed using $^{13}C/^{12}C$ ratios. *Ecology 60(1):* 48-56.

HOLADAY, A.S. AND G. BOWES. 1980. C4 acid metabolism and dark CO_2 fixation in a submersed aquatic macrophyte *(Hydrilla verticillata). Plant Physiol. 65:* 331-335.

MANCILLA PERAZA, M. AND P. VARGAS FLORES. 1980. Los primeros estudios sobre la circulación y el flujo neto de agua a través de la Laguna de Términos, Campeche. *Anales Centro Ci. Mar y Limnol. Univ. Nal. Auton. México. 7(2):* 1-12.

McMILLAN, C., P.L. PARKER AND B. FRY. 1980. $^{13}C/^{12}C$ ratios in seagrasses. *Aquat. Bot. 9:* 237-249.

ORTEGA, M.M. 1984 Catálogo de Algas Continentales Recientes de México. Univ. Nal. Auton. México., México. 561 p.

RASHID, M.A. AND G.E. REINSON. 1979. Organic matter in surficial sediments of the Miramichi Estuary. New Brunswick, Canada. *Est. Coast. Mar. Sci. 8:* 23-38.

RAZ-GUZMAN M., A. 1987. *Proporción isotópica del carbono orgánico en camarones, sedimento y vegetación de la Laguna de Términos, Campeche.* Tesis de Maestría. Inst. Ci. Mar y Limnol. Unidad Académica de los Ciclos Profesional y de Posgrado — Colegio de Ciencias y Humanidades. Universidad Nacional Autónoma de México., México. 45 p.

RENFRO, W.C. 1962. Small beam net for sampling postlarval shrimp. *In:* Galveston Biological Lab., Jun 30, 1962. *U.S. Fish. Wildl. Serv. Circ. 161:* 86-87.

SACKETT, W.M. AND R.R. THOMPSON. 1963. Isotopic organic carbon composition of recent continental derived clastic sediments of the eastern Gulf of Mexico. *Bull. Amer. Assoc. Petr. Geol. 47:* 525-531.

SHACKLEY, M.L. 1975. *Archaeological sediments.* Butterworths. London. 159 p.

SHERR, E.B. 1982. Carbon isotope composition of organic seston and sediments in a Georgia salt marsh estuary. *Geochim. et Cosmochim. Acta 46:* 1227-1232.

SHULTZ, D.J. AND J.A. CALDER. 1976. Organic carbon $^{13}C/^{12}C$ variations in estuarine sediments. *Geochim. et Cosmochim. Acta 40:* 381-385.

SMITH, B.N. AND S. EPSTEIN. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. *Plant. Physiol. 47:* 380-384.

TAN, F.C. AND P.M. STRAIN. 1979. Organic carbon isotope ratios in recent sediments in the St. Lawrence Estuary and the Gulf of St. Lawrence. *Est. Coast. Mar. Sci. 8:* 213-225.

ZAR, J.H., 1974. *Biostatistical Analysis.* Prentice-Hall, Inc. Englewood Cliffs, N.J. 620 p.